

1 **Title page**

2 **Bark beetle outbreaks in Europe:**
3 **State of knowledge and ways forward for management**
4

5 **Authors:** Tomáš Hlásny^{1*}, Louis König², Paal Krokene³, Marcus Lindner⁴, Claire Montagné-
6 Huck⁵, Jörg Müller⁶, Hua Qin⁷, Kenneth F. Raffa⁸, Mart-Jan Schelhaas², Miroslav Svoboda¹, Heli
7 Viiri⁹, Rupert Seidl¹⁰

8
9 ***Corresponding author:** Tomáš Hlásny, Czech University of Life Sciences Prague, Faculty of
10 Forestry and Wood Sciences, Kamýcká 129, 165 21 Prague 6, Czech Republic; e-mail:
11 hlasny@fld.czu.cz, phone: 0421 905 708 539
12

13 **Affiliations:**

14 ¹Czech University of Life Sciences in Prague, Faculty of Forestry and Wood Sciences, the Czech
15 Republic

16 ²Wageningen Environmental Research, Wageningen University and Research, Wageningen,
17 Netherlands

18 ³Norwegian Institute of Bioeconomy Research, Norway

19 ⁴European Forest Institute, Bonn, Germany

20 ⁵Université de Lorraine, Université de Strasbourg, AgroParisTech, CNRS, INRAE, BETA, 54000
21 Nancy, France

22 ⁶Julius-Maximilians-University Würzburg, Bavarian Forest National Park, Germany

23 ⁷University of Missouri-Columbia, Division of Applied Social Sciences, USA

24 ⁸University of Wisconsin – Madison, USA

25 ⁹Natural Resources Institute, Finland

26 ¹⁰School of Life Sciences, Technical University of Munich, Freising, Germany and
27 Berchtesgaden National Park, Germany
28

29 **Author contribution:**

30 TH, RS, KFR, JM, PK, CMH, HQ – Conceptualization and Methodology; M-JS, LK – Formal
31 analysis and Data curation; ML, MS, HV – Review & Editing
32

Declaration:

The submitted work has not been published or is not under consideration for publication in any other journal or book.

Conflicts of interest/Competing interests:

Not applicable

Availability of data and material:

All data and material will be made available via the Zenodo repository upon paper's acceptance

Code availability:

Not applicable

Funding:

Writing and reviewing of the paper by TH and MS was supported by the grant "EVA4.0", No. CZ.02.1.01/0.0/0.0/16_019/0000803 financed by OP RDE.

ML was supported by the project "SURE-- SUSTaining and Enhancing RESilience of European Forests" financed by the German Federal Ministry of Food and Agriculture.

CMH was supported by a grant overseen by the French National Research Agency (ANR) as part of the "Investissements d'Avenir" program (ANR-11-LABX-0002-01, Lab of Excellence ARBRE).

MJS was supported by project Innovative forest MANagEment STRategies for a Resilient biOeconomy under climate change and disturbances (I-MAESTRO; ForestValue Eranet, FNR project ID 2219NR189).

HQ was supported by the Decision, Risk and Management Sciences Program of the USA's National Science Foundation, Award #1733990.

LK was funded by the PE&RC Graduate Programme of the Graduate School for Production Ecology & Resource Conservation (PE&RC) of Wageningen University

Acknowledgments:

We thank Sandy Liebhold for his valuable insights in the early phases of our work. We also acknowledge the European Forest Institute for initiating the research leading to this publication. We thank JRC/EU AGRI4CAST for making available the used climate data.

Abstract

Purpose of review: Outbreaks of tree-killing bark beetles have reached unprecedented levels in conifer forests in the northern hemisphere and are expected to further intensify due to climate change. In parts of Europe, bark beetle outbreaks and efforts to manage them have even triggered social unrests and political instability. These events have increasingly challenged traditional responses to outbreaks, and highlight the need for a more comprehensive management framework.

Recent findings: Several synthesis papers on different aspects of bark beetle ecology and management exist. However, our understanding of outbreak drivers and impacts, principles of ecosystem management, governance, and the role of climate change in the dynamics of ecological and social systems has rapidly advanced in recent years. These advances are suggesting a reconsideration of previous management strategies.

Summary: We synthesize the state of knowledge on drivers and impacts of bark beetle outbreaks in Europe and propose a comprehensive context-dependent framework for their management. We illustrate our ideas for two contrasting societal objectives that represent the end-members of a continuum of forest management goals: wood and biomass production and the conservation of biodiversity and natural processes. For production forests, we propose a management approach addressing economic, social, ecological, infrastructural and legislative aspects of bark beetle disturbances. In conservation forests, where non-intervention is the default option, we elaborate under which circumstances an active intervention is necessary, and whether such an intervention is in conflict with the objective to conserve biodiversity. Our approach revises the current management response to bark beetles in Europe and promotes an interdisciplinary social-ecological approach to dealing with disturbances.

Key words: bark beetle outbreaks, climate change, forest disturbances, societal objectives, forest ecosystem services

1. Introduction

Disturbances by tree-killing bark beetles have strongly increased in conifer forests in the northern hemisphere over the last four decades [1,2]. Available projections indicate that this trend will continue [1], mainly due to warmer temperatures and the increasing frequency of drought events [3,4]. It is estimated that the European spruce bark beetle *Ips typographus* has caused as much as 8% of all tree mortality due to natural disturbances in Europe between 1850-2000 [5], and this proportion has increased since 2000 [6]. A similar trend is observed in western Canada and the United States, where recent tree mortality due to the mountain pine beetle *Dendroctonus ponderosae* has exceeded 28 million ha [7,8].

Bark beetle outbreaks have manifold impacts on ecosystems, affecting water, climate, and nutrient cycles [9–11]. Outbreaks increase net carbon fluxes from the land to the atmosphere and thus provide a positive feedback to climate change [12]. For example, the *D. ponderosae* outbreak in British Columbia changed forests from a net carbon sink to a carbon source, and increased net carbon emissions by 270 megatons over the period 2000-2020 [13]. Outbreaks may also affect regional economies and markets via a range of cascading impacts [14,15]. These include short-term negative impacts on timber markets (e.g. oversupply, declining timber prices) and non-market values such as tourism, but also increased demands for forestry workers with short-term positive effects on regional labour markets [16,17]. Outbreaks often result in large-scale transformations of forest landscapes and may have profound social consequences, such as reduced life quality and economic well-being of forest owners, loss in aesthetic qualities, reduced trail access, land use conflicts, or loss of community identity [18–21]. A manifestation of the potentially high social impacts [22] are political conflicts that have recently emerged after bark beetle outbreaks in European countries such as Germany, Czech Republic, Poland and Slovakia [e.g. 23–25].

While most forests affected by bark beetle outbreaks in Europe are managed for timber production and economic values, outbreaks occurring in ecosystems managed for biodiversity and nature conservation likewise have received much recent attention [24,26–28]. In such forests, bark beetle disturbances are often valued because they contribute to ecosystem functioning and create more heterogeneous tree cover patterns, leading to more complex forests in the future [29–31]. Furthermore, bark beetle outbreaks have generally positive effects on biodiversity [32–35], and thus contribute to the primary management objectives of these areas. However, outbreaks can also have negative effects in forests managed for biodiversity and nature conservation, such as reducing populations of some endangered species, reducing the quality of the recreational experience of

visitors, and compromising the provisioning of ecosystem services such as clean drinking water [32,36,37].

The many different perspectives on bark beetle outbreaks highlight the complex roles these mostly native insects play in forest ecosystems. Depending on what values we primarily derive from forests these roles can be regarded as highly positive, such as fostering biodiversity, or highly negative, such as reducing economic returns and ecosystem services (e.g. carbon storage, water purification), and disrupting a continuous timber supply to the forest-wood-chain [26,38,39]. The context-specific role of bark beetles suggests that differentiated management approaches are required beyond current practices. Currently, the most widely practiced responses to bark beetles in Europe are (i) to employ measures minimizing the outbreak risk, such as clearing of freshly windthrown trees [40,41], and (ii) to contain an outbreak once it is ongoing, for example by using sanitation logging, trap trees or pheromone traps [42–44]. Current management strategies often do not adequately incorporate proactive measures to control beetle outbreak dynamics, fail to consider diverse local contexts and the role of natural disturbances in ecosystem dynamics, lack adequate empirical support, and thus can devolve into what has been termed ‘command-and-control’ management [45]. Such a centralized, unidimensional and disciplinarily isolated approach is unlikely to adequately address the complex, multidimensional, and rapidly changing social-ecological challenges that typify disturbance management [46].

The recent *I. typographus* outbreaks in Europe and their management have precipitated often contradictory reactions among forest professionals, scientists, the general public and other stakeholders [23,28,34,47]. Concerns have been raised about the ability of ‘command-and-control’ tactics [48] to stop outbreaks that largely are driven by extreme weather [49], about the ecological impacts of large-scale salvage felling [50], and about how to promote the economic and environmental recovery of disturbed forests [27,51]. Recent events have also revealed a limited degree of social capacity to address bark beetle outbreaks in parts of Europe, e.g., concerning technical and human resources, legislation and other aspects. More broadly, recent outbreaks have also revealed that control measures in some regions are often applied as a somewhat ‘knee-jerk’ reaction rather than being based on sound evidence on their efficacy, public perception, or effects on ecosystem services [49,52–54]. The unprecedented size of some recent outbreaks has also revealed new challenges, such as the need for coordinated international actions, recognition of the social dimension of forest disturbances, and impacts on international timber markets [16,22].

In this paper, we address these challenges by (i) synthesizing the state of knowledge on bark beetle outbreaks, and (ii) proposing a novel holistic and context-dependent management framework. Our framework combines ecological knowledge about the role of bark beetles in ecosystem dynamics with

tactical management tools that consider a broad suite of potential management objectives such as biodiversity, timber production, or recreation. We acknowledge that efficient management systems need to provide solutions tailored to specific places and situations by addressing the complexity and uncertainty of transforming social-ecological systems [55]. We here focus mainly on *I. typographus* outbreaks in Europe's Norway spruce *Picea abies* forests, but we also draw on notable examples from North America where applicable. We note, however, that the framework proposed here may likewise have implications for the management of other insect-induced disturbances worldwide.

2. Bark beetles and their impacts

2.1 Bark beetle ecology and outbreak dynamics

Bark beetles belong to a diverse subfamily of weevils (Coleoptera: Curculionidae, Scolytinae) with a worldwide distribution. Most of the world's roughly 6,000 bark beetle species breed only in dead trees and tree parts, and thus play important ecological roles in nutrient cycling and as food for other animals [56]. However, a few species colonize stressed and dying trees when their populations are low, but then successfully mass-attack and kill large numbers of healthy trees once their populations are high [57–59, **58].

Adult bark beetles locate and enter suitable trees, then mate and lay their eggs under the bark; the larvae feed and develop to maturity in the phloem and the brood adults emerge to locate new hosts. This lifestyle can lead to economic losses because bark beetles and humans essentially compete for the same resource [56]. Successful beetle colonization is typically fatal to trees, because hundreds of simultaneously attacking beetles destroy the inner bark and disrupt nutrient transport to the roots. The beetles also infect the trees with moderately phytopathogenic fungi that eventually metabolize tree defence chemicals and block water transport in the sapwood [60]. Species of tree-killing bark beetles are commonly able to breed in only one genus of trees and can exploit a tree for only one or two generations before the resources in the bark are exhausted.

Trees have elaborated chemical, anatomical, and physiological defences that enable them to resist attack by bark beetles most of the time. Examples of tree defences include necrotic lesions that form around beetle attacks in the phloem, production of terpenes and other toxic chemicals, and resin flow [60,61]. These defences can be lethal to adult beetles, their offspring, and the beetles' fungal associates [56].

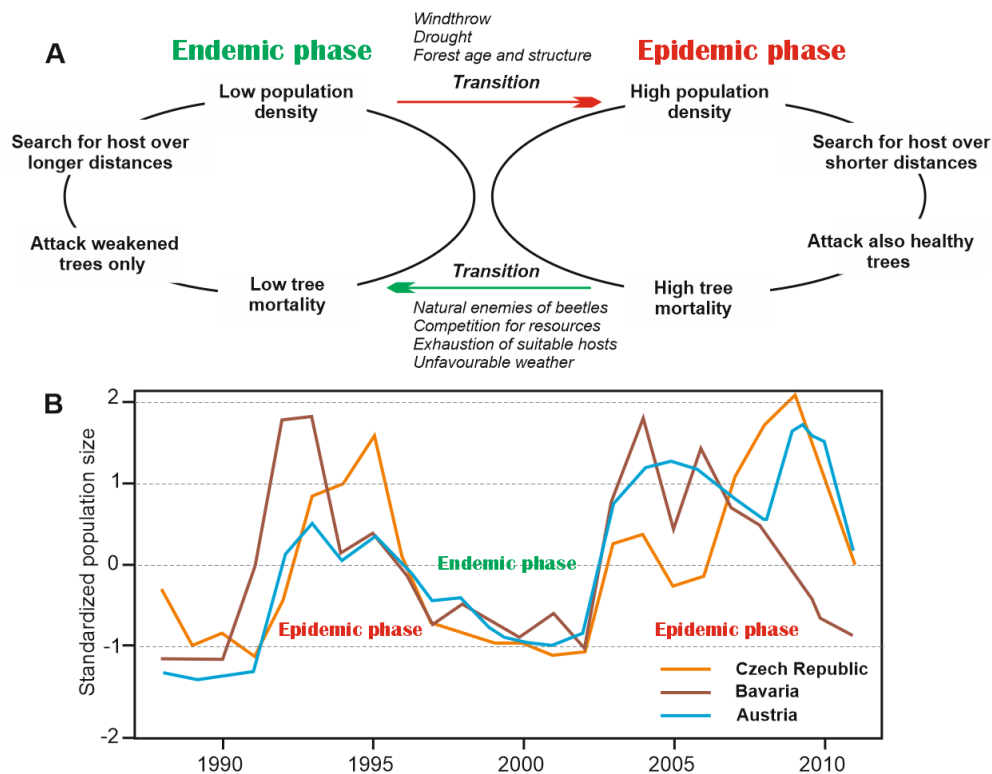


Fig. 1 Scheme of bark beetle population dynamics. A) Low and stable bark beetle populations (endemic phase) can be periodically disrupted by external factors such as droughts and windthrows, which trigger a transition to the epidemic phase (upper panel, adopted from [62]). For *Ips typographus*, the epidemic phase may typically last several years. B) The transition between endemic and epidemic phases over time during synchronous *I. typographus* outbreaks in the Czech Republic, Bavaria (Germany) and Austria. Population values have been standardized for comparison across regions (adopted from [30]).

Beetles have two major ways of reproducing despite these defences; they can avoid defences or they can exhaust them. Beetles can avoid most defences by only entering trees that have recently died, such as windfelled trees, or trees that are under severe physiological stress from drought or other factors [63]. This is the strategy used by so-called non-aggressive or semi-aggressive species (such as *I. amitinus* and *Pityogenes chalcographus* in Europe, and *I. pini* and *Scolytus ventralis* in North America) that can only sustain outbreaks in stressed stands [57]. Alternatively, beetles can exhaust tree defences through mass-attacks coordinated by powerful chemical signals (aggregation pheromones) that rapidly direct hundreds of beetle attacks to a single tree. A tree can resist a certain number of attacks, but beyond this threshold the tree can no longer fend off the attackers [60]. This ability to mass-attack trees is a key adaptation that enables outbreaking bark beetle species to kill healthy trees once their populations have risen and to sustain outbreaks in relatively healthy stands even after the inciting stress is relaxed [57].

