



气候变化背景下针叶林小蠹灾害发生机制与防控策略研究进展

任利利 裴玉亮 伍永明 俞琳锋 陶静 裴佳禾 焦继鹏 骆有庆

Research advances on the occurrence mechanisms and management strategies of bark beetle outbreaks in coniferous forests under climate change

Ren Lili, Pei Yuliang, Wu Yongming, Yu Linfeng, Tao Jing, Pei Jiahe, Jiao Jipeng, Luo Youqing

引用本文:

任利利, 裴玉亮, 伍永明, 俞琳锋, 陶静, 裴佳禾, 焦继鹏, 骆有庆. 气候变化背景下针叶林小蠹灾害发生机制与防控策略研究进展[J]. 北京林业大学学报, 2026, 48(9):1–12. doi: 10.12171/j.1000–1522.20260296

Ren Lili, Pei Yuliang, Wu Yongming, Yu Linfeng, Tao Jing, Pei Jiahe, Jiao Jipeng, Luo Youqing. Research advances on the occurrence mechanisms and management strategies of bark beetle outbreaks in coniferous forests under climate change[J]. *Journal of Beijing Forestry University*, 2026, 48(9):1–12. doi: 10.12171/j.1000–1522.20260296

在线阅读 View online: <https://doi.org/10.12171/j.1000–1522.20260296>

您可能感兴趣的其他文章

Articles you may be interested in

东北针叶林与阔叶林乔灌木组成特征及碳汇功能对比研究

Comparative study on tree, shrub and herb composition and carbon sink function between coniferous and broadleaved forests in Northeast China

北京林业大学学报, 2022, 44(10): 52–67. <https://doi.org/10.12171/j.1000–1522.20220202>

气候变化对我国油松人工林适生区分布的影响

Effects of climate change on distribution of suitable area of *Pinus tabulaeformis* plantation in China

北京林业大学学报, 2024, 46(6): 82–92. <https://doi.org/10.12171/j.1000–1522.20230072>

长白山云冷杉针阔混交林3种常见树种径向生长对气候变化的响应

Response of radial growth of three common tree species to climate change in a spruce–fir mixed stand in Changbai Mountain of northeastern China

北京林业大学学报, 2023, 45(4): 1–10. <https://doi.org/10.12171/j.1000–1522.20210479>

气候变化下黄枝油杉与江南油杉的潜在适生区预测

Prediction of potential suitable areas of *Keteleeria calcarea* and *Keteleeria cyclolepis* under climate change

北京林业大学学报, 2025, 47(6): 30–42. <https://doi.org/10.12171/j.1000–1522.20240094>

气候变化对北京近远郊地区油松径向生长影响的比较研究

Comparative study on the effects of climate change on radial growth of *Pinus tabulaeformis* in near and outer suburbs of Beijing

北京林业大学学报, 2022, 44(1): 19–28. <https://doi.org/10.12171/j.1000–1522.20200329>

贵州喀斯特生态系统典型针叶林地表火蔓延速度影响因子及预测模型

Influencing factors and prediction models of surface fire spreading rate of typical coniferous forest in karst ecosystem of Guizhou Province, southwestern China

北京林业大学学报, 2024, 46(5): 37–45. <https://doi.org/10.12171/j.1000–1522.20220348>

DOI:10.12171/j.1000-1522.20260296

气候变化背景下针叶林小蠹灾害发生机制与 防控策略研究进展

任利利¹ 裴玉亮² 伍永明³ 俞琳锋⁴ 陶 静¹ 裴佳禾¹ 焦继鹏⁵ 骆有庆¹

(1. 北京林业大学林木有害生物防治北京市重点实验室, 北京 100083; 2. 新疆林业有害生物防治检疫中心, 新疆 乌鲁木齐 830099;

3. 新疆维吾尔自治区天山东部国有林管理局, 新疆 乌鲁木齐 830099; 4. 中国林业科学研究院资源信息研究所, 北京 100091;

5. 新疆农业大学林学与风景园林学院, 新疆 乌鲁木齐 830052)

摘要:气候变化正在改变全球针叶林小蠹灾害格局, 并使我国天然针叶林面临虫害发生频率升高、暴发强度增强和危害范围扩大的新风险。本文以全球针叶林小蠹灾害变化为主线, 以我国天然针叶林, 尤其天山雪岭云杉林为落脚点, 系统梳理主要致灾类群、区域发生格局、气候驱动机制和综合防控策略, 按照“全球格局—气候响应—暴发机制—监测预警与综合防控技术—中国天然林启示”的逻辑主线展开归纳评述。齿小蠹属、大小蠹属和切梢小蠹属等主要致灾类群在北美、欧洲和亚洲针叶林中造成显著危害, 并在气候变暖背景下呈现出发育加快、世代数增加、越冬存活率提高、分布区向高纬度和高海拔扩展等响应特征。我国天然针叶林小蠹灾害具有发生区域广、致灾种类杂、基础研究薄弱和防控难度高等特点; 此外, 天山东部雪岭云杉林灾害还体现出“异常气候—树势衰弱—小蠹暴发—林分衰退”的级联过程。在驱动机制上, 环境升温通过促进小蠹发育和延长有效扬花期提高种群增长潜力; 干旱与高温复合胁迫通过削弱寄主水分平衡调节、碳同化代谢和树脂(萜烯类)防御能力降低寄主防御阈值; 风倒、干旱、火灾等复合扰动造成虫源积累, 林分结构同质化则进一步推动灾害的空间扩展。未来应加强本土致灾种生物生态学、级联成灾机制、寄主易感性定量评估、物候与风险预测模型、“天空地”一体化监测预警和天然林分阶段综合防控技术研究, 推动小蠹灾害防控由经验处置转向机制驱动、模型支撑的精准决策和以生态韧性提升为目标的全周期管理。

关键词: 气候变化; 小蠹; 针叶林; 暴发机制; 种群动态; 监测预警; 天然林保护

中图分类号: S763 **文献标志码:** A **文章编号:** 1000-1522(2026)09-0001-12

引文格式: 任利利, 裴玉亮, 伍永明, 等. 气候变化背景下针叶林小蠹灾害发生机制与防控策略研究进展 [J]. 北京林业大学学报, 2026, 48(9): 1-12. Ren Lili, Pei Yuliang, Wu Yongming, et al. Research advances on the occurrence mechanisms and management strategies of bark beetle outbreaks in coniferous forests under climate change[J]. Journal of Beijing Forestry University, 2026, 48(9): 1-12.

Research advances on the occurrence mechanisms and management strategies of bark beetle outbreaks in coniferous forests under climate change

Ren Lili¹ Pei Yuliang² Wu Yongming³ Yu Linfeng⁴ Tao Jing¹
Pei Jiahe¹ Jiao Jipeng⁵ Luo Youqing¹

(1. Beijing Key Laboratory for Forest Pest Control, Beijing Forestry University, Beijing 100083, China;

2. Xinjiang Uygur Autonomous Region Forestry Pest Control and Quarantine Center, Urumqi 830099,
Xinjiang Uygur Autonomous Region, China;

3. Eastern Tianshan State-owned Forest Bureau, Urumqi 830099, Xinjiang Uygur Autonomous Region, China;

4. Institute of Forest Resource Information Techniques, Chinese Academy of Forestry, Beijing 100091, China;

5. College of Forestry and Horticulture, Xinjiang Agricultural University, Urumqi 830052,
Xinjiang Uygur Autonomous Region, China)

收稿日期: 2026-06-15 修回日期: 2026-07-28

基金项目: 天山东部国有林管理局研究类项目: 天山东部天然针叶林钻蛀性害虫监测预警和生态调控技术研究项目。

第一作者: 任利利, 博士。主要研究方向: 森林保护。Email: lily_ren@bjfu.edu.cn 地址: 100083 北京市海淀区清华东路 35 号北京林业大学林学院。

责任作者: 骆有庆, 博士生导师, 教授。主要研究方向: 森林保护。Email: youqingluo@126.com 地址: 同上。

本刊网址: <https://j.bjfu.edu.cn>; <https://journal.bjfu.edu.cn>

Abstract: Climate change is reshaping the global pattern of bark beetle outbreaks in coniferous forests and is exposing China's natural coniferous forests to emerging risks of increasing outbreak frequency, intensity, and spatial extent. Taking global changes in conifer-infesting bark beetle outbreaks as the main framework and China's natural coniferous forests, particularly the *Picea schrenkiana* forests in the Tianshan Mountains, as the focal context, this review systematically synthesizes the major damaging taxa, regional outbreak patterns, climate-driven mechanisms, and integrated management strategies. Based on domestic and international literature, this review follows the logic of 'global patterns-climate responses-outbreak mechanisms-monitoring, early warning, and integrated management-implications for China's natural forests' to summarize and evaluate current research progress. Major damaging taxa, including *Ips*, *Dendroctonus*, and *Tomicus*, have caused substantial damage to coniferous forests in North America, Europe, and Asia. Under climate warming, these taxa show pronounced responses, including accelerated development, increased voltinism, higher overwintering survival, and range expansion toward higher latitudes and elevations. Bark beetle outbreaks in China's natural coniferous forests are characterized by broad geographic occurrence, diverse damaging species, insufficient basic research, and high management difficulty. For example, bark beetle outbreaks in eastern Tianshan spruce forests reflect a cascading process of 'climate anomaly-host decline-bark beetle outbreak-stand deterioration'. Warming increases population growth potential by accelerating beetle development and prolonging the effective flight period. Compound drought and heat stress lowers host defense thresholds by impairing water regulation, carbon metabolism, and resin-terpene defenses. Compound disturbances, including windthrow, drought, fire, and stand homogenization, further promote beetle population build-up and spatial spread. Future research should strengthen studies on the biology and ecology of native damaging species, cascading outbreak mechanisms, quantitative assessment of host susceptibility, phenology and risk prediction models, integrated space-air-ground monitoring and early warning, and stage-specific integrated management technologies for natural forests. These efforts will support a shift in bark beetle management from experience-based intervention toward mechanism-driven, model-supported, and resilience-oriented strategies.

Key words: climate change; bark beetle; coniferous forest; outbreak mechanism; population dynamics; monitoring and early warning; natural forest conservation

21 世纪以来,干旱、高温、强降水等极端气候事件日益频发,削弱了树木长势,使更多健康立木转变为适宜小蠹定殖的易感寄主,进一步加剧了全球针叶林衰退^[1-2]。大多数小蠹是典型的次期性害虫,通常需要寄主树势衰弱后才能完成定殖;在气候异常导致寄主防御能力下降时,其凭借隐蔽生活、信息素介导的聚集攻击与伴生真菌的协同作用,可使种群迅速跨越暴发阈值,成为针叶林生态安全的重要威胁^[3-4]。例如,欧洲中部和北美西部针叶林小蠹灾害发生频率增加、危害面积扩大、分布范围向高纬度和高海拔扩展^[5-6];我国天山、贺兰山等西北山地针叶林区也出现了类似趋势。总体来看,气候变化背景下,针叶林小蠹灾害已由局部地区性次生灾害,逐步演变为区域乃至全球尺度森林衰退的重要驱动因子。

近年来,多项国际研究及国际林业研究组织联盟(IUFRO)相关学术会议(如 2025 年 9 月“气候危机:针叶林面临的风险”专题会议)均强调,气候变化

叠加小蠹扰动已成为针叶林健康的重要威胁。过去被视为生物灾害低风险的天然针叶林正成为新的暴发区,但相关成灾机制研究和防控技术储备仍显不足。在此背景下,本文以全球针叶林小蠹灾害变化为综述框架,系统梳理气候变化驱动下小蠹灾害的主要类群、区域发生格局、种群暴发机制与综合防控策略,并结合我国天然针叶林,尤其关注天山雪岭云杉林(天山东部林区)面临的小蠹灾害新风险,提出未来研究与防控重点^[7]。

1 针叶林小蠹灾害的主要类群、区域格局与气候变化响应

全球针叶林小蠹灾害正由局部、次生性危害转向区域性森林扰动,并呈现向高纬度、高海拔扩展以及新寄主系统形成等趋势。本节先概述主要致灾类群及其区域代表性种类,再归纳气候变化背景下灾害格局和生活史响应的变化,最后结合我国天然针

叶林分析面临的防控风险。

1.1 主要致灾类群与代表性种类

小蠹隶属鞘翅目象甲科(Curculionidae)小蠹亚科(Scolytinae)。针叶林中的致灾小蠹主要为取食韧皮部、可在适宜条件下造成活立木死亡的树皮小蠹,其中最具代表性的类群包括齿小蠹属(*Ips*)、大小蠹属(*Dendroctonus*)和切梢小蠹属(*Tomicus*)。其他造成针叶林小蠹灾害的类群还包括瘤小蠹属(*Orthotomicus*)、星坑小蠹属(*Pityogenes*)、根小蠹属(*Hylastes*)、林小蠹属(*Hylurgus*)和四眼小蠹属(*Polygraphus*)等十余个属^[3-4],不同类群在寄主、生活史和危害特性上存在差异。

北美针叶林小蠹灾害以大小蠹属为代表。山松大小蠹(*Dendroctonus ponderosae*)主要危害扭叶松(*Pinus contorta*)、西黄松(*Pinus ponderosa*)等松属树种,是北美西部最具代表性的致灾种;南方松大小蠹(*Dendroctonus frontalis*)主要危害火炬松(*Pinus taeda*)、北美短叶松(*Pinus banksiana*)等,是美国东南部和中美洲松林的重要害虫;北美云杉大小蠹(*Dendroctonus rufipennis*)主要危害云杉属(*Picea*)树种。除大小蠹属外,美松齿小蠹(*Ips pini*)、加州齿小蠹(*Ips confusus*)、粗齿小蠹(*Ips calligraphus*)、南部松齿小蠹(*Ips grandicollis*)等齿小蠹属种类也常在干旱、火烧、风倒或采伐扰动后侵染松林,参与局部或区域性针叶林衰退过程^[8-10]。

欧洲针叶林小蠹灾害以齿小蠹属为核心。云杉八齿小蠹(*Ips typographus*)是欧洲北方云杉林中最重要致灾种,主要危害欧洲云杉(*Picea abies*),在中欧、北欧和东欧均可形成大范围暴发。松十二齿小蠹(*Ips sexdentatus*)主要危害松属(*Pinus*)树种,在南欧和西欧松林中具有较高致灾风险;重齿小蠹(*Ips duplicatus*)与云杉林衰退密切相关,在中欧和东欧部分地区危害加重;中穴星坑小蠹(*Pityogenes chalcographus*)常与云杉八齿小蠹共同发生,危害较细径云杉枝干;纵坑切梢小蠹(*Tomicus piniperda*)和横坑切梢小蠹(*Tomicus minor*)则兼具嫩梢取食和树干繁殖阶段,是欧洲松林中重要的小蠹类群^[5-6, 11]。

亚洲针叶林小蠹种类组成更为复杂,既包括与欧洲共有或近缘的云杉、落叶松(*Larix* spp.)和松林小蠹种类,也包括具有区域特色的本土种类。我国西南地区以云南切梢小蠹(*Tomicus yunnanensis*)、横坑切梢小蠹等危害云南松(*Pinus yunnanensis*)为主^[12-13];秦岭-大巴山区域以华山松大小蠹(*Dendroctonus armandi*)危害华山松(*Pinus armandii*)为代表^[14];东北和西北针叶林中可见多种齿小蠹类群危害落叶松、云杉和松类。新疆雪岭云杉林中,天

山重齿小蠹(*Ips hauseri*)和天山星坑小蠹(*Pityogenes spessivtsevi*)是重要的蛀干害虫。与欧美代表性种类相比,我国这些本土致灾种的基础生物学、化学生态学、物候模型和暴发动态研究仍明显不足,难以支撑精准预警与防控决策。

外来入侵种是我国针叶林小蠹灾害格局的重要组成部分。红脂大小蠹(*Dendroctonus valens*)原产北美,自1998年在山西暴发以来,已扩散至华北、东北和西北多省区,主要危害油松(*Pinus tabulaeformis*)和华山松^[15-16]。长林小蠹(*Hylurgus ligniperda*)原产欧洲、北非及地中海区域,已在山东多地发现并造成入侵危害,部分地区危害较重,其基因组研究显示该虫具有较强的环境耐受和寄主适应潜力^[17-21]。入侵小蠹在新分布区可能因天敌制约不足、寄主防御不匹配和气候适宜而形成较高的致害风险。

1.2 气候变化下小蠹灾害格局变化

气候变化正在通过两条路径改变针叶林小蠹灾害格局:一是直接改变小蠹的发育速率、世代数、越冬存活率和扬飞物候,二是间接削弱寄主树势并增加风倒木、火烧木、衰弱木等低防御繁殖资源^[10, 22-23]。此外,温度升高也会促进小蠹适宜的分布区扩展^[4, 23]。总体上,全球针叶林小蠹危害呈现“原生危害加剧、入侵种扩展、新区域暴发”3条主线并行发展的态势,但不同系统中气候、寄主和林分结构对灾害的相对贡献并不相同^[3, 6, 8, 10]。