Bark beetle outbreaks are intermittent events separated by lengthy non-outbreak periods during which the beetles' reproductive gains are offset by population losses [58]. During this 'endemic

phase', beetle populations are constrained by tree resistance, certain forest structural features (young age, high diversity, low competitive stress), weather, competitors and natural enemies, and the beetles breed only in sparsely distributed dead or severely weakened trees [57,64]. Region-wide disturbances and climatic events, such as windstorms, drought or heatwaves, can raise populations by reducing tree resistance and/or increasing beetle numbers [3,65]. If the reproductive increase is great enough, beetle populations surpass a critical threshold and become capable of overcoming healthy, well-defended trees via their aggregation mechanism. During this 'epidemic phase' beetles no longer focus solely on weakened trees, which tend to support low brood production, but also include healthy trees which tend to support higher brood production, thus releasing strong positive feedback [59,66,67].

2.1.1 The European spruce bark beetle as a model system

The European spruce bark beetle *I. typographus* is the primary outbreak species of bark beetles in Europe (Fig. 2). This small (~5 mm long) beetle is widely distributed across Eurasia where its range largely corresponds to that of its major host, Norway spruce. The total growing stock of Norway spruce in Europe is currently estimated to be 7.0 billion m³, suggesting that more than a quarter of Europe's total growing stock of 27.4 billion m³ is potentially exposed to *I. typographus* outbreaks (Fig. 3, Appendix A).

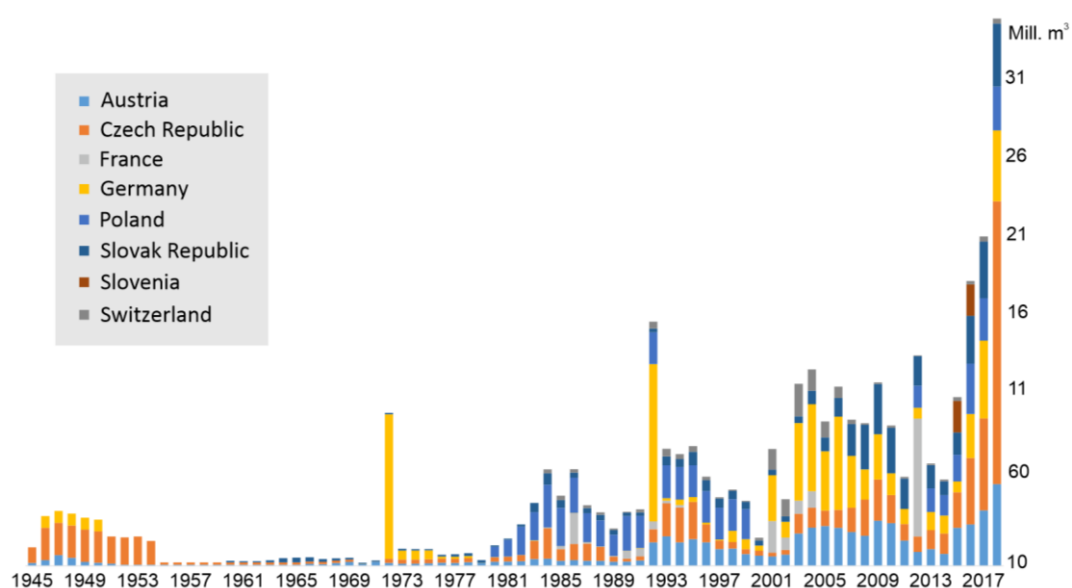


Fig. 2 Volume of Norway spruce killed by *Ips typographus* (and other bark beetles) in selected countries in Europe since 1945.

Like other tree-killing bark beetles, *I. typographus* needs fresh spruce phloem for brood development. It typically favours trees older than 60 years that have a diameter at breast height larger than 20-25 cm, but at high population levels beetles may also attack and reproduce in smaller and younger trees. *Ips typographus* has large phenological plasticity in thermally-regulated traits and this allows it to

adjust its number of annual generations and generation timing to local climates [68]. Depending on the annual heat sum, *I. typographus* can thus complete more than one generation per year in large parts of Europe [69], a typical trait for bark beetles that are economic pests in Europe [70].

Outbreaks of *I. typographus* are often triggered by windstorms. Storms can provide large amounts of mechanically damaged trees, which is a less well defended breeding substrate than healthy standing trees [58,63]. Outbreaks can also be triggered by other factors that compromise tree vigour and support the build-up of bark beetle populations, particularly hot and dry weather [3,71,72]. The mechanisms by which outbreaks collapse are not fully understood [58], but include depletion of remaining suitable breeding substrate, cold temperatures, density-dependent build-up of natural enemies, and various interactions among these factors.

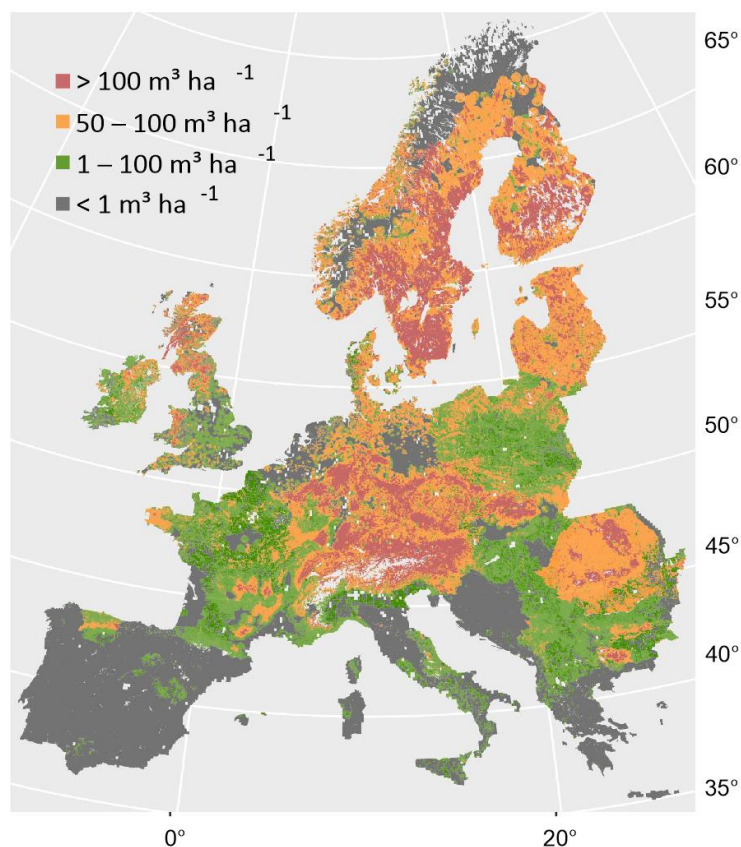


Fig. 3 The current geographical distribution and growing stock of Norway spruce, the main host of *Ips typographus*. Description of used data and methods is in Appendix A.

Management of *I. typographus* either aims to directly reduce beetle populations (immediate control responses) or to modify forest structure and composition to create environments less conducive to outbreaks (long-term preventive management) [42]. Immediate control mainly endeavours to reduce the amount of breeding substrate for beetles by removing trees damaged by wind, snow, rime and

other predisposing agents, removing infested trees from the forest before the new beetle generation emerges, and reducing beetle populations using insecticide application or various trapping devices [41,43,44,73]. Preventive management includes different silvicultural practices such as thinning to support tree vigour by reducing tree competition for resources [74], reducing the amount of host trees by changing species compositions [75,76], or shortening rotation periods to reduce the share of mature, vulnerable trees [74,77].

2.2 Effects of climate change

Climate change has a strong amplifying effect on bark beetle population irruptions [57]: (1) it facilitates bark beetle survival and development (e.g. by reducing winter mortality and allowing the completion of additional beetle generations per year [69,78]; (2) it increases potential beetle habitat by allowing beetles to spread into higher altitudes and latitudes [79,80]; and (3) it increases the probability of extreme, region-wide weather events such as drought, which reduces tree resistance [63,81]. Due to these mechanisms, disturbances caused by bark beetles are projected to increase in Europe in the coming decades. Based on statistical models parameterized with past disturbance data and data on forest structure and composition [82], the strongest relative short-term increase in bark beetle irruptions is expected in the Sub-Atlantic region of Europe, i.e. Germany, France, Denmark, the Netherlands, Belgium, and Luxemburg. The average annual damage caused by bark beetles in this region is for 2021-2030 projected to be almost six times higher than during 1971-2010 [1]. These trends are expected to continue throughout the 21st century. Under a warming of +4 °C virtually all spruce forests in temperate Europe will be at high or very high risk from bark beetle infestation (Fig. 4, Appendix B). In general, areas and/or time periods that experience a combination of warmer and drier conditions will undergo particularly strong population irruptions [59,83]. These increases will not occur at a consistent rate, but rather are expected to come in waves that are synchronized across several hundred kilometres and will be triggered by climatic extremes such as cyclonal storms and large-scale droughts [84].

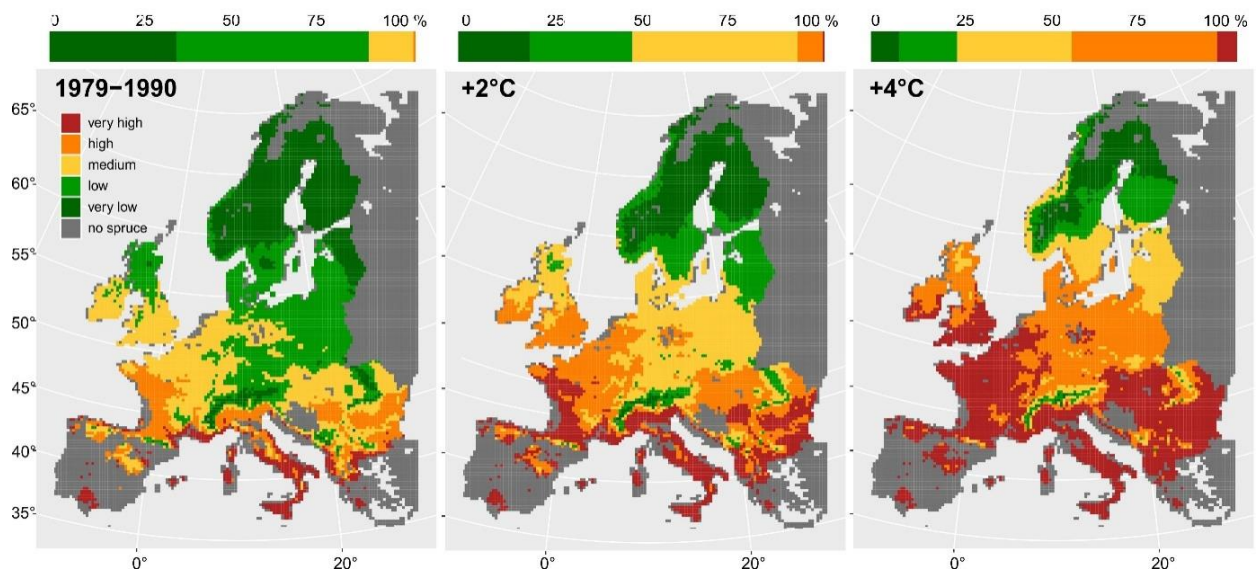


Fig. 4 Probability of a model Norway spruce stand (fully stocked, 100-year-old) being disturbed by bark beetles under historical temperature conditions (1979-1990), and under +2 °C and +4 °C temperature scenarios. Drought conditions were assumed to remain unchanged at the level of 1979-1990, the maps therefore present a conservative estimate. Bars on the top show the relative share of Norway spruce growing stock in Europe in different risk classes. For description of data and methods, see Appendix B.

2.3 Impacts of bark beetle outbreaks

Bark beetle outbreaks affect forest ecosystems and societies in multiple ways, ranging from altered element cycles, to shocks in the provisioning of ecosystems services, to diverse economic and social impacts. We here provide a short synthesis of these diverse impacts as background for the bark beetle management strategy formulated in the following sections.

Element cycles

Large-scale bark beetle outbreaks can have substantial impacts on the biogeochemical cycles of forest ecosystems. Outbreaks reduce the amount of carbon stored in forest ecosystems because of reduced carbon uptake due to a mortality-related reduction in leaf area [85] and increased carbon loss from litter and soil due to increased activity of decomposers [9]. Even though the young forests that emerge after an outbreak may act as sinks for atmospheric carbon [86], a Central European landscape heavily disturbed by bark beetles may require 30 years to reach carbon parity with undisturbed forests [12]. Outbreaks can also result in increased nitrogen mineralization rates and a better nitrogen supply to the foliage of regenerating trees [87]. However, outbreaks might also induce short-term nitrogen losses from the system, for example in the form of nitrate leaching [88]. Due to a reduction in the water use of attacked trees, both water availability in the soil and water runoff increase after a bark beetle outbreak [10]. Also the timing of water runoff can change, as canopy interception is reduced and snowmelt is accelerated in beetle-disturbed systems [11].

297 *Biodiversity*

298 Bark beetle outbreaks strongly alter forest structure [85,89], reset forest succession [90], and create
299 heterogeneous tree cover patterns that lead to more complex forests in the future [29,30,64,91,92].
300 Outbreaks also increase light availability and the amount of dead wood in forest stands, which is
301 beneficial for many forest-dwelling species [93]. Consequently, many species, including some
302 important red-listed species, respond positively to bark beetle disturbances [32]. The complex post-
303 outbreak landscape patterns can provide habitat for species such as the small hazel grouse *Tetrastes*
304 *bonasia* and important flagship species of conservation, such as capercaillie *Tetrao urogallus* [94,95].
305 Nonetheless, the effect of outbreaks on individual species strongly depends on their particular habitat
306 requirements and life history strategy, with both positive and negative effects being reported [54,96].
307 Stand-replacing tree mortality from bark beetles can cause a decline in endangered species,
308 particularly species that have a limited distribution area. Such examples have been reported after
309 mountain pine beetle and southern pine beetle *Dendroctonus frontalis* outbreaks in the USA [97–100],
310 but there are no cases reported to date in Europe.

311 *Ecosystem services*

312 A meta-analysis has shown that all categories of ecosystem services, i.e. provisioning, regulating,
313 cultural and supporting services, are negatively impacted by bark beetle outbreaks [39, Fig. 5]. The
314 provisioning of timber is affected by bark beetle outbreaks through the need to harvest stands
315 prematurely and a quality reduction of harvested timber caused by beetle-associated blue-stain fungi
316 [101]. Impacts on regulating ecosystem services include an increasing risk of natural hazards such as
317 mudslides and debris flows [102,103]. Also, changes in N cycling can temporarily reduce water quality
318 after bark beetle outbreaks at the local scale, whereas effects at larger scales and over longer time
319 periods are minor [32,104]. Impacts on cultural ecosystem services are manifested by decreased
320 recreational value of bark beetle-affected landscapes [37,105].

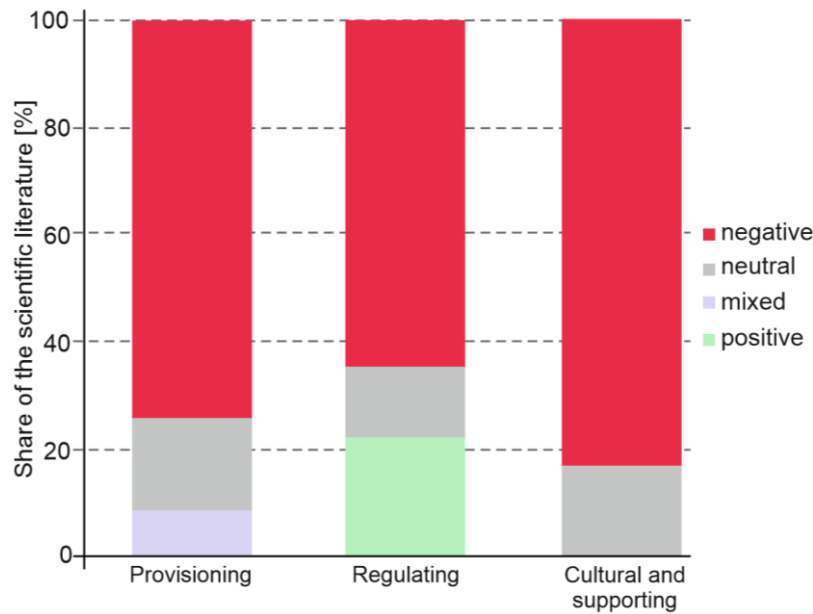


Fig. 5 Impacts of bark beetle outbreaks on ecosystem services. The figure shows the distribution of the evidence of bark beetle impacts collected from 41 scientific papers over different categories of ecosystem services. Source: [39]

Economic impacts

Economic consequences of outbreaks arise from both the direct losses of trees and the market impacts of resulting massive, synchronous salvage and sanitation harvesting [106,107]. Outbreaks result in a pulse of timber supplied to the market and this can lead to positive short-term market dynamics, including a temporary increase in employment, activity (logging, transportation, sawing, wood processing, etc.) and timber exports. However, markets may eventually become saturated with wood, as market participants increasingly attempt to liquidate beetle-killed timber, or even harvest healthy stands in anticipation of decreasing timber prices or future expansion of outbreaks [106]. For example, in 2005 the storm Gudrun and a subsequent bark beetle outbreak caused a temporary decrease in Swedish timber prices from 40 to 25 €/m³, though prices recovered in the next years [108].

In the short-term, timber-processing companies tend to benefit from the cheap timber generated by bark beetle outbreaks. Timber producers are negatively impacted by reduced timber prices and increased logging, sanitation and regeneration costs. For example, the southern pine beetle caused a short-term economic loss of about \$375 million from 1977 to 2004, (in 2004 constant dollars) to the timber market in the southern US. Timber producers lost about \$1,200 million, while timber-processing companies gained about \$837 million from lower roundwood prices [16]. Similar data for Europe are not available. In the longer-term, as the forests recover, timber supplies and exports are expected to decline and timber prices to rise due to a reduced availability of timber on the market.

However, this increase in timber prices typically does not compensate for the initial price decline, and thus also the long-term economic effect of outbreaks for forest owners is negative [16,107].

Economic consequences of bark beetle outbreaks also include reduced property values [109] and reduced income from tourism [110]. For example, tree mortality caused by the mountain pine beetle in Colorado, USA, induced a 5-22% loss in home values depending on county, timing and severity of the outbreak. By comparison, there was a general increase in home prices in areas not affected by beetle outbreaks during the same period [109]. Effects on recreation values are not so clear; for example, Rosenberger et al. [110] reported that moderate to severe mountain pine beetle outbreaks in the Rocky Mountain National Park (USA) caused important losses in total recreation value. Conversely, Dhar et al. [111], found that overall visitation and revenue earnings were not affected by beetle outbreaks in Canadian national parks. Similar research is currently lacking in Europe and constitutes a major knowledge gap regarding the impacts of bark beetle outbreaks.

Social impacts

Despite the importance and scale of bark beetle outbreaks in Europe now and historically, there is surprisingly little empirical research on the social aspects of outbreaks in the European context. When we did a systematic review of the social dimensions of bark beetle outbreaks, we identified 41 case studies from North America, but only six from Europe during 1978 – 2018 [18,24,37,112–114]. The major social impacts identified in the literature are due to falling trees, fire hazard, aesthetic loss, reduced trail access, land use conflicts, loss of community identity, and affected park visitor experience [e.g. 18–20,24,115,116]. In parts of Europe, bark beetle outbreaks have even triggered social unrests and political instability. In Poland, for example, efforts to control the outbreak in the Białowieża Forest led to public demonstrations of disagreement with forestry policy, resulting in the involvement of EU authorities [117]. Contrary to these negative impacts, some studies suggest that impacts such as emergent views for tourists and increased ecological awareness of some social groups are positive societal effects [19,37].

When formulating management strategies, it is important to understand the sociological factors that affect how people perceive and respond to natural disturbances. For example, Müller [24] showed how political conflicts over the management of bark beetle disturbance in Germany's Bavarian Forest National Park were rooted in opposite sociocultural attitudes toward the disturbed landscape. Different social groups often perceive and respond to outbreaks in distinct ways. For example, park visitors from local areas often have a more negative view of bark beetle impacts than tourists traveling a longer distance to visit a park [37,116]. Compared to longer-time residents, newcomers report lower

375 satisfaction with land management entities and are less likely to act in response to forest disturbance
376 [118,119].

377 As human responses to beetle disturbance are directly influenced by the socioeconomic and
378 biophysical characteristics of local communities [120], it is essential to maintain a good balance
379 between diverse community contexts and landscape-scale forest management by incorporating local
380 perspectives into risk mitigation strategies. Perception of threat also varies with time and proximity.
381 For example, research on community responses to a North American spruce beetle *Dendroctonus*
382 *rufipennis* outbreak on the Kenai Peninsula, Alaska showed that although local residents' perception
383 of beetle-related risks generally decreased over time, concerns remained high about immediate
384 threats to personal property and safety (e.g., forest or grass fire). This suggests the social ramification
385 process of forest risks related to insect disturbances is much more complicated than usually assumed
386 [121].

3. A context-dependent framework for managing bark beetles

Currently applied disturbance management in Europe has emerged based on experiences acquired over the last two centuries. Most European countries have adopted legislations on the management of natural disturbances that require monitoring, control and interventions to mitigate negative impacts on forest resources and economies [122]. Though the level of obligation and details of the prescribed procedures differ among countries, top-down approaches that strive to exert control over the disturbance and the post-disturbance vegetation development prevail. In the case of *I. typographus*, for example, the concept of ‘forest hygiene’ [e.g. 123] has been broadly advocated. The current disturbance management approach in many parts of Europe thus exhibits features of the *command-and-control pathology* originally described by Holling and Meffe [45] and recently summarized by Cox [48]. This concept describes a problematically large degree of authoritative centralization and control in a governance system. It is characterized, for example, by an inadequate analytical simplification of the problems in question, a preference for ‘one-size-fits-all’ solutions (the panacea approach), and a lacking acknowledgement of local social and ecological knowledge and practices. The command-and-control approach can lead to deterioration of social-ecological systems and loss of resilience. Recent events have demonstrated the inefficiency of current management approaches to address the intensifying bark beetle outbreaks and an increasing desire of the general public to participate in forestry policy decision-making.

Here we propose a context-dependent management framework that incorporates emergent understanding from disturbance ecology, population dynamics, economics, social sciences, and other research fields. The context-dependency of the proposed approach means that we differentiate between forests managed for different societal objectives. Our approach emphasizes tailor-made solutions for different social-ecological contexts rather than any uniform solution. In particular, we begin with the recognition that effects of bark beetles range from highly positive (fostering biodiversity and contributing to nutrient cycling) to highly negative (reducing desired ecosystem services), depending on site-specific management objectives and the human values that are emphasized. Accordingly, management responses should span the full range from non-intervention (in environments where conservation of natural ecosystem processes is the main management objective) to active prevention and mitigation of excessive population levels (in environments where the main objective is to create economic value from timber production). For the sake of clarity, we first present our ideas for two contrasting societal objectives that represent the end-members of what is actually a continuum of forest management goals:

1. Wood and biomass production to generate economic values: forests managed under this objective dominate in Europe, and a large share of them is stocked with Norway spruce and thus may be affected by *I. typographus* outbreaks (Appendix E). Because bark beetles directly threaten economic values and because the timber industry is an important part of many national economies, interventions against bark beetles are typically legally required in these systems.
2. Conservation of biodiversity, natural processes and other conservation values: forests managed under this objective (henceforth referred to as High Conservation Value Forests; HCVF) include national parks, biological reserves, and wilderness areas. A restricted range of management measures is allowed in these forests, which are designated to conservation by law. Most HCVF are categorized as Wilderness Areas (categories Ia and Ib) or National Parks (category II) according to the International Union for Conservation of Nature (IUCN). Other HCVF include small, strictly protected reserves embedded in production forest landscapes. In Europe, 3.6% of spruce growing stock is located in the IUCN categories I and II, while 23.5 % of the growing stock is located inside protected areas in general. At the same time, 88.9 % of the IUCN categories I and II are estimated to contain spruce and may thus face infestation of *I. typographus* (according to the World Database of Protected Areas; Appendix E).

We do, however, recognize the fact that a large share of Europe's forests is managed for multi-functionality, generating finer-scale trade-offs between the two end-member categories described above. After developing management approaches for production forests and HCVF we therefore elaborate on how management principles may be integrated also into the context of multi-purpose forest management.

3.1 Forests managed for timber production and economic values

A growing body of evidence suggests that many of the present-day production forests stocked with Norway spruce in Europe cannot be sustained under climate change [82,*124]. Still, active management of bark beetles will remain an important task for the coming decades, in parallel with an overall transition of forest management to different tree species and management systems. Effective outbreak management needs to be embedded into a broader agenda of climate change adaptation and a comprehensive risk management framework for the entire forestry sector. To facilitate an integration of the ideas presented here into such efforts we present a framework for comprehensive bark beetle management that includes four complementary components: preparedness, prevention, response, and recovery (Table 1). These phases incorporate infrastructural, legislative, ecological, and

social components in a structured but overlapping progression. Some overlap between phases is inevitable, as some specific practices can achieve multiple functions.

We deliberately deviate from the traditional sequence of management phases by placing preparedness before prevention. This allows us to first address numerous legislative, infrastructural and other aspects that operate at largely national and regional scales, thereby facilitating activities in the remaining phases. Preparedness differs from prevention, as prevention mostly addresses bark beetle and vegetation management measures at a scale of forest management units, yet its efficiency is contingent on the level of preparedness. Moreover, management of bark beetle populations often differs from management of other pulse disturbances such as floods and wildfires [125,126], because biotic systems are often characterized by unique density-dependent sources, rates, and degrees of internally generated positive and negative feedbacks [57,64].

Preparedness

From an ecological perspective, preparedness addresses a complex set of measures fostering forest resilience, i.e., the ability to swiftly recover from disturbances caused by population irruptions [51,127,128]. Resilience-oriented management focuses, for example, on maintaining a vital layer of advanced regeneration in the forest, management of disturbance legacies, and maintaining a balanced distribution of late- and early-seral species in the forest to facilitate fast recovery after future disturbances [92,129]. Resilience is an overarching concept that helps to cope with the high level of uncertainty related to future disturbance dynamics and shifting social objectives, and thus underlies all the remaining phases.

The *social aspects* of the preparedness phase includes a number of factors, such as improved education about disturbance management and bark beetle ecology, maintaining sufficient levels of trained professionals on site, strengthening international cooperation in population monitoring and management, developing communication platforms that increase the awareness of all relevant social groups about the multiple roles of forest disturbances, and building relationships with local stakeholders and communities [130]. Involving local communities in the designation of management objectives is a key element in developing a shared understanding of natural disturbances in forests. Such a shared understanding is, in turn, a prerequisite for successful disturbance management [131].

Preparing forest *infrastructure* for bark beetle outbreaks includes the provisioning of ample timber storage capacities to cope with large amounts of salvaged timber and buffer negative impacts on timber markets [132]. Improved forest road networks allow the timely implementation of management responses (including salvage and sanitation fellings) throughout the landscape [133], and sufficient nursery capacities provide enough seedlings of diverse genetic stock of desired tree species

for (partial) replanting of disturbed sites [134]. Development of early-warning and hazard rating systems that combine near-real time meteorological data, remote sensing and field surveys can help to identify vulnerable stands and better target scarce management resources [135–138].

Finally, *adaptive legislative frameworks* are an important component of preparing for bark beetle outbreaks. These frameworks should contain evidence-based guidelines for conducting salvage and sanitation operations, and for when it is necessary to plant in order to aid post-disturbance recovery. Legislative frameworks should also provide guidance on the geographical transfer of reproductive material [139] and could be complemented by incentive schemes that support efficient disturbance responses and recovery operations [140]. These instruments also need to be supported by a certain level of international harmonization. Each of these legislative elements must be put into place well in advance of an outbreak so that they can take effect once a disturbance occurs.

Prevention

Prevention mainly focuses on *ecological aspects* and includes population-based measures aimed at preventing the build-up of bark beetle populations, as well as stand-/landscape-based measures that manipulate forest conditions to create environments that reduce the probability of outbreak initiation and spread [30,141]. Prevention addresses a complex set of measures aimed to reduce the likelihood and extent of outbreaks. For example, resistance to outbreaks can be improved by increasing tree species, age, and genetic diversity, by judicious site selection (i.e., planting on sites for which a tree species is well adapted and that has water retention and soil nutrient properties supporting tree resistance to attack), and by promoting natural enemies of bark beetles. By increasing forest diversity, beetle population increases and decreases are distributed more evenly over space and time, thus making large-scale outbreaks less likely. Furthermore, a key element of prevention is quantitative monitoring, tracking changes in populations of native bark beetles and their natural enemies, as well as changes in host tree resistance to attack. In addition, monitoring can track the occurrence and tree-killing capacity of emerging invasive or native pests [142–144].

All these preventive measures include elements such as timely detection and removal of infested trees [41], maintaining compositionally and structurally diverse stands [75,76], increasing host tree resistance by e.g. thinning [74], creating habitats for natural enemies of bark beetles [145], and decreasing landscape-scale host connectivity [30,146]. As these measures are largely consistent with broader objectives of climate change adaptation in Europe's forests they are likely beneficial beyond the specific aim of bark beetle management [147].

Social aspects of prevention include the coordination of preventive measures across the landscape, particularly when there are multiple owners and when forest lands are managed for different

objectives. For example, small-scale owners may not be able to manage scattered windthrows or implement plans on large-scale transformation of forest species composition in an efficient manner without established coordination platforms. Ongoing prevention measures must be effectively communicated to reach wide acceptance of the applied management among forest owners and other stakeholders, although measures included in the prevention phase are typically not a subject of public outcry.

Response

The aims of responding to bark beetle outbreaks are to mitigate outbreak impacts and prevent negative effects on management objectives. *Ecological aspects* include the removal of freshly killed and infested trees to reduce the amount of available breeding substrate and prevent deterioration of timber quality and further reduction of timber value [107,148,149]. The latter aspect is particularly important in Europe's production forests where management decisions are chiefly driven by economic considerations. However, an important management response to outbreaks that should be considered more often is the deliberate decision to make no intervention. This can be the most efficient option when tree removal is likely to have little effect on bark beetle populations, may compromise the provisioning of ecosystem services, and interferes with post-outbreak recovery [49,52,150]. *Infrastructure* supporting evidence-based responses to bark beetle outbreaks includes the development and application of formal models that help decision makers evaluate the inherent trade-offs of various response measures [151,152]. *Social responses* to bark beetle outbreaks include the decision to reduce planned harvests elsewhere (in order to compensate for high levels of salvage harvesting in disturbed parts of the landscape), and the temporary storage of salvaged timber to buffer market impacts. Preventing injuries by falling dead trees, e.g. along hiking routes, is another important response measure. Finally, maintaining an open dialogue with stakeholders can reduce the risk of negative reactions towards the applied response measures [23].