小蠹暴发并非单一气候因子作用的结果,而是气候异常、寄主易感性、虫口密度、化学通讯、林分结构和景观连通性等因素跨尺度耦合的产物。小蠹种群能否由常发状态转入暴发状态,取决于虫口密度、寄主防御阈值、资源可利用性之间的相互作用^[3]。全球变暖还会增强干旱、火灾、风倒等扰动,并通过虫害复合扰动放大森林退化风险^[2]。近年研究认为,小蠹暴发是阶段性种群动态过程,暴发的启动、扩展和衰退分别受寄主抗性、种内竞争、天敌、共生微生物和景观结构等因素的协同调控^[4, 23]。

升温首先改变小蠹的生活史和物候过程,可加快发育速率、缩短发育历期、增加世代数、提前春季扬飞并延长有效繁殖期。云杉八齿小蠹完成发育约需334℃·d,发育起始温度约为8.3℃;中欧升温已使低海拔种群由一年一代向稳定二代、局部三代转变,未来世代数仍可能增加,潜在适生范围也将进一步扩大^[24-27]。北美大小蠹类群表现出相似响应:山松大小蠹在部分高海拔区出现一年二代记录,表明升温可能打破以往由低温和短生长季限制的生活史格局^[28-29];北美云杉大小蠹在连续暖夏条件下可由两年一代缩短为一年一代,显著提高种群增长速率,是

美国阿拉斯加和加拿大育空地区暴发的重要驱动因素^[9,30]。这些变化表明,升温不仅增加单代种群增长潜力,还可能通过世代重叠和繁殖期延长提高暴发概率。

冬季极端低温减少和春季物候提前共同推动小蠹分布区向高纬度和高海拔扩展。南方松大小蠹原主要分布于美国东南部,随着冬季低温限制减弱,近年在新泽西、纽约、新罕布什尔和缅因等地的新记录已经证实其北扩趋势^[31-34]。山松大小蠹在北美西部的暴发也突破了部分历史气候限制,在高纬度和高海拔松林中造成大面积树木死亡^[8,10,35-36]。这些案例说明,升温不仅改变已有分布区内的种群动态,也在推动小蠹地理分布范围的扩展。

全球气候变化还可能推动寄主范围扩大和新寄主系统形成。小蠹与寄主长期共演化关系决定其定殖成功率,但当升温、干旱或入侵导致小蠹进入新的气候区和寄主组合时,原有的寄主防御匹配关系可能被打破。例如,红脂大小蠹在北美通常多侵染衰弱木、伐桩和受伤木,但入侵我国后在油松林中表现出更强的致害性,成为入侵种由低危种转变为重大害虫的典型示例^[15-16]。

寄主种类和林分结构变化也会改变小蠹危害方式。许多小蠹在常发状态下主要危害风倒木、伐桩、火烧木或干旱衰弱木等,但当气候胁迫造成活立木衰弱、同时虫源种群升高时,原本以衰弱木为主的次期性种类也可能侵入活立木并形成区域性危害。欧洲云杉八齿小蠹暴发案例显示,极端干旱正在使部分地区由风倒驱动型暴发转向干旱驱动型暴发^[5]。我国西南地区切梢小蠹危害已成为与气候因子密切耦合的区域性灾害问题^[37]。

多类同步发生和联合危害是全球变化背景下小蠹灾害加重的另一重要趋势。在干旱、风倒、火灾等复合扰动和林分同质化背景下,不同小蠹种类可在同一林分或相邻寄主系统中同步增长,形成多类共同参与的树木死亡过程。例如,欧洲云杉林中云杉八齿小蠹常与中穴星坑小蠹、重齿小蠹等共同发生,不同种类利用不同树干部位或不同径级资源,加重云杉林衰退风险^[5-6,11]。北美松林中,山松大小蠹、南方松大小蠹及多种齿小蠹种类可在干旱、火烧或采伐扰动后形成复合危害^[8,10]。我国天山雪岭云杉林中,天山重齿小蠹、天山星坑小蠹、云杉大小蠹、云杉根小蠹(*Hylastes cunicularius*)和木小蠹属(*Trypodendron* sp.)种类可在不同程度上共同参与衰弱木和枯死木利用,表明我国天然针叶林小蠹灾害可能具有多类、多阶段和多生态位共同作用的特征。

我国本土致灾小蠹的生活史变化与全球趋势具有一致性。天山重齿小蠹历史记录为一年一代、成虫在土壤越冬^[38-39];2025年在乌鲁木齐县白杨沟调查显示,其年生活史趋于复杂,可能增至每年至少2代,越冬虫态和越冬场所也趋于多样化(课题组待发表数据)。PHENIPS、RITY等积温模型已能较好预测其出蛰和世代发育,但不同类群的关键驱动因子并不一致^[22,25-27,40]。我国本土致灾种仍缺乏积温-物候模型、越冬存活参数、寄主易感性评价和空间扩散模型,这些不足已成为精准预警和阶段化防控的关键短板。

1.3 我国天然针叶林小蠹灾害的新风险

我国天然针叶林小蠹灾害正在由局部、次期性危害转向气候变化背景下的区域性复合扰动。近年来,西北、东北、秦岭、西南、横断山脉区域等天然或次生针叶林区均出现小蠹危害加重现象,其中天山、贺兰山等区域风险尤为突出,迫切需要建立以早期预警、阶段诊断和生态韧性提升为核心的防控策略。

以天山雪岭云杉林(天山东部林区)为例,天山重齿小蠹近年来在暖干化背景下引发大面积云杉异常枯死。现有证据表明,该灾害并非单一虫口增长过程,而是“异常气候—树势衰弱—小蠹暴发—林分衰退”的级联过程。该虫研究基础薄弱,其发育阈值、扬飞物候、越冬虫态、寄主选择、信息素系统和暴发终止机制仍缺乏系统研究。

从灾害特征和防控难度来看,我国天然针叶林小蠹灾害可概括为“重、广、新、特、杂、难”:重,即已造成局部天然林大面积枯死并威胁区域生态安全;广,即风险覆盖东北、西北和西南主要针叶林区;新,即异常气候诱导树势下降后,次期性害虫可出现暴发性扩张;特,即部分灾害发生在过去生物灾害风险较低的天然林中;杂,即不同区域建群树种和优势小蠹不同,成灾机制具有显著区域差异;难,即小蠹隐蔽危害、天然林干预受限,防控难度远高于多数食叶害虫。因此,我国天然针叶林小蠹灾害防控应在明确本土致灾种生物生态学特征的基础上,建立适合天然林保护目标的监测预警、阶段诊断和综合治理体系,为从经验处置转向机制驱动和模型支撑的科学防控提供基础。

2 气候因子驱动的小蠹种群动态与暴发机制

2.1 升温、干旱与寄主防御下降的级联作用

小蠹暴发源于虫口增长潜力提高与寄主防御能力下降的共同作用。当虫口密度超过寄主抗性所决定的防御阈值后,小蠹种群即由常发状态转入暴发

状态,并在聚集信息素介导的密度正反馈下快速扩张^[3-4, 10, 41-42](图1)。

衰弱针叶树释放的单萜、乙醇等挥发物可增强小蠹对寄主的定位能力;寄主防御削弱后,先锋虫更易成功侵入并释放聚集信息素,诱导同种个体集中攻击。多数致灾小蠹还与长喙壳类真菌等微生物共生,共生真菌可削弱寄主防御、影响水分运输并参与营养供给,部分共生真菌甚至可能参与聚集信息素合成。因此,气候变化背景下的小蠹危害本质上是“小蠹、共生微生物、寄主、环境”多因子互作的结果^[43-50]。

干旱与高温通过水分-碳代谢瓶颈削弱针叶树防御能力。水分胁迫降低气孔导度、光合碳输入和非结构性碳水化合物积累,进而削弱树脂流速、萜烯类树脂防御反应,使小蠹在较低攻击密度下也可能突破寄主防御阈值^[48, 51-52]。林分结构进一步调节这一过程:高密度纯林会加剧资源竞争并提高寄主易感性,而混交林中的非寄主挥发物可干扰小蠹寄主定位,降低连续侵染概率^[53-56]。我国天山东部雪岭云杉林小蠹灾害与“气候异常—寄主防御下降与虫口增长—攻击密度突破阈值—局地暴发”的级联机制基本一致。持续暖干化、寄主连续分布和近纯林结构可能共同为天山重齿小蠹的扩散和区域性暴发提供条件^[37, 42, 57]。