Recovery

Recovery measures aim to support the establishment of a new tree cohort on disturbed sites and the recovery of forestry economies affected by a disturbance. Recovery measures thus focus on creating forest structures that are consistent with management objectives and are resilient to future changes in climate and disturbance regimes [51,153]. Measures include silvicultural approaches to foster diverse stands [154,155], maintain sufficient early-successional species across the landscape (due to their ability to swiftly recolonize disturbed patches), and integrate disturbance legacies (e.g., individual surviving trees, standing and downed deadwood) into the recovering forest [156]. In order to enable natural regeneration, ungulate populations should be kept low, particularly during the initial recovery

550 phase. A *social aspect* of disturbance recovery includes subsidies for recovery measures. Such subsidies
551 could, for instance, support the planting of new species that are better adapted to future conditions,
552 or distribute economic risks among forest owners via forest insurance schemes [157]. Still, negative
553 aspects of subsidy policies, such as a reluctance of forest owner to insure and invest in prevention,
554 need to be considered [17]. Maintaining a dialogue with all stakeholders allows tracking changes in risk
555 perceptions. We note that many recovery measures are contingent on measures taken to increase the
556 preparedness to bark beetle outbreaks (e.g., an increased capacity of nurseries, the presence of a vital
557 cohort of advanced regeneration, an adapted density of ungulates), illustrating the interconnectedness
558 of measures taken along the four steps proposed here.

	Preparedness	Prevention	Response	Recovery
Objectives	<p>Revise forestry education</p> <p>Strengthen international collaboration in disturbance management and monitoring</p> <p>Build relationships with local communities</p> <p>Establish forest and pest monitoring systems and data dissemination protocols</p> <p>Support advanced regeneration</p> <p>Secure coordination of disturbance management in multi-owner landscapes</p> <p>Monitor forest conditions and pest populations</p> <p>Maintain and enhance the level of forestry infrastructure</p>	<p>Reduce the risk of outbreaks</p> <p>Keep high level of awareness about forest conditions and pest populations</p> <p>Maintain a high level of forestry infrastructure</p> <p>Reduce the risk of negative public response to preventative measures</p>	<p>Prevent outbreak expansion</p> <p>Mitigate social, economic and environmental impacts</p> <p>Monitor and forecast outbreak development</p> <p>Reduce the risk of negative public perception of applied response measures</p> <p>Secure coordination of disturbance management in multi-owner landscapes</p>	<p>Secure regeneration of disturbed stands</p> <p>Foster climate-adaptedness and resilience of the new forest generation</p> <p>Monitor recovery dynamics</p> <p>Consolidate affected forestry economies</p> <p>Inform the previous management phases about the effect of measures taken</p>
Measures	<p>Develop new curricula for education and training at all levels of forest policy- and decision-making.</p> <p>Develop communication platforms for multi-stakeholder dialogue, and engage social scientists and professionals</p>	<p>Quantitatively sample populations of bark beetles and predators using pheromone traps and remote-sensing systems, and disseminate data</p> <p>Apply knowledge-driven sanitary operations</p>	<p>Apply knowledge-driven sanitary operations</p> <p>Apply salvage operations addressing trade-offs between the mitigation of economic impacts, and collateral impacts on the environment and the recovery process</p>	<p>Maintain high nursery production of seedlings of desirable species and provenances</p> <p>Subsidize recovery measures</p>

	<p>Develop data-driven crises plans for managing large-scale forest disturbances</p> <p>Develop high-level timber storage, nursery, and transportation infrastructure</p> <p>Develop decision-support systems to guide salvage and sanitation operations with regard to multiple objectives</p>	<p>Maintain tree vitality using silviculture operations</p> <p>Foster complex forest structures and diverse species compositions, reduce the share of spruce</p> <p>Create forest landscapes that prevent a large-scale spread of outbreaks</p> <p>Communicate preventative measures to the public via diverse dissemination platforms</p>	<p>Reduce regular harvests and exploit storage capacities for salvaged timber to buffer impacts on the market</p> <p>Subsidize response measures, including tax reductions and other indirect measures</p> <p>Communicate response measures to the public to prevent undesired responses</p>	<p>Support affected forest owners and economies to speed-up their recovery</p> <p>Keep density of ungulates low to protect forest regeneration</p>
Tools	<p>Modern teaching materials</p> <p>Improved monitoring tools, such as intelligent pheromone traps, semi-automatized detection algorithms for remote sensing data, etc.</p> <p>Models to optimize regional-to-national disturbance management infrastructure</p> <p>Decision support systems optimizing multi-objective disturbance management operations</p>	<p>Improved monitoring tools and protocols</p> <p>Hazard-rating models to target preventative measures to high-risk stands</p> <p>Improved silviculture practices</p> <p>Targeted communications platforms and channels</p>	<p>Models for spatial and temporal optimization of disturbance management operations</p> <p>Wood cycle models to identify the bottlenecks in the disturbance-affected forestry sector</p> <p>Targeted subsidy systems</p> <p>Targeted communications platforms and channels</p>	<p>Tree species distribution models to optimize planting for future climate conditions</p> <p>Sampling design and protocols to permanently monitor forest recovery</p> <p>Targeted subsidy systems</p> <p>New repellents and other technologies to manage ungulates</p>
	Preparedness	Prevention	Response	Recovery

560 Tab. 1 Main elements of a framework for comprehensive bark beetle management distributed along four management phases: preparedness, prevention,
561 response, and recovery. The included elements are representative of a broader set listed in Appendix F. ‘Measures’ indicate specific actions needed to reach
562 different objectives. ‘Tools’ indicate specific technologies, materials, legislation and other means that support individual measures.

3.2 Forests managed for biodiversity and nature conservation

The default approach to managing HCVF is to conserve natural processes and not intervene with ecosystem dynamics [38]. The key question related to the management of natural disturbance in HCVF is thus, under which circumstances an active intervention is necessary, and whether interventions are in conflict with the main management objective for these forests, i.e. the conservation of biodiversity [25]. Important considerations include (i) whether a particular disturbance falls within the historical range of variability of a given forest and thus should be treated as part of the natural forest dynamics; (ii) what the social and economic implications of non-intervention are, including a potential loss of recreational value; (iii) concerns about outbreak expansion to adjacent production forests; and (iv) threats to focal species of conservation in a given territory, from both the disturbance itself and the potential management response.

In Europe, most insect outbreaks in HCVF have been and still are caused by native bark beetles. In these cases, bark beetles and the disturbances that result from their colonization of trees are part of the natural system, contribute to natural ecosystem dynamics and often increase biodiversity [158]. A long history of co-evolution between host tree, bark beetle and associated species [159] ensures that a „correction“ by management is rarely required [17,56]. As a consequence of their co-evolutionary history with disturbance, many species in Europe (including threatened ones) are adapted to the early stages of forest succession following bark beetle outbreaks [32,93]. Even some species that were previously considered specialists dependent on the presence of mature stands (e.g., *Tetrao urogallus*) have been found to thrive in the heterogeneous landscapes that emerge after bark beetle disturbances [160]. Consequently, the early successional habitats resulting from an outbreak of a native bark beetle are valuable for conservation [54].

There are, however, situations when active intervention against bark beetles is a justifiable option in HCVF. These mainly include (i) invasions by non-native pest species, (ii) a range expansion of native bark beetles into habitats that have not been occupied by them previously (e.g., due to climate change), (iii) threats to trees or stands of exceptional conservation value (e.g., the last old-growth remnants of a certain area), and (iv) threats to focal species of conservation. We elaborate below the conditions under which active management interventions might be justifiable in HCVF and how such interventions might differ from those made in commercial forests.

Risk from non-native pests

Invasive species, i.e. the most damaging introduced species, can have severe impacts on HCVF and cause dramatic changes to their historical disturbance regimes [161]. In Europe's Norway spruce forests, no invasive bark beetle species have emerged to date. However, at least 18 non-native bark beetle species have established in Europe already, and introductions occur at an accelerating rate [162]. Because most invasions take place at large spatial scales (i.e., beyond the boundaries of individual conservation areas), management options in HCVF are limited. The most efficient means to halt species invasions are coordinated nationwide or international actions [e.g. 163].

Expansion of native bark beetles into new territories

An emergent situation in some HCVF is that native bark beetle species expand their outbreak range into higher altitudes or latitudes in response to climate change. This might critically impact conservation values and disrupt natural ecosystem dynamics in HCVF. The beetles may encounter evolutionarily naïve or semi-naïve host trees, i.e., trees with no or little prior contact with the beetle over recent evolutionary history, and which therefore lack effective defences [164]. One well documented example is the elevational shift of mountain pine beetle in North America into high-elevation whitebark pine *Pinus albicaulis* forests, which have relatively low resistance against attacks [165]. This has resulted in high tree mortality that reduces the availability of whitebark pine cones as food for grizzly bears (*Ursus arctos horribilis*) and other endangered wildlife, and has created multiple other adverse environmental impacts [166]. In Europe, *I. typographus* expands its range into northern Europe in response to relaxed temperature limitation [167] and its outbreak range into higher elevations in protected areas of the Alps [80]. Further south, the northern bark beetle *Ips duplicatus* is expanding its range southwards in Eurasia, causing considerable damage to spruce forests in some locations [168]. Range expansion of native species needs to be continuously monitored and containment actions could be considered. However, currently no immediate conservation threats are known from range expansions of native bark beetles in Europe [24]. Furthermore, these expansions could conceivably help forests in high latitudes and elevations adapt more quickly to the emerging climatic conditions [169].

Risk to trees and stands with high conservation value

Old-growth forests are rare in most parts of Europe [170]. They typically have forest structures that are associated with high resilience to disturbances and have high biodiversity. Moreover, old-growth forests show lower climate sensitivity than younger forests [171]. Relict stands of old trees are thus highly valued by conservation managers and the general public, and are frequently under strict protection [172]. Because these stands are usually small, active management tools such as anti-

aggregation pheromones or sticky traps can be considered in efforts to sustain such stands in the face of a bark beetle outbreak. However, whether such relict stands can be protected from bark beetles in the long run remains uncertain.

Risk to focal species of conservation

Large stand-replacing bark beetle outbreaks can threaten local populations of species of conservation concern, particularly if their remaining habitat is small. To date, no threats from bark beetles to species of conservation concern have been reported for Norway spruce forests in Europe. However, examples from North America illustrate the potential for negative effects of bark beetle outbreaks. Populations of the endemic squirrel *Tamiasciurus hudsonicus grahamensis* declined sharply in response to an extensive mountain pine beetle outbreak [97], and the endangered red-cockaded woodpecker *Leuconotopicus borealis* suffered from the loss of cavity trees after bark beetle attacks [100].

Management options

The most common tools for controlling outbreaks by native bark beetles in HCVF are similar to those applied in production forests [*173]. However, several recent studies have shown that management measures such as salvage logging can have adverse impacts on conservation goals [174,175]. These impacts include the declines in native species populations [54], a shift in community assembly processes [50], reduced natural regeneration [176], and the loss of key forest structures, such as abundant deadwood and old legacy trees surviving the disturbance [177]. If bark beetle control measures are implemented in HCVF, their benefits need to be balanced against their negative impacts, and measures to minimize negative impacts need to be taken.

Beyond the measures already discussed for production forests, a widespread approach for managing bark beetles in conservation areas of Europe is zoning, i.e. designating a non-intervention zone at the core of a protected area that is buffered by a management zone of sufficient width to prevent bark beetle spread into surrounding managed forests [178]. Typical buffer widths for management zones are between 200m and 500m for *I. typographus*. Zoning also increases the social acceptance of non-intervention in core zones of protected areas, as it dispels the widely held belief that protected areas act as sources or epicentres for bark beetle outbreaks. In fact, recent research indicates that large, unmanaged HCVFs in Europe often attract more bark beetles from surrounding managed forests than they export [179].

Another regularly applied management approach for bark beetles in HCVF areas is “low impact” salvage logging that preserves part of the biologically legacies created by the disturbance. This can be done for instance by debarking infested trees to effectively destroy the beetle brood but retain the deadwood in the forest. This approach is expensive and also has negative effects on a broad

community of organisms that depend on the specific microclimate under the bark of beetle-infested trees. In recent years, an equally efficient tree-level approach with lower biodiversity impact has been developed (“bark scratching”), in which multiple longitudinal strips of bark are removed from fallen trees [180]. In addition to benefiting biodiversity, bark scratching has also proven to be economically and aesthetically advantageous compared to complete debarking of beetle-infested trees.

3.3 Multifunctional forests

The two approaches to dealing with bark beetle disturbances described above are representative for the end-members of management objectives along a production – conservation gradient. As such they can be applied in areas where commodity production and conservation are spatially segregated, and where buffer zones between the two categories mitigate undesired interactions. However, in many parts of Europe an integrative, multi-functional approach to forest management prevails. In forests managed for multiple objectives managers usually aim to simultaneously produce timber and maximize the habitat value of the forest ecosystem [181]. Consequently, reconciling the two alternative approaches to dealing with bark beetle outbreaks remains a challenge for multifunctional forest management. No general recommendations for how to address these challenges can be given, as the success of management depends strongly on the specific management objectives and local contexts, which are highly diverse across Europe. Nonetheless, we here formulate some general ideas that can guide the development of a tailor-made bark beetle management strategy within the frame of the end-member approaches described above:

- The spatial scale of integrative, multi-functional forestry should be reconsidered. Traditionally, the stand scale has been the focus of management considerations in Europe, and the goals of multi-functionality have also largely been assessed at this scale. However, achieving multifunctionality at the stand scale might be near impossible in the face of landscape-scale drivers such as bark beetle disturbances. Instead, we propose to adopt a landscape-scale approach in which the benefits of bark beetle containment on forest production can be maximized by focusing on particularly valuable and vulnerable stands, while natural disturbance dynamics can be allowed in other parts of the landscape (with lower importance for the locally relevant portfolio of ecosystem services) [e.g., 182].
- Non-intervention should not be categorically rejected as a management option in multifunctional forests, especially if salvage and sanitation logging are not feasible due to market, logistic and other reasons. In such cases, non-intervention could limit disturbance-induced losses and increase forest biodiversity through deadwood retention. Advanced

planning tools for multi-criterial optimisation of salvaging decision can be used to support such considerations [183].

- Financial incentives should be established that facilitate integration of natural disturbance dynamics into landscapes managed for multiple ecosystem services. These incentives could compensate forest owners for (i) potential losses of marketable ecosystem services due to bark beetles, and (ii) losses due to management restrictions resulting from natural disturbances. As bark beetle disturbances are a potent means to increase the biodiversity of managed forests (e.g., by enriching their deadwood stocks; [158]) funds for biodiversity conservation could be used to incentivize a more balanced disturbance management in multi-functional forests.

- Improved information about the potential roles and effects of bark beetles are particularly needed in multi-functional forest landscapes. Because such landscapes aim to fulfil many functions simultaneously they usually also have a large and diverse set of stakeholders. Raising awareness of the trade-offs involved in bark beetle management and clearly communicating the rationale behind individual management decisions (e.g., salvage logging in some parts of the landscape, no intervention in others) is of paramount importance to increase the local acceptance of bark beetle management in multi-functional forests.

4. Discussion and conclusions

Recent decades have seen a dramatic change both in the dynamics of bark beetle outbreaks and in public attitudes to and perceptions of natural disturbances [26,37,96]. The adaptation of management strategies, however, lags behind these social-ecological changes, eroding the ability of management to address the emerging challenges. Although several synthesis papers on different aspects of bark beetle ecology and management have been published recently [*14,**58,63], Wermelinger [42] – published 17 years ago – remains the latest comprehensive review paper on the management of *I. typographus* in Europe (but see relevant syntheses of bark beetle management by Fettig and Hilszczański [184] and the work of Fettig et al. [141] for *D. ponderosae*). The last decades have seen a remarkable advance in our understanding of outbreak drivers and impacts, principles of ecosystem management, governance, and the prominent role of climate change in the dynamics of ecological and social systems. These advances suggested the need to reconsider previous strategies for bark beetle management. In this paper we have synthesized the current understanding of bark beetle ecology and formulated a new management framework to address the bark beetle outbreaks of the coming period. Cornerstones of the management strategy outlined here are context-dependency, a holistic integration across the entire management cycle, consideration of how ecosystem dynamics are

affected by climate change, and recognition of the social-ecological complexity of managing bark beetle outbreaks.

4.1 Context-dependency

Current outbreak or, more broadly disturbance management often applies a unified set of measures across diverse environments and management objectives. Yet such measures can fit some social and ecological conditions better than others. For example, a global survey revealed that salvage felling is frequently implemented in protected areas to control outbreaks and recover economic values [*173], even though this practice contradicts the main management objective in these areas, i.e. nature conservation. Insufficient coordination between societal objectives and management strategies often stems from poor understanding of the role of natural disturbances in ecosystem dynamics and an absence of shared management objectives [*14,131]. In HCVF, for example, efforts to control disturbance dynamics are often motivated by unrealistic expectations of how much mature and old-growth stands there should be on the landscape, and the perception of disturbed forest as a less desirable state [17,56]. This implies that clear formulations of management objectives based on a consensus among relevant stakeholders is a precondition for successful management, an aspect that remains largely underappreciated in the current bark beetle management practices.

Apart from differences in local management objectives, ecological and geographical gradients form another dimension along which management strategies need to be organized. For example, bark beetle management can be more successful in thermally limited environments, such as mountain regions and high latitudes, where a harsh climate keeps bark beetle populations below the eruptive threshold. This, however, may differ at lower elevations and latitudes, where spruce has often been artificially introduced and where biotic risks are generally high [4]. Therefore, while management can succeed in controlling bark beetle populations in harsher climates, management should predominantly focus on transforming forest structure and composition in regions that are more favourable to the beetles. Here, outbreaks can also effectively catalyse forest transformation and provide negative feedback to future disturbances [64,169]. We also note that our Europe-wide projections of bark beetle risks show that the extent of low-risk areas will decrease dramatically with increasing temperature (Fig. 4), and options for active containment of beetle populations will thus likely diminish.

To address the problem of context-dependency, we organized our framework around two contrasting management objectives that represent end points along a management continuum relevant for European forestry: delivery of timber production and economic values versus biodiversity and nature conservation [185]. Still, since much of Europe's forests are managed for multi-functionality our proposed framework must be adapted to address challenges arising from e.g. conflicts between

concurrent management objectives [186,187]) or from beetles migrating between forests with different management objectives [179,188]. Such problems cannot be addressed effectively in the face of an outbreak, but rather require extensive and long-term institutional and legislative adaptation (e.g. improved education, development of compensation payment systems; [189,190]). This highlights the importance of preparedness for effective disturbance management. However, while a firm and evidence-based approach to the two major management objectives should be taken at the sectoral level (forestry vs. nature conservation), there is a range of embedded contexts, which need to be addressed at decision-making and operational levels.

In the case of production forests, active management of bark beetle populations is the default option because outbreaks threaten the desired ecosystem services [39,102]. However, many situations may call for differentiated treatments, such as different bark beetle population levels, the distribution and conditions of host trees, institutional settings and market conditions. Therefore, centralized management that applies a unified set of measures without considering the local context will often be a misguided strategy. Instead, tailored management approaches that include balanced combinations of monitoring and forecasting, preventive measures, salvage and sanitary operations, silviculture and non-intervention need to be formulated. For example, as opposed to the current European practice, we suggest that non-intervention could become an increasingly used response if outbreaks are strongly driven by external factors, such as climate change and if timber prices are depressed by large pulses of disturbed timber. Obviously, formulating management systems tailored to such a broad range of contexts requires new management planning tools. We therefore encourage the scientific community to develop tools coupling process understanding of climate-sensitive disturbance dynamics with decision support systems, and develop a portfolio of management strategies for different contexts. Implementation of such context-specific management will increase the demand on human resources, education and training.

Contrary to production forests, non-intervention is a default management option in HCVF because it is most compatible with efforts to preserve biodiversity and other conservation values [38]. Still, climate change and other anthropogenic processes, such as increasing rates of biological invasion, challenge the current static conservation paradigm [191]. This may shift disturbance regimes from their historical ranges and put conservation values at risk. To date, the management of HCVF only rarely considers challenges due to shifting climate and disturbance regimes, and relevant policies and operational guidelines are missing. To address this gap, we have summarized situations where bark beetle outbreaks interfere with conservation objectives and require active intervention [161,192]. We suggest that Europe's conservation policies should incorporate the lessons learned in North America and Asia [e.g. 193], where conservation objectives have already been put at risk from altered biotic

disturbance regimes in the recent past. Such insights can inform European conservation policies, improve monitoring networks and management guidelines, and help Europe reach its conservation targets.

4.2 Holistic perception

Centralized and reductionist ‘command-and-control’ strategies for outbreak management are becoming less efficient in the highly complex, uncertain, and rapidly changing conditions that forest ecosystems are confronted with today [133,194]. Therefore, decentralization and development of strategies tailored to the local context is a key premise for sustainable management [195]. By decentralization we mean the transfer of power from central authorities to lower levels of the administrative and territorial hierarchy with the aim to improve efficiency and accountability, and to better address differences in local contexts [e.g. 196]. The need for decentralization is, however, stage specific – while centralized actions are needed in the preparedness phase (e.g. legislative changes and education), a higher degree of context-dependency is required in the remaining phases. At the same time, managing large-scale outbreaks requires a high-level of cross-sectoral mobilization and formulation of roles, institutions and incentives [197] that support individual (decentralized) actions. We have therefore formulated a holistic framework, which strives to address social and ecological conditions related to managing bark beetles and the disturbances they cause. This framework extends beyond existing approaches in several ways.

First, current management of bark beetles in Europe typically emphasizes direct control of beetle populations, while maintaining only a loose connection with fields such as silviculture, economics, monitoring, infrastructure development, and stakeholder interaction. For example, silviculture can be a critical element in the prevention and recovery phases of the management cycle in production forests, but it can also counteract disturbance management objectives. Although there exist systems that consider trade-offs between the quantity and stability of forest production [198,199], they are rarely deployed (but see [200]). Likewise, Integrated Pest Management [201], which strives to integrate considerations and tactics from a range of disciplines and approaches, has never reached broad acceptance in European forestry [e.g. 202]. We therefore propose that different fields of management, including silviculture, monitoring, economics, ecology, education, and transportation, should be integrated into a holistic outbreak management system. Yet, the complexity of such a system may also hamper practical implementation, as often rigid legislative and organisational settings must be overcome. Recent experiences with bark beetle outbreaks of unprecedented intensity, however, is a strong incentive for changing management strategies.

Second, our framework inherently couples social and ecological dimension of disturbances, and this is recognized to be of utmost importance for resolving different social-ecological problems [55]. Large-scale landscape transformations caused by outbreaks and their management affect human communities and may trigger negative responses towards responsible authorities [e.g. 24,175]. At the same time, the degree of institutional development and cooperation (e.g. between forestry, economy, transportation, and nature conservation) determines our capacity to take appropriate precautionary and responsive measures to face outbreaks, particularly if they occur at large spatial scales. The public is increasingly aware of how forests affect the quality of their lives and thus endeavours to participate in decisions affecting the fate of the forests. This increasingly applies even for countries where participatory approaches do not have a long history, such as the former socialist countries of Europe [203], some of which have become epicentres of the recent bark beetle outbreaks. Such bi-directional social-ecological interactions can determine the overall success of outbreak management and should be addressed across all phases of the management cycle, suggesting that current governance systems need to be revised accordingly.

Third, the behaviour of policy-makers and managers is strongly driven by economic considerations, and these may change over the course of an outbreak, depending on market dynamics. Large-scale and persistent outbreaks may saturate international wood markets and reduce the profitability of selling salvaged wood. Therefore, management decisions need to consider a broader economic context and aim to mitigate negative impacts on the market, for example, by increasing timber storage capacities and reducing planned harvesting and salvaging where possible. More strategic anticipatory decisions may include market diversification and adaptation of regional wood-processing industries towards large amounts of salvaged timber.

Finally, advances in different fields of science have not been adequately implemented into management of bark beetle disturbances. This particularly includes advances in bark beetle monitoring and forecasting based on intelligent trapping devices, remote sensing and machine-learning classification algorithms, process-based ecosystem models addressing climate-sensitive disturbance dynamics, governance systems such as ecosystem management and co-adaptive management, as well as decision-support and resource-allocation systems. We suggest that interdisciplinary methods and technologies need to be organized in a consistent framework throughout all phases of the management cycle.

4.3 Final considerations

Bark beetles are not the only risk that is threatening European forests. Our proposed management framework should thus not be perceived in isolation, but be seen as part of a more comprehensive risk management and climate change adaptation agenda. This particularly applies for the management phases of preparedness and recovery, which are the most forward-looking elements in our framework. We here have included several management options that are broadly beneficial for addressing different types of future risks, such as options aiming to increase the ability to take timely actions (via monitoring, forecasting, social acceptance) and fostering social and ecological resilience [51,128].

In many European countries, rigid legislation, institutions, and logistic limitations can hamper the implementation of here proposed framework, and the mismatch between legal and institutional frameworks and the requirements of bark beetle management could increase further as outbreaks intensify. Insufficient infrastructural and legislative preparedness, along with the low resilience of many European forests, will limit the options for mitigation. The framework proposed here can help to facilitate transitions to new management systems and provide a starting point for managing the forests emerging from the current wave of bark beetle disturbance. Moreover, societal awareness of climate change-driven risks is increasing in many parts of Europe as a result of ongoing outbreaks, potentially supporting a shift in the current bark beetle management paradigm.

References

1. Seidl R, Schelhaas M-J, Rammer W, Verkerk PJ. Increasing forest disturbances in Europe and their impact on carbon storage. *Nature Climate Change*. Nature Publishing Group; 2014;4:806.
2. Bentz BJ, Régnière J, Fettig CJ, Hansen EM, Hayes JL, Hicke JA, et al. Climate Change and Bark Beetles of the Western United States and Canada: Direct and Indirect Effects. *BioScience*. 2010;60:602–13.
3. Marini L, Økland B, Jönsson AM, Bentz B, Carroll A, Forster B, et al. Climate drivers of bark beetle outbreak dynamics in Norway spruce forests. *Ecography*. 2017;40:1426–35.
4. Jactel H, Branco M, Duncker P, Gardiner B, Grodzki W, Langstrom B. A Multicriteria Risk Analysis to Evaluate Impacts of Forest Management Alternatives on Forest Health in Europe. *Ecology and Society*. 2012;17.
5. Schelhaas M-J, Nabuurs G-J, Schuck A. Natural disturbances in the European forests in the 19th and 20th centuries. *Global Change Biology*. 2003;9:1620–33.
6. *Senf C, Pflugmacher D, Zhiqiang Y, Sebald J, Knorn J, Neumann M, et al. Canopy mortality has doubled in Europe's temperate forests over the last three decades. *Nature Communications*. 2018;9:1–8. **This paper provides sound evidence for increasing forest mortality in the temperate forests of Europe, and attributes these changes to climate change and land-use. It supported the need of revising current disturbance management strategies.**
7. Hicke JA, Meddens AJH, Kolden CA. Recent Tree Mortality in the Western United States from Bark Beetles and Forest Fires. *Forest Science*. Oxford University Press (OUP); 2015;62:141–53.
8. Cooke BJ, Carroll AL. Predicting the risk of mountain pine beetle spread to eastern pine forests: Considering uncertainty in uncertain times. *Forest Ecology and Management*. Elsevier B.V.; 2017. p. 11–25.
9. Mayer M, Sandén H, Rewald B, Godbold DL, Katzensteiner K. Increase in heterotrophic soil respiration by temperature drives decline in soil organic carbon stocks after forest windthrow in a mountainous ecosystem. *Functional Ecology*. 2016.
10. Bearup LA, Maxwell RM, Clow DW, McCray JE. Hydrological effects of forest transpiration loss in bark beetle-impacted watersheds. *Nature Climate Change*. 2014;4:481–6.
11. Edburg SL, Hicke JA, Brooks PD, Pendall EG, Ewers BE, Norton U, et al. Cascading impacts of bark beetle-caused tree mortality on coupled biogeophysical and biogeochemical processes. *Frontiers in Ecology and the Environment*. 2012;10:416–24.
12. Dobor L, Hlásny T, Rammer W, Barka I, Trombik J, Pavlenda P, et al. Post-disturbance recovery of forest carbon in a temperate forest landscape under climate change. *Agricultural and Forest Meteorology*. 2018;263:308–22.
13. Kurz WA, Dymond CC, Stinson G, Rampley GJ, Neilson ET, Carroll AL, et al. Mountain pine beetle and forest carbon feedback to climate change. *Nature*. 2008;452:987–90.
14. *Morris JL, Cottrell S, Fettig CJ, Hansen WD, Sherriff RL, Carter VA, et al. Managing bark beetle impacts on ecosystems and society: priority questions to motivate future research. *Journal of Applied Ecology*. 2017;54:750–60. **This paper collates major questions about bark beetle management, emphasizing the importance of interdisciplinary solutions and integrated social-ecological perception of the outbreaks like we advocated in the current study.**
15. Montagné-Huck C, Brunette M. Economic analysis of natural forest disturbances: A century of

913 research. *Journal of Forest Economics* [Internet]. 2018;32:42–71. Available from:
 914 <http://dx.doi.org/10.1016/j.jfe.2018.03.002>

915 16. Pye JM, Holmes TP, Prestemon JP, Wear DN. Economic Impacts of the Southern Pine Beetle.
 916 Coulson, RN; Klepzig, KD (2011) Southern Pine Beetle II Gen Tech Rep SRS-140. Asheville, NC: US
 917 Department of Agriculture Forest Service, Southern Research Station.; 2011. p. 213–22.

918 17. Grégoire J-C, Raffa KF, Lindgren BS. Economics and Politics of Bark Beetles. In: Vega FE, Hofstetter
 919 RW, editors. *Bark Beetles Biology and Ecology of Native and Invasive Species* [Internet]. London:
 920 Elsevier, Academic Press; 2015. p. 585–613. Available from:
 921 <http://linkinghub.elsevier.com/retrieve/pii/B9780124171565000150>

922 18. Arnberger A, Ebenberger M, Schneider IE, Cottrell S, Schlueter AC, von Ruschkowski E, et al.
 923 Visitor Preferences for Visual Changes in Bark Beetle-Impacted Forest Recreation Settings in the
 924 United States and Germany. *Environmental Management*. 2018;61:209–23.

925 19. Flint CG. Community perspectives on spruce beetle impacts on the Kenai Peninsula, Alaska.
 926 *Forest Ecology and Management*. 2006;227:207–18.

927 20. Kooistra CM, Hall TE. Understanding Public Support for Forest Management and Economic
 928 Development Options after a Mountain Pine Beetle Outbreak. *Journal of Forestry*. 2014;112:221–9.

929 21. McFarlane BL, Parkins JR, Watson DOT. Risk, knowledge, and trust in managing forest insect
 930 disturbance. *Canadian Journal of Forest Research* [Internet]. 2012;42:710–9. Available from:
 931 <https://doi.org/10.1139/x2012-030>

932 22. Morris JL, Cottrell S, Fettig CJ, DeRose RJ, Mattor KM, Carter VA, et al. Bark beetles as agents of
 933 change in social–ecological systems. *Frontiers in Ecology and the Environment*. 2018;16:S34–43.