2.2 小蠹种群暴发的启动、维持与衰退

小蠹暴发本质上是种群由常发状态跨越生态阈值进入暴发状态,在正反馈放大后又因资源耗竭和密度制约而回落的“启动—放大—自限—衰退”过程^[3-4, 23](图2)。在非暴发期,小蠹通常依赖风倒木、火烧木或衰弱木等低防御或无防御寄主维持低密度

种群。大规模风倒、干旱和高温可同时增加衰弱寄主并削弱周围活立木的防御能力,从而推动种群积累、降低小蠹虫种群暴发阈值^[5, 11, 42, 52]。

暴发启动的关键在于攻击密度是否超过寄主防御所能承受的临界阈值。不同小蠹对寄主树种的临界攻击密度存在差异;当聚集攻击强度超过寄主防御阈值并导致树脂分泌和次生代谢防御失效后,小蠹的危害对象即可由衰弱木扩展至健康活立木。例如,松十二齿小蠹侵入健康海岸松(*Pinus pinaster*)所需的临界攻击密度(critical threshold of attack density, CTAD)约为142个入侵孔/m²;山松大小蠹在扭叶松上的最优攻击密度约为60头雌虫/m²^[58-59]。超过阈值后,聚集信息素驱动的集中侵入可进一步提高繁殖回报,形成持续虫源并推动斑块扩展^[4, 23, 60]。

然而,小蠹暴发并不会无限持续。当定殖密度过高时,种内竞争增强,后代数量和个体适合度下降,种群净增殖率最终降至1以下,暴发随之进入自限和衰退阶段。多项研究均显示,随着母坑道密度或攻击密度升高,小蠹繁殖成功率显著下降,种内竞争是暴发后期种群回落的核心机制^[24, 58-59, 61-62]。Schroeder等^[62]对瑞典南部由风倒触发的云杉八齿小蠹暴发进行了7年连续追踪:活立木受害初期定殖密度较低,约为218条母坑道/m²,每头雌虫可产生下一代雌虫约5.7头;暴发后期,活立木上的定殖密度总体升高,最高可达717条母坑道/m²,而繁殖成功率显著下降,每头雌虫产生的下一代雌虫数降至1头以下。易感寄主减少和天敌滞后响应也可促进暴发终止,但其作用通常弱于密度制约效应;过度清除枯死木还可能削弱天敌维持基础,不利于常发状态下的自然调控^[11, 61, 63]。



图1 气候变化下物候重塑与寄主树势衰弱驱动小蠹暴发机制示意图(以天山雪岭云杉与天山重齿小蠹为例)

Fig. 1 Schematic diagram showing how phenological reshaping and host tree weakening drive bark beetle outbreaks under climate change (taking *Picea schrenkiana* and *Ips hauseri* as an example)

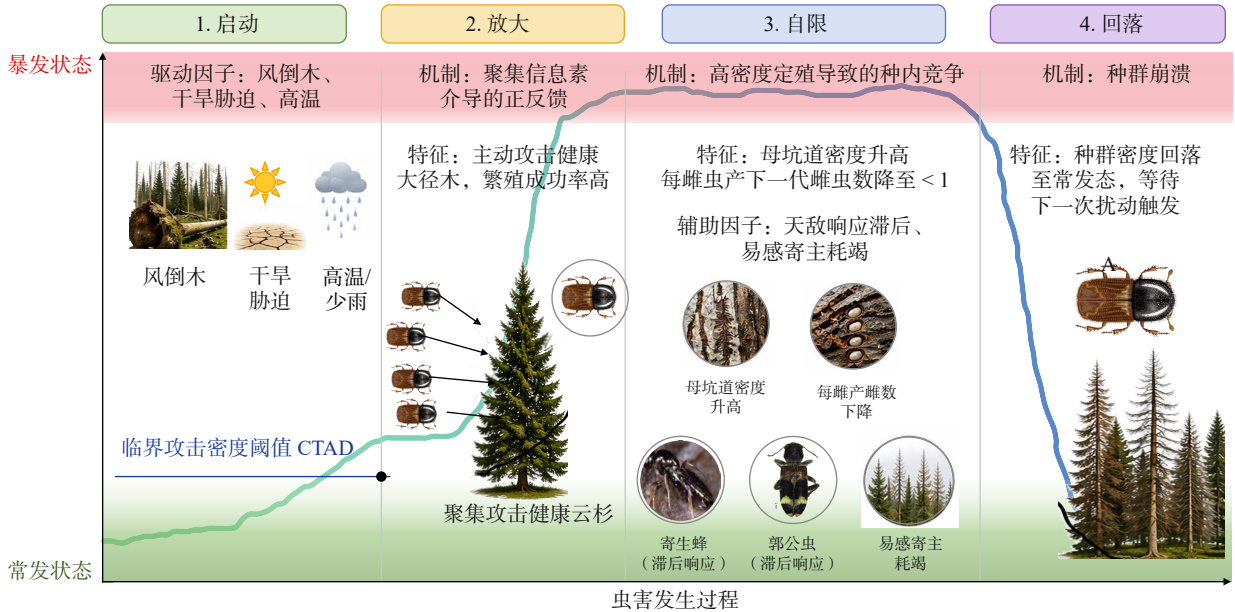


图2 小蠹种群暴发的“启动—放大—自限—衰退”过程示意图

Fig. 2 Schematic diagram of the initiation–amplification–self-limitation–collapse process of bark beetle outbreaks

诱捕器捕获量是判断小蠹种群阶段的常用指标,但绝对捕获数量受虫种、寄主、诱芯释放速率、诱捕器位置和区域环境影响较大,不能简单跨区域套用^[64–66]。相比单一绝对捕获量,春季越冬亲代与夏季子代的捕获量比值更能反映种群趋势:该比值大于1通常提示种群仍在增长,小于1则提示种群趋于下降^[67–68]。因此,诱捕量应与林分健康状况、气候胁迫指标、虫口密度和繁殖成功率等指标综合使用。

在无人工干预的自然条件下,云杉八齿小蠹暴发通常持续3~6年后自然终止^[11,61]。因此,小蠹防控不应依赖固定的单一阈值,而应转向种群阶段识别和过程管理:在启动前控制低防御寄主资源,在暴发中抑制虫源扩散,在衰退期结合种内竞争、寄主资源变化和天敌调控,形成阶段差异化的综合管理策略。

2.3 暴发的空间扩展与复合扰动的放大效应

小蠹暴发启动后,灾害扩展通常表现为近距离斑块扩展与远距离跳跃传播并存的多尺度过程。以云杉八齿小蠹为例,新侵染斑块多形成于上一年虫源附近,早期主要表现为原有斑块边缘扩展和邻近新斑块形成;随着虫口密度升高,聚集攻击推动小蠹侵入周边活立木,零星受害点逐步扩大为斑块状或片状危害^[69–70]。在高虫口密度区域,相邻侵染斑块可相互连接并形成连续受害廊道;同时,气流辅助迁飞和人为木材调运也可能造成远距离跳跃式传播,增加跨区域扩散风险^[71]。

景观连通性决定了局部斑块能否发展为区域性蔓延。寄主树种连续分布、林分同质化和高密度纯林可降低扩散阻力,促进小蠹沿连续寄主林带扩展;而树种混交、非寄主林分和景观异质性可增加扩散

阻力,降低斑块连通性和同步暴发风险^[72–73]。长期追踪研究表明,小蠹暴发可由早期“寄主资源驱动”逐步转向“种群扩散驱动”,景观尺度暴发本质上是虫源数量、寄主连通性和扩散阻力共同作用的结果^[70]。风倒、干旱、火灾和小蠹暴发常形成复合扰动,并进一步放大扩展效应,使暴发更易由局部虫源点扩展为景观尺度灾害,并提高暴发强度和持续时间^[74]。

天山东部雪岭云杉林小蠹灾害也表现出类似的斑块扩展和空间级联特征。基于已有高分辨率遥感和野外调查数据初步分析,近年云杉枯死由零星点状发生逐步发展为斑块状和片状危害,主要集中于前山浅山带,并在局部区域呈现向中山带扩展趋势。持续暖干化、雪岭云杉沿山脉连续分布、近纯林斑块较多,三者可能共同促进局部虫源点沿连续寄主林带扩展,最终在相邻斑块连接后形成区域性危害。

3 针叶林小蠹灾害监测预警与综合防控策略

小蠹灾害防控应以监测预警为基础,结合化学生态调控、虫源木管理、天敌利用和林分经营等措施,形成分阶段、分区域的综合治理体系。由于小蠹多在树皮隐蔽危害,单一技术难以满足早期发现、风险判断和应急处置需求,需构建“监测预警—应急控制—长期预防”相衔接的综合管理框架。