934 23. Blicharska M, Angelstam P, Giessen L, Hilszczański J, Hermanowicz E, Holeksa J, et al. Between
 935 biodiversity conservation and sustainable forest management – A multidisciplinary assessment of the
 936 emblematic Białowieża Forest case. *Biological Conservation* [Internet]. Elsevier; 2020;248:1–15.
 937 Available from: <https://doi.org/10.1016/j.biocon.2020.108614>

938 24. Müller M. How natural disturbance triggers political conflict: Bark beetles and the meaning of
 939 landscape in the Bavarian Forest. *Global Environmental Change*. 2011;21:935–46.

940 25. Schiermeier Q. European Commission urges logging ban in ancient Białowieża Forest. *Nature*
 941 [Internet]. 2017;547:267–8. Available from: <http://www.nature.com/articles/nature.2017.22309>

942 26. Müller J, Bußler H, Goßner M, Rettelbach T, Duelli P. The European spruce bark beetle *Ips*
 943 *typographus* in a national park: From pest to keystone species. *Biodiversity and Conservation*.
 944 2008;17:2979–3001.

945 27. Michalová Z, Morrissey RC, Wohlgemuth T, Bače R, Fleischer P, Svoboda M. Salvage-logging
 946 after windstorm leads to structural and functional homogenization of understory layer and delayed
 947 spruce tree recovery in Tatra Mts., Slovakia. *Forests*. 2017;8.

948 28. Kulakowski D. Managing bark beetle outbreaks (*Ips typographus*, *Dendroctonus* spp.) in
 949 conservation areas in the 21st century. *Forest Research Papers*. 2016;77:352–7.

950 29. Donato DC, Campbell JL, Franklin JF. Multiple successional pathways and precocity in forest
 951 development: Can some forests be born complex? *Journal of Vegetation Science*. 2012;23:576–84.

952 30. Seidl R, Müller J, Hothorn T, Bässler C, Heurich M, Kautz M. Small beetle, large-scale drivers: How
 953 regional and landscape factors affect outbreaks of the European spruce bark beetle. *Journal of*
 954 *Applied Ecology*. 2016;53:530–40.

- 955 31. Svoboda M, Janda P, Nagel TA, Fraver S, Rejzek J, Bače R. Disturbance history of an old-growth
956 sub-alpine *Picea abies* stand in the Bohemian Forest, Czech Republic. *Journal of Vegetation Science*.
957 2012;23:86–97.
- 958 32. Beudert B, Bässler C, Thorn S, Noss R, Schröder B, Dieffenbach-Fries H, et al. Bark Beetles Increase
959 Biodiversity While Maintaining Drinking Water Quality. *Conservation Letters*. 2015;8:272–81.
- 960 33. Hilmers T, Avdagic A, Bartkowicz L, Bielak K, Binder F, Bončina A, et al. The productivity of mixed
961 mountain forests comprised of *Fagus sylvatica*, *Picea abies*, and *Abies alba* across Europe. *Forestry*.
962 2019;0:1–11.
- 963 34. Thorn S, Müller J, Leverkus AB. Preventing European forest diebacks. *Science* [Internet].
964 2019;365. Available from: <https://www.sciencemag.org/lookup/doi/10.1126/science.aaz3476>
- 965 35. Georgiev KB, Chao A, Castro J, Chen Y, Choi C, Fontaine JB, et al. Salvage logging changes the
966 taxonomic, phylogenetic and functional successional trajectories of forest bird communities. *Journal*
967 *of Applied Ecology* [Internet]. 2020;1365–2664.13599. Available from:
968 <https://onlinelibrary.wiley.com/doi/abs/10.1111/1365-2664.13599>
- 969 36. McFarlane BL, Stumpf-Allen RCG, Watson DO. Public perceptions of natural disturbance in
970 Canada’s national parks: The case of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins).
971 *Biological Conservation*. 2006;130:340–8.
- 972 37. Müller M, Job H. Managing natural disturbance in protected areas: Tourists’ attitude towards the
973 bark beetle in a German national park. *Biological Conservation*. 2009;142:375–83.
- 974 38. Lindenmayer DB, Franklin JF, Fischer J. General management principles and a checklist of
975 strategies to guide forest biodiversity conservation. *Biological Conservation*. 2006;131:433–45.
- 976 39. Thom D, Seidl R. Natural disturbance impacts on ecosystem services and biodiversity in
977 temperate and boreal forests. *Biological reviews of the Cambridge Philosophical Society*.
978 2016;91:760–81.
- 979 40. Forster B, Meier F, Gall R. Bark Beetle Management After a Mass Attack-Some Swiss Experiences.
980 McManus, Michael L; Liebhold, Andrew M, eds *Proceedings: Ecology, Survey and Management of*
981 *Forest Insects*; 2002 September 1-5; Krakow, Poland. Gen. Tech. Rep. NE-311. Newtown Square, PA:
982 U.S. Dept. of Agriculture, Forest Service, Northeastern Research Station.; 2003. p. 10–5.
- 983 41. Stadelmann G, Bugmann H, Meier F, Wermelinger B, Bigler C. Effects of salvage logging and
984 sanitation felling on bark beetle (*Ips typographus* L.) infestations. *Forest Ecology and Management*
985 [Internet]. Elsevier B.V.; 2013;305:273–81. Available from:
986 <http://dx.doi.org/10.1016/j.foreco.2013.06.003>
- 987 42. Wermelinger B. Ecology and management of the spruce bark beetle *Ips typographus* - A review of
988 recent research. *Forest Ecology and Management*. 2004;202:67–82.
- 989 43. Holuša J, Hlásny T, Modlinger R, Lukášová K, Kula E. Felled trap trees as the traditional method for
990 bark beetle control: Can the trapping performance be increased? *Forest Ecology and Management*.
991 2017;404:165–73.
- 992 44. Faccoli M, Stergulc F. Damage reduction and performance of mass trapping devices for forest
993 protection against the spruce bark beetle, *Ips typographus* (Coleoptera Curculionidae Scolytinae).
994 *Annals of Forest Science* [Internet]. 2008;65:309. Available from:
995 <http://dx.doi.org/10.1051/forest:2008010>
- 996 45. Holling CS, Meffe GK. Command and Control and the Pathology of Natural Resource
997 Management. *Conservation Biology* [Internet]. 1996;10:328–37. Available from:

998 <https://onlinelibrary.wiley.com/doi/abs/10.1046/j.1523-1739.1996.10020328.x>

999 46. Levin SA. Fragile dominion: complexity and the commons [Internet]. Perseus Books; 1999.

1000 Available from: <https://books.google.cz/books?id=TpfuAAAAMAAJ>

1001 47. Grodzki W. Mass outbreaks of the spruce bark beetle *Ips typographus* in the context of the

1002 controversies around the Białowieża Primeval Forest. Forest Research Papers. Walter de Gruyter

1003 GmbH; 2017;77:324–31.

1004 48. Cox M. The pathology of command and control: a formal synthesis. Ecology and Society.

1005 2016;21:1–8.

1006 49. *Dobor L, Hlásny T, Rammer W, Zimová S, Barka I, Seidl R. Is salvage logging effectively

1007 dampening bark beetle outbreaks and preserving forest carbon stocks? Journal of Applied Ecology.

1008 2019;57:67–76. **This paper provides an important revision of salvage logging as a tool to control**

1009 **bark beetle outbreaks in Europe. The paper highlights some controversies related to this practise**

1010 **and quantifies its effects on beetle outbreak dynamics and forest carbon pools.**

1011 50. Thorn S, Bässler C, Brandl R, Burton PJ, Cahall R, Campbell JL, et al. Impacts of salvage logging on

1012 biodiversity: A meta-analysis. Journal of Applied Ecology. 2017;55:279–89.

1013 51. Seidl R. The Shape of Ecosystem Management to Come : Anticipating Risks and Fostering

1014 Resilience. Bioscience. 2014;64:1159–69.

1015 52. Leverkus AB, Lindenmayer DB, Thorn S, Gustafsson L. Salvage logging in the world 's forests:

1016 Interactions between natural disturbance and logging need recognition. Global Ecology and

1017 Biogeography. 2018;27:1140–54.

1018 53. Leverkus AB, Benayas JMR, Castro J, Boucher D, Brewer S, Collins BM, et al. Salvage logging

1019 effects on regulating and supporting ecosystem services — a systematic map. Canadian Journal of

1020 Forest Research. 2018;48:983–1000.

1021 54. Thorn S, Bässler C, Svoboda M, Müller J. Effects of natural disturbances and salvage logging on

1022 biodiversity – Lessons from the Bohemian Forest. Forest Ecology and Management [Internet].

1023 Elsevier B.V.; 2017;388:113–9. Available from: <http://dx.doi.org/10.1016/j.foreco.2016.06.006>

1024 55. Armitage DR, Plummer R, Berkes F, Arthur RI, Charles AT, Davidson-Hunt IJ, et al. Adaptive co-

1025 management for social-ecological complexity. Frontiers in Ecology and the Environment. 2009;7:95–

1026 102.

1027 56. Raffa KF, Grégoire J-C, Lindgren BS. Natural History and Ecology of Bark Beetles. In: Vega FE,

1028 Hofstetter RW, editors. Bark Beetles [Internet]. San Diego: Academic Press; 2015. p. 1–40. Available

1029 from: <http://www.sciencedirect.com/science/article/pii/B9780124171565000010>

1030 57. Raffa KF, Aukema BH, Bentz BJ, Carroll AL, Hicke JA, Turner MG, et al. Cross-scale Drivers of

1031 Natural Disturbances Prone to Anthropogenic Amplification : The Dynamics of Bark Beetle Eruptions.

1032 BioScience. 2008;58:501–17.

1033 58. **Biedermann PHW, Müller J, Grégoire J, Gruppe A, Hagge J, Hammerbacher A, et al. Bark Beetle

1034 Population Dynamics in the Anthropocene : Challenges and Solutions. Trends in Ecology & Evolution.

1035 2019;34:914–24. **This paper provides an excellent review of our understanding of tree-killing bark**

1036 **beetles and presents a multivariate approach that integrates the many drivers governing bark**

1037 **beetle systems.**

1038 59. Kausrud K, Økland B, Skarpaas O, Grégoire J-C, Erbilgin N, Stenseth NC. Population dynamics in

1039 changing environments: the case of an eruptive forest pest species. Biological Reviews. 2012;87:34–

1040 51.

1041 60. Krokene P. Conifer Defense and Resistance to Bark Beetles. In: Vega FE, Hofstetter RW, editors.
 1042 Bark Beetles [Internet]. San Diego: Academic Press; 2015. p. 177–207. Available from:
 1043 <http://www.sciencedirect.com/science/article/pii/B9780124171565000058>

1044 61. Celedon JM, Bohlmann J. Oleoresin defenses in conifers: chemical diversity, terpene synthases
 1045 and limitations of oleoresin defense under climate change. *New Phytologist*. 2019;224:1444–63.

1046 62. Kautz M, Schopf R, Imron MA. Individual traits as drivers of spatial dispersal and infestation
 1047 patterns in a host-bark beetle system. *Ecological Modelling* [Internet]. Elsevier B.V.; 2014;273:264–
 1048 76. Available from: <http://dx.doi.org/10.1016/j.ecolmodel.2013.11.022>

1049 63. Huang J, Kautz M, Trowbridge AM, Hammerbacher A, Raffa KF, Adams HD, et al. Tree defence and
 1050 bark beetles in a drying world: carbon partitioning, functioning and modelling. *New Phytologist*.
 1051 2020;225:26–36.

1052 64. Sommerfeld A, Rammer W, Heurich M, Hilmers T, Müller J, Seidl R. Do bark beetle outbreaks
 1053 amplify or dampen future bark beetle disturbances in Central Europe? *Journal of Ecology*. 2020;1–13.

1054 65. Mezei P, Jakuš R, Pennerstorfer J, Havašová M, Škvarenina J, Ferenčík J, et al. Storms,
 1055 temperature maxima and the Eurasian spruce bark beetle *Ips typographus*—An infernal trio in
 1056 Norway spruce forests of the Central European High Tatra. *Agricultural and Forest Meteorology*.
 1057 2017;242:85–95.

1058 66. Wallin K, Raffa K. Feedback between individual host selection behavior and population dynamics
 1059 in an eruptive herbivore. *Ecological Monographs*. 2004;74:101–16.

1060 67. Boone CK, Aukema BH, Bohlmann J, Carroll AL, Raffa KF. Efficacy of tree defense physiology varies
 1061 with bark beetle population density: a basis for positive feedback in eruptive species. *Canadian*
 1062 *Journal of Forest Research* [Internet]. 2011;41:1174–88. Available from: [https://doi.org/10.1139/x11-](https://doi.org/10.1139/x11-041)
 1063 041

1064 68. Bentz B, Jönsson AM, Schroeder M, Weed A, Wilcke RAI, Larsson K. *Ips typographus* and
 1065 *Dendroctonus ponderosae* Models Project Thermal Suitability for Intra- and Inter-Continental
 1066 Establishment in a Changing Climate. *Frontiers in Forests and Global Change*. 2019;2:1–17.

1067 69. Baier P, Pennerstorfer J, Schopf A. PHENIPS-A comprehensive phenology model of *Ips*
 1068 *typographus* (L.) (Col., Scolytinae) as a tool for hazard rating of bark beetle infestation. *Forest Ecology*
 1069 *and Management*. 2007;249:171–86.

1070 70. Bussler H, Bouget C, Brustel H, Brändle M, Riedinger V, Brandl R, et al. Abundance and pest
 1071 classification of scolytid species (Coleoptera: Curculionidae, Scolytinae) follow different patterns.
 1072 *Forest Ecology and Management* [Internet]. Elsevier B.V.; 2011;262:1887–94. Available from:
 1073 <http://dx.doi.org/10.1016/j.foreco.2011.08.011>

1074 71. Seidl R, Vigl F, Rössler G, Neumann M, Rammer W. Assessing the resilience of Norway spruce
 1075 forests through a model-based reanalysis of thinning trials. *Forest Ecology and Management*
 1076 [Internet]. Elsevier B.V.; 2016;388:3–12. Available from:
 1077 <http://dx.doi.org/10.1016/j.foreco.2016.11.030>

1078 72. Netherer S, Panassiti B, Pennerstorfer J, Matthews B. Acute Drought Is an Important Driver of Bark
 1079 Beetle Infestation in Austrian Norway Spruce Stands. *Frontiers in Forests and Global Change*
 1080 2019;2:2. Important Driver of Bark Be. *Frontiers in Forests and Global Change*. 2019;2.

1082 73. Schlyter F, Zhang QH, Liu GT, Ji LZ. A successful case of pheromone mass trapping of the bark
 1083 beetle *Ips duplicatus* in a forest island, analysed by 20-year time-series data. *Integrated Pest*
 1084 *Management Reviews*. 2001;6:185–96.

- 1085 74. Björkman C, Bylund H, Nilsson U, Nordlander G, Schroeder M. Effects of New Forest Management
1086 on Insect Damage Risk in a Changing Climate. In: Björkman C, Niemelä P, editors. Climate Change and
1087 Insect Pests. CABI Clima. Preston, UK: Antony Rowe, CPI Group (UK) Ltd.; 2015. p. 291.
- 1088 75. Griess VC, Acevedo R, Härtl F, Staupendahl K, Knoke T. Does mixing tree species enhance stand
1089 resistance against natural hazards? A case study for spruce. Forest Ecology and Management.
1090 2012;267:284–96.
- 1091 76. Neuner S, Albrecht A, Cullmann D, Engels F, Griess VC, Hahn WA, et al. Survival of Norway spruce
1092 remains higher in mixed stands under a dryer and warmer climate. Global Change Biology.
1093 2015;21:935–46.
- 1094 77. Jactel H, Nicoll BC, Branco M, Gonzalez-Olabarria JR, Grodzki W, Långström B, et al. The
1095 influences of forest stand management on biotic and abiotic risks of damage. Annals of Forest
1096 Science. 2009;66:1–18.
- 1097 78. Berec L, Doležal P, Hais M. Population dynamics of *Ips typographus* in the Bohemian Forest
1098 (Czech Republic): Validation of the phenology model PHENIPS and impacts of climate change. Forest
1099 Ecology and Management. 2013;292:1–9.
- 1100 79. Jönsson AM, Appelberg G, Harding S, Bärning L. Spatio-temporal impact of climate change on the
1101 activity and voltinism of the spruce bark beetle , *Ips typographus*. Global Change Biology.
1102 2009;15:486–99.
- 1103 80. Jakoby O, Lischke H, Wermelinger B. Climate change alters elevational phenology patterns of the
1104 European spruce bark beetle (*Ips typographus*). Global Change Biology. 2019;25:4048–63.
- 1105 81. Matthews B, Netherer S, Katzensteiner K, Pennerstorfer J, Blackwell E, Henschke P, et al.
1106 Transpiration deficits increase host susceptibility to bark beetle attack: Experimental observations
1107 and practical outcomes for *Ips typographus* hazard assessment. Agricultural and Forest Meteorology
1108 [Internet]. Elsevier; 2018;263:69–89. Available from:
1109 <https://doi.org/10.1016/j.agrformet.2018.08.004>
- 1110 82. Seidl R, Rammer W, Lexer MJ. Climate change vulnerability of sustainable forest management in
1111 the Eastern Alps. Climatic Change. 2011;106:225–54.
- 1112 83. Sommerfeld A, Senf C, Buma B, Amato AWD, Després T, Díaz-Hormazábal I, et al. Patterns and
1113 drivers of recent disturbances across the temperate forest biome. Nature Communications.
1114 2018;9:1–9.
- 1115 84. **Senf C, Seidl R. Natural disturbances are spatially diverse but temporally synchronized across
1116 temperate forest landscapes in Europe. Global Change Biology. 2018;24:1201–11. **This paper**
1117 **provides important evidence of large-scale spatial synchrony of forest disturbance in Europe. Such**
1118 **a synchrony highlights the limitations of the current mostly stand-scale oriented management and**
1119 **emphasizes the importance of the landscape-scale perspective we advocate here.**
- 1120 85. Peters EB, Wythers KR, Bradford JB, Reich PB. Influence of Disturbance on Temperate Forest
1121 Productivity. Ecosystems. 2013;16:95–110.
- 1122 86. Williams CA, Collatz GJ, Masek J, Goward SN. Carbon consequences of forest disturbance and
1123 recovery across the conterminous United States. Global Biogeochem Cycles. 2012;26:1–13.
- 1124 87. Griffin JM, Turner MG, Simard M. Nitrogen cycling following mountain pine beetle disturbance in
1125 lodgepole pine forests of Greater Yellowstone. Forest Ecology and Management. Elsevier B.V.;
1126 2011;261:1077–89.
- 1127 88. Oulehle F, Wright RF, Svoboda M, Bače R, Matějka K, Kaňa J, et al. Effects of Bark Beetle

1128 Disturbance on Soil Nutrient Retention and Lake Chemistry in Glacial Catchment. *Ecosystems*.
1129 2019;22:725–41.

1130 89. Seidl R, Rammer W, Jäger D, Lexer MJ. Impact of bark beetle (*Ips typographus* L.) disturbance on
1131 timber production and carbon sequestration in different management strategies under climate
1132 change. *Forest Ecology and Management*. 2008;256:209–20.

1133 90. Zeppenfeld T, Svoboda M, Deroose RJ, Heurich M, Müller J, Čížková P, et al. Response of mountain
1134 *Picea abies* forests to stand-replacing bark beetle outbreaks: Neighbourhood effects lead to self-
1135 replacement. *Journal of Applied Ecology*. 2015;52:1402–11.

1136 91. Wild J, Kopecký M, Svoboda M, Zenáhlíková J, Edwards-Jonášová M, Herben T. Spatial patterns
1137 with memory: Tree regeneration after stand-replacing disturbance in *Picea abies* mountain forests.
1138 *Journal of Vegetation Science*. 2014;25:1327–40.

1139 92. Bače R, Svoboda M, Janda P, Morrissey RC, Wild J, Clear JL, et al. Legacy of pre-disturbance spatial
1140 pattern determines early structural diversity following severe disturbance in montane spruce forests.
1141 *PLoS ONE*. 2015;10:1–18.

1142 93. Hilmers T, Friess N, Bässler C, Heurich M, Brandl R, Pretzsch H, et al. Biodiversity along temperate
1143 forest succession. *Journal of Applied Ecology*. 2018;1–11.

1144 94. Kortmann M, Heurich M, Latifi H, Rösner S, Seidl R, Müller J, et al. Forest structure following
1145 natural disturbances and early succession provides habitat for two avian flagship species, capercaillie
1146 (*Tetrao urogallus*) and hazel grouse (*Tetrastes bonasia*). *Biological Conservation*. 2018;226.

1147 95. Müller D, Schröder B, Müller J. Modelling habitat selection of the cryptic Hazel Grouse *Bonasa*
1148 *bonasia* in a montane forest. *Journal of Ornithology*. 2009;150:717–32.

1149 96. Kortmann M, Müller JC, Baier R, Bässler C, Buse J, Cholewińska O, et al. Ecology versus society:
1150 Impacts of bark beetle infestations on biodiversity and restorativeness in protected areas of Central
1151 Europe. *Biological Conservation*. 2021;254:108931.

1152 97. Koprowski JL, Alanen MI, Lynch AM. Nowhere to run and nowhere to hide: Response of endemic
1153 Mt. Graham red squirrels to catastrophic forest damage. *Biological Conservation*. 2005;126:491–8.

1154 98. Zugmeyer C, Koprowski J. Habitat Selection is Unaltered After Severe Insect Infestation: Concerns
1155 for Forest-Dependent Species. *Journal of Mammalogy - J MAMMAL*. 2009;90:175–82.

1156 99. Conner RN, Rudolph DC. Losses of red-cockaded woodpecker cavity trees to southern pine
1157 beetles. *Wilson Bulletin*. 1995;107:81–92.

1158 100. Conner RN, Rudolph DC, Kulhavy DL, Snow AE. Causes of mortality of red-cockaded woodpecker
1159 cavity trees. *Journal of Wildlife Management*. 55(3): 531-537. 1991.

1160 101. Jonsson M. Live storage of *Picea abies* in Sweden after storm felling. *Scandinavian Journal of*
1161 *Forest Research* [Internet]. Taylor & Francis; 2007;22:344–50. Available from:
1162 <https://doi.org/10.1080/02827580701478404>

1163 102. Bebi P, Teich M, Hagedorn F, Zurbriggen N, Brunner SH, Grêt-Regamey A. Veränderung von
1164 Wald und Waldleistungen in der Landschaft Davos im Zuge des Klimawandels. *Schweizerische*
1165 *Zeitschrift für Forstwesen*. 2012;163:493–501.

1166 103. Sebold J, Senf C, Heiser M, Scheidl C, Pflugmacher D, Seidl R. The effects of forest cover and
1167 disturbance on torrential hazards : large- scale evidence from the Eastern Alps. *Environmental*
1168 *Research Letters*. 2019;14:1–12.

1169 104. Mikkelsen KM, Dickenson ER V, Maxwell RM, McCray JE, Sharp JO. Water-quality impacts from

1170 climate-induced forest die-off. *Nature Climate Change* [Internet]. Nature Publishing Group;
 1171 2013;3:218–22. Available from: <https://doi.org/10.1038/nclimate1724>

1172 105. Flint C, Qin H, Ganning JP. Linking local perceptions to the biophysical and amenity contexts of
 1173 forest disturbance in Colorado. *Environmental Management*. 2012;49:553–69.

1174 106. Holmes TP. Price and Welfare Effects of Catastrophic Forest Damage From Southern Pine Beetle
 1175 Epidemics. *Forest Science*. 1991.

1176 107. Bogdanski B, Sun L, Peter B, Stennes B. Markets for forest products following a large
 1177 disturbance : opportunities and challenges from the mountain pine beetle outbreak in western
 1178 Canada [Internet]. 2011. Available from: <https://www.researchgate.net/publication/264040371>

1179 108. SFA. SFA - Swedish statistical yearbook of forestry. Jönköping: Swedish Forest Agency.; 2010.

1180 109. Cohen J, Blinn CE, Boyle KJ, Holmes TP, Moeltner K. Hedonic Valuation with Translating
 1181 Amenities: Mountain Pine Beetles and Host Trees in the Colorado Front Range. *Environmental and*
 1182 *Resource Economics*. Springer Netherlands; 2016;63:613–42.

1183 110. Rosenberger RS, Bell LA, Champ PA, White EM. Estimating the Economic Value of Recreation
 1184 Losses in Rocky Mountain National Park Due to a Mountain Pine Beetle Outbreak. *Western*
 1185 *Economics Forum*. 2013;12:31–9.

1186 111. Dhar A, Parrott L, Heckbert S. Consequences of mountain pine beetle outbreak on forest
 1187 ecosystem services in western Canada. *Canadian Journal of Forest Research* [Internet]. 2016;46:987–
 1188 99. Available from: <http://www.nrcresearchpress.com/doi/10.1139/cjfr-2016-0137>

1189 112. Arnberger A, Eder R, Alex B, Preisel H, Ebenberger M, Husslein M. Trade-offs between wind
 1190 energy, recreational, and bark-beetle impacts on visual preferences of national park visitors. *Land*
 1191 *Use Policy* [Internet]. Elsevier; 2018;76:166–77. Available from:
 1192 <https://doi.org/10.1016/j.landusepol.2018.05.007>

1193 113. Keskitalo ECH, Pettersson M, Ambjörnsson EL, Davis EJ. Agenda-setting and framing of policy
 1194 solutions for forest pests in Canada and Sweden: Avoiding beetle outbreaks? *Forest Policy and*
 1195 *Economics* [Internet]. Elsevier B.V.; 2016;65:59–68. Available from:
 1196 <http://dx.doi.org/10.1016/j.forpol.2015.10.011>

1197 114. Švajda J, Koróny S, Zięba A, Adamski P. Perceptions of natural disturbance in Tatra National Park,
 1198 Poland. *Forestry Journal*. 2016;62:105–9.

1199 115. Buhyoff GJ, Leuschner WA, Wellman JD. Aesthetic impacts of southern pine beetle damage(US).
 1200 *Journal of Environmental Management*. 1979;8:261–7.

1201 116. McFarlane BL, Watson DOT. Perceptions of ecological risk associated with mountain pine beetle
 1202 (*Dendroctonus ponderosae*) infestations in Banff and Kootenay National Parks of Canada. *Risk*
 1203 *analysis: an official publication of the Society for Risk Analysis*. United States; 2008;28:203–12.

1204 117. Blicharska M, Smithers RJ. Białowieża Forest: Political stands. *Science* [Internet]. 2018;359.
 1205 Available from: <https://www.sciencemag.org/lookup/doi/10.1126/science.aar7173>

1206 118. Gordon JS, Gruver JB, Flint CG, Luloff AE. Perceptions of wildfire and landscape change in the
 1207 Kenai Peninsula, Alaska. *Environmental Management*. 2013;52:807–20.

1208 119. Qin H. Comparing newer and longer-term residents’ perceptions and actions in response to
 1209 forest insect disturbance on Alaska’s Kenai Peninsula: A longitudinal perspective. *Journal of Rural*
 1210 *Studies* [Internet]. Elsevier Ltd; 2015;39:51–62. Available from:
 1211 <http://dx.doi.org/10.1016/j.jrurstud.2015.03.007>

- 1212 120. Qin H, Flint CG. Capturing community context of human response to forest disturbance by
1213 insects: a multi-method assessment. *Human Ecology* [Internet]. 2010;38:567–79. Available from:
1214 <https://doi.org/10.1007/s10745-010-9334-2>
- 1215 121. Qin H, Flint CG, Luloff AE. Tracing temporal changes in the human dimensions of forest insect
1216 disturbance on the Kenai Peninsula, Alaska. *Human Ecology*. 2015;43:43–59.
- 1217 122. Edwards P, Kleinschmit D. Towards a European forest policy - Conflicting courses. *Forest Policy*
1218 *and Economics*. 2013;33:87–93.
- 1219 123. Christiansen E. Eurasian Spruce Bark Beetle, *Ips typographus* Linnaeus (Coleoptera:
1220 Curculionidae, Scolytinae). In: Capinera JL, editor. *Encyclopedia of Entomology* [Internet]. Dordrecht:
1221 Springer Netherlands; 2008. p. 1363–6. Available from: [https://doi.org/10.1007/978-1-4020-6359-](https://doi.org/10.1007/978-1-4020-6359-6_3684)
1222 [6_3684](https://doi.org/10.1007/978-1-4020-6359-6_3684)
- 1223 124. *Albrich K, Rammer W, Seidl R. Climate change causes critical transitions and irreversible
1224 alterations of mountain forests. *Global Change Biology*. Wiley; 2020. **This paper highlights the role**
1225 **of climate change as a driver of forest transition in Europe. It emphasizes the vulnerability of**
1226 **mountain spruce forests and describes a cascade of processes driving their transition to alternative**
1227 **ecological states.**
- 1228 125. Alexander D. Towards the Development of a Standard in Emergency Planning. *Disaster*
1229 *Prevention and Management*. 2005;14:158–75.
- 1230 126. Kelly C. A framework for improving operational effectiveness and cost efficiency in emergency
1231 planning and response. *Disaster Prevention and Management: An International Journal* [Internet].
1232 MCB UP Ltd; 1995;4:25–31. Available from: <https://doi.org/10.1108/09653569510088041>
- 1233 127. Ingrisch J, Bahn M. Towards a Comparable Quantofication of Resilience. *Trends in Ecology &*
1234 *Evolution*. 2018;1–9.
- 1235 128. Nikinmaa L, Lindner M, Cantarello E, Jump AS, Seidl R, Winkel G, et al. Reviewing the Use of
1236 Resilience Concepts in Forest Sciences. *Current Forestry Reports*. *Current Forestry Reports*;
1237 2020;6:61-80.
- 1238 129. Szwagrzyk J, Maciejewski Z, Maciejewska E, Tomski A, Gazda A. Forest recovery in set-aside
1239 windthrow is facilitated by fast growth of advance regeneration. *Annals of Forest Science*. Springer-
1240 Verlag France; 2018;75.
- 1241 130. Nelson HW, Williamson TB, Macaulay C, Mahony C. Assessing the potential for forest
1242 management practitioner participation in climate change adaptation. *Forest Ecology and*
1243 *Management*. Elsevier; 2016;360:388–99.
- 1244 131. Flint CG, McFarlane B, Müller M. Human dimensions of forest disturbance by insects: An
1245 international synthesis. *Environmental Management*. 2009;43:1174–86.
- 1246 132. USDA Forest Service. Economic Use of Beetle - Killed Trees. 2011.
- 1247 133. Dobor L, Hlásny T, Rammer W, Zimová S, Barka I, Seidl R. Spatial configuration matters when
1248 removing windfelled trees to manage bark beetle disturbances in Central European forest
1249 landscapes. *Journal of Environmental Management*. 2020;254:1–12.
- 1250 134. Tepe TL, Meretsky VJ. Forward-looking forest restoration under climate change-Are U.S.
1251 nurseries ready? *Restoration Ecology*. 2011;19:295–8.
- 1252 135. Netherer S, Nopp-Mayr U. Predisposition assessment systems (PAS) as supportive tools in forest
1253 management - Rating of site and stand-related hazards of bark beetle infestation in the High Tatra
1254 Mountains as an example for system application and verification. *Forest Ecology and Management*.