3.1 多源监测预警与化学生态调控

小蠹危害具有隐蔽性和滞后显症特征,传统地面调查难以及时覆盖大范围林区。当前监测技术主要包括卫星遥感、无人机遥感、地面信息素诱捕和林分风险评估,并正向“天空地”一体化方向发展^[75]。

卫星遥感适合区域尺度监测,可识别红冠木(树冠变红)、灰冠木(树冠变灰)等冠层变色特征及大范围冠层异常,判断灾害发生范围与程度。Sentinel-2、高分二号、WorldView-3等影像已被用于云杉八齿小蠹、红脂大小蠹和切梢小蠹危害识别,并显示出较好的应用潜力^[76-78]。但受光谱分辨率和空间分辨率的限制,在受害初期冠层尚未明显变色的“绿冠期”,实现早期侵染木的精准识别仍是卫星遥感的主要瓶颈^[79]。

无人机多光谱、高光谱和热成像技术具有高空分辨率、灵活部署等优势,可实现单木尺度的受害树木识别。相关研究表明,红边波段、高光谱植被指数以及热红外信息有助于提高绿冠期早期侵染木的识别精度^[80-85]。除直接识别受害木外,结合林分、地形、景观、虫情、人为干扰等因素还可构建空间风险预测模型,为重点区域巡查和防控资源配置提供依据^[86-88]。

基于信息素的监测和化学生态调控是小蠹灾害监测预警与精准防控的重要技术途径,主要包括信息素诱捕、抗聚集化合物驱避和“推-拉”调控策略。信息素诱捕可用于监测成虫扬飞期、评估种群动态和判断暴发风险^[6,11]。目前,部分小蠹类的商品化引诱剂已较为成熟^[15-16,60,89]。将驱避剂与引诱剂进行空间组合的“推-拉”策略,可在一定程度上降低立木受害率,尤其对齿小蠹属具有较好的应用潜力^[90-92]。但其效果受虫种、虫口密度、释放剂型、布设密度和空间配置影响较大。

总体而言,卫星遥感适合大范围发生区域识别、定位、发生面积勾绘和灾害发生历史追溯,无人机遥感适合重点区域和单木尺度精准早期识别,信息素诱捕可提供种群物候和动态信息。多源遥感、地面信息素诱捕和林分风险因子相结合的“天空地”一体化监测体系,是提升小蠹早期识别、风险预警和精准防控能力的重要方向。

3.2 生物防治

小蠹在自然条件下受到捕食性天敌、寄生性天敌和病原微生物的共同调控。欧洲已记录与云杉八齿小蠹(*Ips typographus*)相关联的寄生蜂和捕食天敌种类繁多,其中捕食性甲虫以郭公虫科(Cleridae)和啮蠹甲科(Rhizophagidae = Monotomidae)研究最为深入^[93]。天敌在常发状态下可对小蠹种群起到一定调节作用,但在暴发状态下,其种群数量增长(数值响应)通常滞后于小蠹的快速增长,因此难以单独遏制大规模暴发^[4,11]。我国红脂大小蠹的昆虫类天敌主要有大啮蠹甲(*Rhizophagus grandis*)、环斑猛猎蝽(*Sphedanolestes impressicollis*)、西岳蒙蛇蛉(*Mongoloraphidia xiyue*)、日本弓背蚁(*Camponotus*

japonicus)、中华红林蚁(*Formica sinensis*)、拟蚁态郭公虫(*Thanasimus lewisi*)、纤细阎甲(*Niponius* sp.)、寄生蝇(Tachinidae)和茧蜂(Braconidae)等。其中,大啮蠹甲的成功引进与应用是我国小蠹生物防治的重要实践,该虫已在我国山西红脂大小蠹发生区成功定殖,并在防治实验中取得成效^[94-95]。在欧洲也曾利用大啮蠹甲防治云杉大小蠹(*Dendroctonus micans*),取得良好效果^[96]。此外,球孢白僵菌(*Beauveria bassiana*)、绿僵菌(*Metarhizium* spp.)等昆虫病原真菌在实验室和部分林间试验中显示出一定防治潜力,但其林间尺度稳定应用仍受环境条件、施用方式和持效期等因素限制^[93]。从基础研究和未来技术储备角度看,RNAi和CRISPR/Cas9等新兴分子技术为小蠹防控提供了新的研究方向,但目前仍处于功能验证和应用探索阶段^[6]。总体而言,天敌利用和生物防治技术仍是综合治理体系中相对薄弱的一环,有待进一步研发,并与监测预警、虫源控制和林分经营等措施协同使用。

3.3 林分经营与韧性提升

通过林分经营降低寄主易感性、提高森林韧性,是气候变化背景下小蠹灾害适应性管理的重要方向。林分密度、树种组成和径阶结构共同影响寄主树势、资源竞争和小蠹扩散风险^[54,97-99]。

虫源木管理是小蠹灾害防控中应用最广泛的措施,主要包括清除已受侵染树木(卫生伐),以及清理风倒木、衰弱木和采伐剩余物等。其防控效果高度依赖种群发生阶段和作业时效。在种群积累阶段,风倒木、衰弱木和新伐桩等低防御水平寄主可为小蠹提供繁殖场所,及时清理有助于减少虫源积累并降低暴发风险;进入暴发阶段后,小蠹已可通过聚集攻击侵入健康活立木并持续产生新虫源,单纯清理枯死木的效果明显下降^[100-102]。虫源木清理也存在明显的生态权衡。过度或均匀清除枯死木可能影响生物多样性和天敌种群,可能增加林缘破碎化和局部微气候变化风险。因此,虫源木管理应注重空间优化和阶段化处置,在控制虫源扩散的同时兼顾碳储量、生物多样性和天然更新^[6,103]。增加树种多样性和景观异质性可通过降低寄主连续性、增强非寄主干扰和维持天敌群落,降低小蠹暴发风险^[55-56]。近年研究和模拟结果表明,提高阔叶树比例、优化龄级结构并营造景观尺度异质性,有助于降低林分受害风险,提升森林生态系统对干旱、风倒和虫害复合扰动的抵抗力与恢复力^[104-105]。

在我国天山雪岭云杉天然林中,小蠹灾害防控应坚持“监测预警为基、生态调控为本、辅以生态修复”的总体思路。异常气候难以直接调控,但其变化

趋势和高风险时空窗口可以预测;在此基础上,应通过早期预报预警、精准清理、林窗更新和天然恢复促进灾害减缓与生态修复。对于天然林,应避免单纯追求彻底清除虫源,而应以遏制扩散、降低灾害等级和促进森林自我恢复为主要目标,形成与天然林保护目标相协调的阶段化综合管理策略。

4 小结与展望

综上,气候变化正在推动针叶林小蠹灾害由局地次期性危害向区域性复合危害转变。升温提高小蠹发育速率、越冬存活率和世代数增加(多化性)风险;干旱和高温复合胁迫削弱寄主水分平衡调节、碳同化代谢和树脂(萜烯类)防御能力;风倒、干旱和火灾等复合扰动进一步增加低防御繁殖资源,林分同质化和景观连通性则共同放大灾害的空间扩展。小蠹暴发的核心机制可概括为“气候异常、寄主防御下降与虫口增长、虫口密度突破阈值聚集攻击”。因此,未来研究不应仅关注单一气候因子或单一虫种,而应整合个体寄主选择、信息素通讯、共生微生物、寄主防御、种群密度反馈和景观扩散等过程,建立跨尺度的暴发机制研究框架。

天然针叶林因树种组成相对单一、林龄结构偏老、景观连通性高且人为干预受限,对气候变化驱动的小蠹灾害尤为敏感。我国天然针叶林小蠹灾害研究仍存在明显短板:本土重要种类在发育阈值、扬飞物候、越冬存活、寄主选择、聚集与抗聚集信息素、共生微生物功能和种群动态参数方面仍缺乏系统数据,限制了精准监测和模型化预警能力的提升。

未来应重点推进五方面工作:一是解析异常气候、寄主衰弱和小蠹暴发之间的级联成灾机制;二是建立本土致灾小蠹的生物生态学、化学生态学和共生微生物基础数据;三是构建寄主易感性评价指标,量化树脂流量、针叶水分、光合作用、冠层温度和光谱特征等指标;四是耦合物候模型、扩散模型、寄主动态和景观结构,构建适用于中国主要针叶林区的风险预测模型;五是完善“天空地”一体化监测预警和天然林分阶段综合防控技术体系。对我国而言,应坚持“监测预警为基、生态调控为本、辅以生态修复”的总体策略,重点推进本土致灾小蠹生物学和化学生态学研究、精准监测预警、分阶段虫源木管理、天敌保护利用和生态恢复,实现更为科学的小蠹灾害防控。

参 考 文 献

[1] Allen C D, Macalady A K, Chenchouni H, et al. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests [J]. *Forest Ecology and*

Management, 2010, 259(4): 660–684.

- [2] Seidl R, Thom D, Kautz M, et al. Forest disturbances under climate change [J]. *Nature Climate Change*, 2017, 7(6): 395–402.
- [3] Raffa K F, Aukema B H, Bentz B J, et al. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions [J]. *BioScience*, 2008, 58(6): 501–517.
- [4] Biedermann P H W, Müller J, Grégoire J C, et al. Bark beetle population dynamics in the Anthropocene: challenges and solutions [J]. *Trends in Ecology & Evolution*, 2019, 34(10): 914–924.
- [5] Hlásny T, Zimová S, Merganičová K, et al. Devastating outbreak of bark beetles in the Czech Republic: drivers, impacts, and management implications [J]. *Forest Ecology and Management*, 2021, 490: 119075.
- [6] Singh V V, Naseer A, Mogilicherla K, et al. Understanding bark beetle outbreaks: exploring the impact of changing temperature regimes, droughts, forest structure, and prospects for future forest pest management [J]. *Reviews in Environmental Science and Bio/Technology*, 2024, 23(2): 257–290.
- [7] IUFRO. Climate crisis: conifer forests at risk 2025[R]. Jeju, Republic of Korea: International Union of Forest Research Organizations, 2025.
- [8] Fettig C J, Asaro C, Nowak J T, et al. Trends in bark beetle impacts in North America during a period (2000–2020) of rapid environmental change [J]. *Journal of Forestry*, 2022, 120(6): 693–713.
- [9] Berg E E, Henry J D, Fastie C L, et al. Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: relationship to summer temperatures and regional differences in disturbance regimes [J]. *Forest Ecology and Management*, 2006, 227(3): 219–232.
- [10] Bentz B J, Régnière J, Fettig C J, et al. Climate change and bark beetles of the western United States and Canada: direct and indirect effects [J]. *BioScience*, 2010, 60(8): 602–613.
- [11] Wermelinger B. Ecology and management of the spruce bark beetle *Ips typographus*: a review of recent research [J]. *Forest Ecology and Management*, 2004, 202(1/3): 67–82.
- [12] Kirkendall L R, Faccoli M, Ye H. Description of the Yunnan shoot borer, *Tomicus yunnanensis* Kirkendall & Faccoli sp. n. (Curculionidae, Scolytinae), an unusually aggressive pine shoot beetle from southern China, with a key to the species of *Tomicus* [J]. *Zootaxa*, 2008, 1819(1): 25–39.
- [13] Lu J, Zhao T, François L, et al. The shoot-feeding ecology of three *Tomicus* species in Yunnan Province, southwestern China [J]. *Journal of Insect Science*, 2014, 14(1): 37.
- [14] Ning H, Tang M, Chen H. Impact of climate change on potential distribution of Chinese white pine beetle *Dendroctonus armandi* in China [J]. *Forests*, 2021, 12(5): 544.
- [15] Yan Z, Sun J, Don O, et al. The red turpentine beetle, *Dendroctonus valens* LeConte (Scolytidae): an exotic invasive

- pest of pine in China [J]. *Biodiversity and Conservation*, 2005, 14(7): 1735–1760.
- [16] Sun J, Lu M, Gillette N E, et al. Red turpentine beetle: innocuous native becomes invasive tree killer in China [J]. *Annual Review of Entomology*, 2013, 58: 293–311.
- [17] 任利利, 陶静, 武海卫, 等. 重大害虫长林小蠹入侵我国的首次发现与侵染特征 [J]. *林业科学*, 2021, 57(5): 140–150.
- Ren L L, Tao J, Wu H W, et al. The first discovery and infective characteristics of a major invasive pest *Hylurgus ligniperda* (Coleoptera: Scolytidae) in China [J]. *Scientia Silvae Sinicae*, 2021, 57(5): 140–150.
- [18] Chen Z Q, Ren L L, Li J X, et al. Chromosomal-level genome assembly of *Hylurgus ligniperda*: insights into host adaptation and environmental tolerance [J]. *BMC Genomics*, 2024, 25: 792.
- [19] 顾颖, 任利利, 骆有庆, 等. 长林小蠹林间种群扬飞日节律观察及飞行能力测定 [J]. *北京林业大学学报*, 2025, 47(4): 1–9.
- Gu Y, Ren L L, Luo Y Q, et al. Flight daily rhythm observation and flight ability assessment of *Hylurgus ligniperda* populations in forest [J]. *Journal of Beijing Forestry University*, 2025, 47(4): 1–9.
- [20] 周玉婷, 葛雪贞, 邹娅, 等. 基于 Maxent 模型的长林小蠹的全球及中国适生区预测 [J]. *北京林业大学学报*, 2022, 44(11): 90–99.
- Zhou Y T, Ge X Z, Zou Y, et al. Prediction of the potential geographical distribution of *Hylurgus ligniperda* at the global scale and in China using the Maxent model [J]. *Journal of Beijing Forestry University*, 2022, 44(11): 90–99.
- [21] 李相淳, 陶静, 李心钰, 等. 长林小蠹气味降解酶基因的鉴定与分子对接 [J]. *北京林业大学学报*, 2025, 47(2): 79–94.
- Li X C, Tao J, Li X Y, et al. Identification and molecular docking of odorant-degrading enzyme genes in *Hylurgus ligniperda* [J]. *Journal of Beijing Forestry University*, 2025, 47(2): 79–94.
- [22] Schebeck M, Hansen E M, Schopf A, et al. Diapause and overwintering of two spruce bark beetle species [J]. *Physiological Entomology*, 2017, 42(3): 200–210.
- [23] Lantschner M V, Corley J C. Spatiotemporal outbreak dynamics of bark and wood-boring insects [J]. *Current Opinion in Insect Science*, 2023, 55: 101003.
- [24] Faccoli M, Bernardinelli I. Breeding performance of the second generation in some bivoltine populations of *Ips typographus* (Coleoptera: Curculionidae) in the south-eastern Alps [J]. *Journal of Pest Science*, 2011, 84(1): 15–23.
- [25] Baier P, Pennerstorfer J, Schopf A. PHENIPS: a comprehensive phenology model of *Ips typographus* (L.) (Col., Scolytinae) as a tool for hazard rating of bark beetle infestation [J]. *Forest Ecology and Management*, 2007, 249(3): 171–186.
- [26] Ogris N, Ferlan M, Hauptman T, et al. RITY: a phenology model of *Ips typographus* as a tool for optimization of its monitoring [J]. *Ecological Modelling*, 2019, 410: 108775.
- [27] Hofmann S, Kautz M, Schebeck M. Increasing spring temperatures advance post-diapause swarming and prolong the reproductive period in the bark beetle *Ips typographus* [J]. *Journal of Applied Entomology*, 2025, 149(2): e13404.
- [28] Bentz B J, Vandygriff J, Jensen C, et al. Mountain pine beetle voltinism and life history characteristics across latitudinal and elevational gradients in the western United States [J]. *Forest Science*, 2014, 60(3): 434–449.
- [29] Mitton J B, Ferrenberg S M. Mountain pine beetle develops an unprecedented summer generation in response to climate warming [J]. *The American Naturalist*, 2012, 179(5): E163–E171.
- [30] Hansen E M, Bentz B J, Turner D L. Temperature-based model for predicting univoltine brood proportions in spruce beetle (Coleoptera: Scolytidae) [J]. *Canadian Entomologist*, 2001, 133(6): 827–841.
- [31] Lesk C, Coffel E, D'Amato A W, et al. Threats to North American forests from southern pine beetle with warming winters [J]. *Nature Climate Change*, 2017, 7(10): 713–717.
- [32] Kanaskie C R, Schmeelk T C, Cancelliere J A, et al. New records of southern pine beetle (*Dendroctonus frontalis* Zimmermann) in New York, New Hampshire, and Maine, USA indicate northward range expansion [J]. *The Coleopterists Bulletin*, 2023, 77(2): 248–251.
- [33] Dodds K J, Aoki C F, Arango-Velez A, et al. Expansion of southern pine beetle into northeastern forests: management and impact of a primary bark beetle in a new region [J]. *Journal of Forestry*, 2018, 116(2): 178–191.
- [34] 李明阳, 巨云为, 吴文浩, 等. 气候变化情景下外来森林病虫害潜在生境动态分析: 以美国南方松大小蠹为例 [J]. *北京林业大学学报*, 2009, 31(4): 64–69.
- Li M Y, Ju Y W, Wu W H, et al. Dynamic analysis of potential habitat of alien forest invasive species under climate change scenarios: a case study of *Dendroctonus frontalis* [J]. *Journal of Beijing Forestry University*, 2009, 31(4): 64–69.
- [35] Nealis V, Peter B. Risk assessment of the threat of mountain pine beetle to Canada's boreal and eastern pine forests[R]. Information Report BC-X-417. Victoria: Canadian Forest Service, 2008.
- [36] Kurz W A, Dymond C C, Stinson G, et al. Mountain pine beetle and forest carbon feedback to climate change [J]. *Nature*, 2008, 452: 987–990.
- [37] Yu L F, Zhan Z Y, Zhou Q, et al. Climate drivers of pine shoot beetle outbreak dynamics in Southwest China [J]. *Remote Sensing*, 2022, 14(12): 2728.
- [38] 文守易. 哈密林区小蠹虫种类初步调查和防治意见 [J]. *新疆农业科学*, 1962(11): 456–457, 466.
- Wen S Y. Preliminary survey of bark beetles in the Hami forest region and recommendations for pest management [J]. *Xinjiang Agricultural Sciences*, 1962(11): 456–457, 466.
- [39] Lynch A M, Mukhamadiev N S, O'Connor C D, et al. Tree-ring reconstruction of bark beetle disturbances in the *Picea schrenkiana* Fisch. et Mey. forests of southeast Kazakhstan [J]. *Forests*, 2019, 10(10): 912.

- [40] Gaylord M L, Williams K K, Hofstetter R W, et al. Influence of temperature on spring flight initiation for southwestern ponderosa pine bark beetles (Coleoptera: Curculionidae, Scolytinae) [J]. *Environmental Entomology*, 2008, 37(1): 57–69.
- [41] McDowell N, Sapes G, Pivovarov A, et al. Mechanisms of woody-plant mortality under rising drought, CO₂ and vapour pressure deficit [J]. *Nature Reviews Earth & Environment*, 2022, 3(5): 294–308.
- [42] Netherer S, Panassiti B, Pennerstorfer J, et al. Acute drought is an important driver of bark beetle infestation in Austrian Norway spruce stands [J]. *Frontiers in Forests and Global Change*, 2019, 2: 39.
- [43] Byers J A, Zhang Q H, Schlyter F, et al. Volatiles from nonhost birch trees inhibit pheromone response in spruce bark beetles [J]. *The Science of Nature*, 1998, 85(12): 557–561.
- [44] Schlyter F, Birgersson G, Byers J A, et al. Field response of spruce bark beetle, *Ips typographus*, to aggregation pheromone candidates [J]. *Journal of Chemical Ecology*, 1987, 13(4): 701–716.
- [45] Blomquist G J, Figueroa-Teran R, Aw M, et al. Pheromone production in bark beetles [J]. *Insect Biochemistry and Molecular Biology*, 2010, 40(10): 699–712.
- [46] Franceschi V R, Krokene P, Christiansen E, et al. Anatomical and chemical defenses of conifer bark against bark beetles and other pests [J]. *New Phytologist*, 2005, 167(2): 353–376.
- [47] Krokene P. Conifer defense and resistance to bark beetles [M]// Vega F E, Hofstetter R W. *Bark beetles: biology and ecology of native and invasive species*. London: Academic Press, 2015: 177–207.
- [48] Boone C K, Aukema B H, Bohlmann J, et al. Efficacy of tree defense physiology varies with bark beetle population density: a basis for positive feedback in eruptive species [J]. *Canadian Journal of Forest Research*, 2011, 41(6): 1174–1188.
- [49] Six D L, Wingfield M J. The role of phytopathogenicity in bark beetle-fungus symbioses: a challenge to the classic paradigm [J]. *Annual Review of Entomology*, 2011, 56: 255–272.
- [50] Zhao T, Axelsson K, Krokene P, et al. Fungal symbionts of the spruce bark beetle synthesize the beetle aggregation pheromone 2-methyl-3-buten-2-ol [J]. *Journal of Chemical Ecology*, 2015, 41(9): 848–852.
- [51] Matthews B, Netherer S, Katzensteiner K, et al. Transpiration deficits increase host susceptibility to bark beetle attack: experimental observations and practical outcomes for *Ips typographus* hazard assessment [J]. *Agricultural and Forest Meteorology*, 2018, 263: 69–89.
- [52] Netherer S, Lehmannski L, Bachlehner A, et al. Drought increases Norway spruce susceptibility to the Eurasian spruce bark beetle and its associated fungi [J]. *New Phytologist*, 2024, 242(3): 1000–1017.
- [53] Christiansen E, Waring R H, Berryman A A. Resistance of conifers to bark beetle attack: searching for general relationships [J]. *Forest Ecology and Management*, 1987, 22(1/2): 89–106.
- [54] Fettig C J, Klepzig K D, Billings R F, et al. The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States [J]. *Forest Ecology and Management*, 2007, 238(1/3): 24–53.
- [55] Zhang Q H, Schlyter F. Redundancy, synergism, and active inhibitory range of non-host volatiles in reducing pheromone attraction in European spruce bark beetle *Ips typographus* [J]. *Oikos*, 2003, 101(2): 299–310.
- [56] Jactel H, Brockerhoff E G. Tree diversity reduces herbivory by forest insects [J]. *Ecology Letters*, 2007, 10(9): 835–848.
- [57] Potterf M, Fröhbrodt T, Thom D, et al. Hotter drought increases population levels and accelerates phenology of the European spruce bark beetle *Ips typographus* [J]. *Forest Ecology and Management*, 2025, 585: 122615.
- [58] Raffa K F, Berryman A A. The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae) [J]. *Ecological Monographs*, 1983, 53(1): 27–49.
- [59] Pineau X, Bourguignon M, Jactel H, et al. Pyrrhic victory for bark beetles: successful standing tree colonization triggers strong intraspecific competition for offspring of *Ips sexdentatus* [J]. *Forest Ecology and Management*, 2017, 399: 188–196.
- [60] Hlásny T, Krokene P, Liebhold A, et al. Living with bark beetles: impacts, outlook and management options [R]. From Science to Policy 8. Joensuu: European Forest Institute, 2019.
- [61] Vanická H, Holuša J, Resnerová K, et al. Interventions have limited effects on the population dynamics of *Ips typographus* and its natural enemies in the western Carpathians (Central Europe) [J]. *Forest Ecology and Management*, 2020, 470: 118209.
- [62] Schroeder M, Knappe J, Kärvmö S. Rise and fall of a spruce bark beetle outbreak: importance of colonisation density and reproductive success [J]. *Forest Ecology and Management*, 2025, 586: 122695.
- [63] Økland B, Bjørnstad O N. A resource-depletion model of forest insect outbreaks [J]. *Ecology*, 2006, 87(2): 283–290.
- [64] Faccoli M, Stergulc F. *Ips typographus* (L.) pheromone trapping in south Alps: spring catches determine damage thresholds [J]. *Journal of Applied Entomology*, 2004, 128(4): 307–311.
- [65] Gohli J, Krokene P, Flo Heggem E S, et al. Climatic and management-related drivers of endemic European spruce bark beetle populations in boreal forests [J]. *Journal of Applied Ecology*, 2024, 61(4): 809–820.
- [66] Hofmann S, Kautz M, Sonnemann S, et al. Significant uncertainty in bark beetle trap catches due to varying pheromone release from dispensers and local trap position [J]. *Journal of Pest Science*, 2025, 98: 2065–2076.
- [67] Faccoli M, Stergulc F. A practical method for predicting the short-time trend of bivoltine populations of *Ips typographus* (L.) (Col., Scolytidae) [J]. *Journal of Applied Entomology*, 2006, 130(2): 61–66.

- [68] Bozzini A, Brugnaro S, Morgante G, et al. Drone-based early detection of bark beetle infested spruce trees differs in endemic and epidemic populations [J]. *Frontiers in Forests and Global Change*, 2024, 7: 1385687.
- [69] Kautz M, Dworschak K, Gruppe A, et al. Quantifying spatio-temporal dispersion of bark beetle infestations in epidemic and non-epidemic conditions [J]. *Forest Ecology and Management*, 2011, 262(4): 598–608.
- [70] Potterf M, Nikolov C, Kočícká E, et al. Landscape-level spread of beetle infestations from windthrown- and beetle-killed trees in the non-intervention zone of the Tatra National Park, Slovakia (Central Europe) [J]. *Forest Ecology and Management*, 2019, 432: 489–500.
- [71] Inward D J G, Caiti E, Barnard K, et al. Evidence of cross-channel dispersal into England of the forest pest *Ips typographus* [J]. *Journal of Pest Science*, 2024, 97(4): 1823–1837.
- [72] Chapman T B, Veblen T T, Schoennagel T. Spatiotemporal patterns of mountain pine beetle activity in the southern Rocky Mountains [J]. *Ecology*, 2012, 93(10): 2175–2185.
- [73] Seidl R, Müller J, Hothorn T, et al. Small beetle, large-scale drivers: how regional and landscape factors affect outbreaks of the European spruce bark beetle [J]. *Journal of Applied Ecology*, 2016, 53(2): 530–540.
- [74] Das A K, Baldo M, Dobor L, et al. The increasing role of drought as an inciting factor of bark beetle outbreaks can cause large-scale transformation of Central European forests [J]. *Landscape Ecology*, 2025, 40: 108.
- [75] Luo Y Q, Huang H G, Roques A. Early monitoring of forest wood-boring pests with remote sensing [J]. *Annual Review of Entomology*, 2023, 68: 277–298.
- [76] Meddens A J H, Hicke J A, Vierling L A, et al. Evaluating methods to detect bark beetle-caused tree mortality using single-date and multi-date Landsat imagery [J]. *Remote Sensing of Environment*, 2013, 132: 49–58.
- [77] Zhan Z Y, Yu L F, Ren L L, et al. Combining GF-2 and Sentinel-2 images to detect tree mortality caused by red turpentine beetle during the early outbreak stage in North China [J]. *Forests*, 2020, 11(2): 172.
- [78] Yu L F, Zhan Z Y, Ren L L, et al. Evaluating the potential of WorldView-3 data to classify different shoot damage ratios of *Pinus yunnanensis* [J]. *Forests*, 2020, 11(4): 417.
- [79] Kautz M, Feurer J, Adler P. Early detection of bark beetle (*Ips typographus*) infestations by remote sensing: a critical review of recent research [J]. *Forest Ecology and Management*, 2024, 556: 121595.
- [80] Näsi R, Honkavaara E, Lyytikäinen-Saarenmaa P, et al. Using UAV-based photogrammetry and hyperspectral imaging for mapping bark beetle damage at tree-level [J]. *Remote Sensing*, 2015, 7(11): 15467–15493.
- [81] Hellwig F M, Stelmaszczuk-Górska M A, Dubois C, et al. Mapping European spruce bark beetle infestation at its early phase using gyrocopter-mounted hyperspectral data and field measurements [J]. *Remote Sensing*, 2021, 13(22): 4659.
- [82] Bárta V, Hanuš J, Dobrovolný L, et al. Comparison of field survey and remote sensing techniques for detection of bark beetle-infested trees [J]. *Forest Ecology and Management*, 2022, 506: 119984.
- [83] Gao B T, Yu L F, Ren L L, et al. Early detection of *Dendroctonus valens* infestation with machine learning algorithms based on hyperspectral reflectance [J]. *Remote Sensing*, 2022, 14(6): 1373.
- [84] Gao B T, Yu L F, Ren L L, et al. Early detection of *Dendroctonus valens* infestation at tree level with a hyperspectral UAV image [J]. *Remote Sensing*, 2023, 15(2): 407.
- [85] Bi P, Yu L, Zhou Q, et al. Early detection of *Dendroctonus valens* infestation with UAV-based thermal and hyperspectral images [J]. *Remote Sensing*, 2024, 16(20): 3840.
- [86] Yu L F, Zhan Z Y, Ren L L, et al. Effects of stand and landscape level variables on shoot damage ratios caused by shoot beetles in Southwest China [J]. *Forest Ecology and Management*, 2022, 507: 120030.
- [87] Zhan Z Y, Yu L F, Ren L L, et al. Infestation patterns of incipient red turpentine beetle populations in fire-affected, logged and undisturbed forest stands of northern China [J]. *Forest Ecology and Management*, 2022, 521: 120424.
- [88] Zhan Z Y, Yu L F, Ren L L, et al. The association between stand and landscape level factors and red turpentine beetle damage in different infestation stages [J]. *Forest Ecology and Management*, 2023, 531: 120790.
- [89] Sullivan B T. Composition of attractant semiochemicals of North American species of *Dendroctonus* bark beetles: a review [J]. *Forests*, 2024, 15(4): 642.
- [90] Schlyter F. Semiochemical diversity in practise: antiattractant semiochemicals reduce bark beetle attacks on standing trees: a first meta-analysis [J]. *Psyche: A Journal of Entomology*, 2012, 2012: 268621.
- [91] Afzal S S, Nahrung H F, Lawson S A, et al. How effective are push-pull semiochemicals as deterrents for bark beetles? A global meta-analysis of thirty years of research [J]. *Insects*, 2023, 14(10): 812.
- [92] Fröhbrodt T, Schebeck M, Andersson M N, et al. Verbenone: the universal bark beetle repellent? Its origin, effects, and ecological roles [J]. *Journal of Pest Science*, 2024, 97(1): 35–71.
- [93] Wegensteiner R, Wermelinger B, Herrmann M. Natural enemies of bark beetles: predators, parasitoids, pathogens, and nematodes [M]// Vega F E, Hofstetter R W. Bark beetles: biology and ecology of native and invasive species. London: Academic Press, 2015: 247–304.
- [94] 张历燕, 陈庆昌, 张小波. 红脂大小蠹形态学特征及生物学特性研究 [J]. *林业科学*, 2002, 38(4): 95–99.
- Zhang L Y, Chen Q C, Zhang X B. Studies on the morphological characters and bionomics of *Dendroctonus valens* Leconte [J]. *Scientia Silvae Sinicae*, 2002, 38(4): 95–99.

- [95] 赵建兴, 杨忠岐, 梁廷杰. 利用捕食性天敌大啮蜡甲防治大小蠹属害虫的研究进展 [J]. *林业科学*, 2008, 44(1): 151–156.
- Zhao J X, Yang Z Q, Liang T J. Research advance on biological control of conifer bark beetles with the predator, *Rhizophagus grandis* (Coleoptera: Rhizophagidae) [J]. *Scientia Silvae Sinicae*, 2008, 44(1): 151–156.
- [96] Gregoire J C, Akıncı H A, Burjanadze M, et al. Successful bark-beetle biocontrol: a review of the only case in history releasing *Rhizophagus grandis* in Georgia, France, Britain and Türkiye against *Dendroctonus micans* [J]. *ARPHA Preprints*, 2026, 7: e205679.
- [97] Fettig C J, Gibson K E, Munson A S, et al. Cultural practices for prevention and mitigation of mountain pine beetle infestations [J]. *Forest Science*, 2014, 60(3): 450–463.
- [98] Hood S M, Baker S, Sala A. Fortifying the forest: thinning and burning increase resistance to a bark beetle outbreak and promote forest resilience [J]. *Ecological Applications*, 2016, 26(7): 1984–2000.
- [99] Morris J E, Buonanduci M S, Agne M C, et al. Does the legacy of historical thinning treatments foster resilience to bark beetle outbreaks in subalpine forests? [J]. *Ecological Applications*, 2022, 32(1): e02474.
- [100] Stadelmann G, Bugmann H, Meier F, et al. Effects of salvage logging and sanitation felling on bark beetle (*Ips typographus* L.) infestations [J]. *Forest Ecology and Management*, 2013, 305: 273–281.
- [101] Augustynczyk A L D, Dobor L, Hlásny T. Controlling landscape-scale bark beetle dynamics: can we hit the right spot? [J]. *Landscape and Urban Planning*, 2021, 209: 104035.
- [102] Dobor L, Hlásny T, Rammer W, et al. Is salvage logging effectively dampening bark beetle outbreaks and preserving forest carbon stocks? [J]. *Journal of Applied Ecology*, 2020, 57(1): 67–76.
- [103] Leverkus A B, Buma B, Wagenbrenner J, et al. Tamm review: does salvage logging mitigate subsequent forest disturbances? [J]. *Forest Ecology and Management*, 2021, 481: 118721.
- [104] Windmuller-Campione M A, DeRose R J, Long J N. Landscape-scale drivers of resistance and resilience to bark beetles: a conceptual susceptibility model [J]. *Forests*, 2021, 12(6): 798.
- [105] López-Andújar F T, Öhman K, Klapwijk M J, et al. Impact of management strategies on forest susceptibility to spruce bark beetle damage and potential trade-offs with timber production and biodiversity [J]. *Forest Ecology and Management*, 2024, 563: 121964.

(责任编辑 范 娟
责任编辑 臧润国)