1255 2005;207:99–107.

1256 136. Weslien J. Monitoring *Ips typographus* (L.) populations and forecasting damage¹. Journal of
1257 Applied Entomology. 2009;114:338–40.

1258 137. de Groot M, Ogris N. Short-term forecasting of bark beetle outbreaks on two economically
1259 important conifer tree species. Forest Ecology and Management. Elsevier B.V.; 2019;450.

1260 138. Abdullah H, Darvishzadeh R, Skidmore AK, Groen TA, Heurich M. European spruce bark beetle
1261 (*Ips typographus* , L.) green attack affects foliar reflectance and biochemical properties. International
1262 Journal of Applied Earth Observation and Geoinformation [Internet]. Elsevier; 2018;64:199–209.
1263 Available from: <http://dx.doi.org/10.1016/j.jag.2017.09.009>

1264 139. Konnert M, Fady B, Gömöry D, A'Hara S, Wolter F, Ducci F, et al. Use and transfer of forest
1265 reproductive material : in Europe in the context of climate change. Rome, Italy: Bioversity
1266 International; 2015.

1267 140. Kolström M, Lindner M, Vilén T, Maroschek M, Seidl R, Lexer MJ, et al. Reviewing the Science
1268 and Implementation of Climate Change Adaptation Measures in European Forestry. Forests.
1269 2011;2:961–82.

1270 141. Fettig CJ, Gibson KE, Munson AS, Negrón JF. Cultural Practices for Prevention and Mitigation of
1271 Mountain Pine Beetle Infestations. Forest Science [Internet]. 2013;60:450–63. Available from:
1272 <https://doi.org/10.5849/forsci.13-032>

1273 142. Fassnacht FE, Latifi H, Ghosh A, Joshi PK, Koch B. Assessing the potential of hyperspectral
1274 imagery to map bark beetle-induced tree mortality. Remote Sensing of Environment. 2014;140:533–
1275 48.

1276 143. Senf C, Seidl R, Hostert P. Remote sensing of forest insect disturbances: Current state and future
1277 directions. International Journal of Applied Earth Observation and Geoinformation. Elsevier B.V.;
1278 2017. p. 49–60.

1279 144. Poland TM, Rassati D. Improved biosecurity surveillance of non-native forest insects: a review of
1280 current methods. Journal of Pest Science. Springer Verlag; 2019. p. 37–49.

1281 145. Wermelinger B, Epper C, Kenis M, Ghosh S, Holdenrieder O. Emergence patterns of univoltine
1282 and bivoltine *Ips typographus* (L.) populations and associated natural enemies. Journal of Applied
1283 Entomology. 2012;136:212–24.

1284 146. Honkaniemi J, Rammer W, Seidl R. Norway spruce at the trailing edge : the effect of landscape
1285 configuration and composition on climate resilience. Landscape Ecology [Internet]. Springer
1286 Netherlands; 2020;35:591–606. Available from: <https://doi.org/10.1007/s10980-019-00964-y>

1287 147. Lindner M, Maroschek M, Netherer S, Kremer A, Barbati A, Garcia-Gonzalo J, et al. Climate
1288 change impacts , adaptive capacity , and vulnerability of European forest ecosystems. Forest Ecology
1289 and Management. 2010;259:698–709.

1290 148. Potterf M, Bone C. Simulating bark beetle population dynamics in response to windthrow
1291 events. Ecological Complexity [Internet]. Elsevier B.V.; 2017;32:21–30. Available from:
1292 <https://doi.org/10.1016/j.ecocom.2017.08.003>

1293 149. Havašová M, Ferencík J, Jakuš R. Interactions between windthrow , bark beetles and forest
1294 management in the Tatra national parks. Forest Ecology and Management. 2017;391:349–61.

1295 150. Taerøe A, de Koning JHC, Löf M, Tolvanen A, Heiðarsson L, Raulund-Rasmussen K. Recovery of
1296 temperate and boreal forests after windthrow and the impacts of salvage logging. A quantitative
1297 review. Forest Ecology and Management. Elsevier B.V.; 2019. p. 304–16.

1298 151. Koch FH, Yemshanov D, McKenney DW, Smith WD. Evaluating Critical Uncertainty Thresholds in
1299 a Spatial Model of Forest Pest Invasion Risk. *Risk Analysis* [Internet]. 2009;29:1227–41. Available
1300 from: <http://doi.wiley.com/10.1111/j.1539-6924.2009.01251.x>

1301 152. Schmolke A, Thorbek P, DeAngelis DL, Grimm V. Ecological models supporting environmental
1302 decision making: A strategy for the future. *Trends in Ecology and Evolution*. 2010. p. 479–86.

1303 153. Johnstone JF, Allen CD, Franklin JF, Frelich LE, Harvey BJ, Higuera PE, et al. Changing disturbance
1304 regimes, ecological memory, and forest resilience. *Frontiers in Ecology and the Environment*. Wiley
1305 Blackwell; 2016. p. 369–78.

1306 154. Bengtsson J, Nilsson SG, Franc A, Menozzi P. Biodiversity, disturbances, ecosystem function and
1307 management of European forests. *Forest Ecology and Management*. 2000;132:39–50.

1308 155. Fares S, Mugnozza GS, Corona P, Palahí M. Sustainability: Five steps for managing Europe's
1309 forests. *Nature* [Internet]. 2015;519:407–9. Available from:
1310 <http://www.nature.com/articles/519407a>

1311 156. Franklin JF, Lindenmayer D, MacMahon JA, McKee A, Magnuson J, Perry DA, et al. Threads of
1312 Continuity. There are immense differences between even-aged silvicultural disturbances (especially
1313 clearcutting) and natural disturbances, such as windthrow, wildfire, and even volcanic eruptions.
1314 *Conservation in Practice* [Internet]. 2000;1:8–17. Available from:
1315 <http://doi.wiley.com/10.1111/j.1526-4629.2000.tb00155.x>

1316 157. Brunette M, Holec J, Sedliak M, Tucek J, Hanewinkel M. An actuarial model of forest insurance
1317 against multiple natural hazards in fir (*Abies Alba* Mill.) stands in Slovakia. *Forest Policy and*
1318 *Economics* [Internet]. Elsevier B.V.; 2015;55:46–57. Available from:
1319 <http://dx.doi.org/10.1016/j.forpol.2015.03.001>

1320 158. Müller J, Noss RF, Bussler H, Brandl R. Learning from a “benign neglect strategy” in a national
1321 park: Response of saproxylic beetles to dead wood accumulation. *Biological Conservation*.
1322 2010;143:2559–69.

1323 159. Raffa KF, Berryman AA. Interacting Selective Pressures in Conifer-Bark Beetle Systems: A Basis
1324 for Reciprocal Adaptations? *The American Naturalist* [Internet]. 1987;129:234–62. Available from:
1325 <https://doi.org/10.1086/284633>

1326 160. Rösner S, Mussard-Forster E, Lorenc T, Müller J. Recreation shapes a “landscape of fear” for a
1327 threatened forest bird species in Central Europe. *Landscape Ecology*. 2014;29:55–66.

1328 161. Seidl R, Klonner G, Rammer W, Essl F, Moreno A, Neumann M, et al. Invasive alien pests
1329 threaten the carbon stored in Europe's forests. *Nature Communications* [Internet]. Springer US;
1330 2018;9:1–10. Available from: <http://dx.doi.org/10.1038/s41467-018-04096-w>

1331 162. Kirkendall LR, Faccoli M. Bark beetles and pinhole borers (Curculionidae , Scolytinae ,
1332 Platypodinae) alien to Europe. *ZooKeys*. 2010;56:227–51.

1333 163. Showalter DN, Raffa KF, Snieszko RA, Herms DA, Liebhold AM, Smith JA, et al. Strategic
1334 Development of Tree Resistance Against Forest Pathogen and Insect Invasions in Defense-Free Space.
1335 *Frontiers in Ecology and Evolution* [Internet]. 2018;6. Available from:
1336 <https://www.frontiersin.org/article/10.3389/fevo.2018.00124/full>

1337 164. Cudmore TJ, Björklund N, Carroll AL, Lindgren BS. Climate change and range expansion of an
1338 aggressive bark beetle: evidence of higher beetle reproduction in naïve host tree populations.
1339 *Journal of Applied Ecology*. 2010;47:1036–43.

1340 165. Raffa KF, Powell EN, Townsend PA. Temperature-driven range expansion of an irruptive insect

- 1341 heightened by weakly coevolved plant defenses. *Proceedings of the National Academy of Sciences of*
1342 *the United States of America*. 2013;110:2193–8.
- 1343 166. Logan JA, MacFarlane WW, Willcox L. Whitebark pine vulnerability to climate-driven mountain
1344 pine beetle disturbance in the Greater Yellowstone Ecosystem. *Ecological Applications*. 2010;20:895–
1345 902.
- 1346 167. Jönsson AM, Harding S, Krokene P, Lange H, Lindelöw Å, Økland B, et al. Modelling the potential
1347 impact of global warming on *Ips typographus* voltinism and reproductive diapause. *Climatic Change*.
1348 2011;109:695–718.
- 1349 168. Wermelinger B, Schneider Mathis D, Knížek M, Forster B. Tracking the spread of the northern
1350 bark beetle (*Ips duplicatus* [Sahlb.]) in Europe and first records from Switzerland and Liechtenstein.
1351 *Alpine Entomology* [Internet]. Pensoft Publishers; 2020;4:179–84. Available from:
1352 <https://doi.org/10.3897/alpento.4.53808>
- 1353 169. Thom D, Rammer W, Seidl R. Disturbances catalyze the adaptation of forest ecosystems to
1354 changing climate conditions. *Global Change Biology*. 2017;23:269–82.
- 1355 170. Sabatini FM, Burrascano S, Keeton WS, Levers C, Lindner M, Pötzschner F, et al. Where are
1356 Europe’s last primary forests? *Diversity and Distributions*. 2018;24:1426–39.
- 1357 171. Thom D, Golivets M, Edling L, Meigs G, Gourevitch J, Sonter L, et al. The climate sensitivity of
1358 carbon, timber, and species richness co-varies with forest age in boreal-temperate North America.
1359 *Global Change Biology*. 2019;25:2446–58.
- 1360 172. Lindenmayer DB, Laurance WF, Franklin JF, Likens GE, Banks SC, Blanchard W, et al. New Policies
1361 for Old Trees : Averting a Global Crisis in a Keystone Ecological Structure. *Conservation Letters*.
1362 2014;7:61–9.
- 1363 173. *Müller J, Noss RF, Thorn S, Bässler C, Leverkus AB, Lindenmayer D. Increasing disturbance
1364 demands new policies to conserve intact forest. *Conservation Letters*. 2018;e12449:1–7. **This study**
1365 **contributes to resolving some conflicts between forest management and nature conservation in**
1366 **Europe, emphasizing the controversies about salvage logging in protected spruce forests. It**
1367 **formulated specific steps to be taken to alleviate the conflicts.**
- 1368 174. Lindenmayer DB, Foster DR, Franklin JF, Hunter ML, Noss RF, Schmiegelow FA, et al. Salvage
1369 Harvesting Policies After Natural Disturbance. *Science* [Internet]. American Association for the
1370 Advancement of Science; 2004;303:1303. Available from:
1371 <https://science.sciencemag.org/content/303/5662/1303>
- 1372 175. Schmiegelow FKA, Stepnisky DP, Stambaugh CA, Koivula M. Reconciling salvage logging of boreal
1373 forests with a natural-disturbance management model. *Conservation Biology*. 2006;20:971–83.
- 1374 176. Leverkus AB, Castro J. An ecosystem services approach to the ecological effects of salvage
1375 logging: Valuation of seed dispersal. *Ecological Applications*. Ecological Society of America;
1376 2017;27:1057–63.
- 1377 177. Lindenmayer DB, Laurance WF. The ecology, distribution, conservation and management of
1378 large old trees. *Biological Reviews*. Blackwell Publishing Ltd; 2017;92:1434–58.
- 1379 178. Kautz M, Dworschak K, Gruppe A, Schopf R. Quantifying spatio-temporal dispersion of bark
1380 beetle infestations in epidemic and non-epidemic conditions. *Forest Ecology and Management*
1381 [Internet]. Elsevier B.V.; 2011;262:598–608. Available from:
1382 <http://dx.doi.org/10.1016/j.foreco.2011.04.023>
- 1383 179. Montano V, Bertheau C, Doležal P, Krumböck S, Okrouhlík J, Stauffer C, et al. How differential

1384 management strategies affect *Ips typographus* L. dispersal. *Forest Ecology and Management*.
1385 2016;360:195–204.

1386 180. Hagge J, Leibl F, Müller J, Plechinger M, Soutinho JG, Thorn S. Reconciling pest control, nature
1387 conservation, and recreation in coniferous forests. *Conservation Letters*. 2019;12:1–8.

1388 181. Krumm F, Schuck A, Rigling A. How to balance forestry and biodiversity conservation ? A view
1389 across Europe. Birmensdorf: European Forest Institute (EFI); Swiss Federal Institute for Forest, Snow
1390 and Landscape Research (WSL); 2020.

1391 182. Seidl R, Albrich K, Thom D, Rammer W. Harnessing landscape heterogeneity for managing future
1392 disturbance risks in forest ecosystems. *Journal of Environmental Management* [Internet]. Elsevier
1393 Ltd; 2018;209:46–56. Available from: <https://doi.org/10.1016/j.jenvman.2017.12.014>

1394 183. Augustynczyk ALD, Dobor L, Hlásny T. Controlling landscape-scale bark beetle dynamics: Can we
1395 hit the right spot? *Landscape and Urban Planning* [Internet]. 2021;209:104035. Available from:
1396 <https://www.sciencedirect.com/science/article/pii/S016920462031519X>

1397 184. Fettig CJ, Hilszczański J. Management Strategies for Bark Beetles in Conifer Forests. In: Vega FE,
1398 Hofstetter RWBT-BB, editors. *Bark Beetles: Biology and Ecology of Native and Invasive Species*
1399 [Internet]. San Diego: Academic Press; 2015. p. 555–84. Available from:
1400 <https://www.sciencedirect.com/science/article/pii/B9780124171565000149>

1401 185. Nabuurs G-J, Verweij P, Van Eupen M, Pérez-Soba M, Pölzl H, Hendriks K. Next-generation
1402 information to support a sustainable course for European forests. *Nature Sustainability* [Internet].
1403 2019;2:815–8. Available from: <https://doi.org/10.1038/s41893-019-0374-3>

1404 186. Niemelä J, Young J, Alard D, Askasibar M, Henle K, Johnson R, et al. Identifying and managing
1405 conflicts between forest conservation and other human interests in Europe. *Forest Policy and*
1406 *Economics* 7 (2005). 2005;6.

1407 187. Kuboń M, Latawiec AE, Scarano FR, Drosik A, Strassburg BBN, Grzebieniowski W, et al. Searching
1408 for solutions to the conflict over Europe’s oldest forest. *Conservation Biology* [Internet].
1409 2019;33:476–9. Available from: <https://conbio.onlinelibrary.wiley.com/doi/abs/10.1111/cobi.13229>

1410 188. Mezei P, Blaženec M, Grodzki W, Škvarenina J, Jakuš R. Influence of different forest protection
1411 strategies on spruce tree mortality during a bark beetle outbreak. *Annals of Forest Science* [Internet].
1412 2017;74:65. Available from: <https://doi.org/10.1007/s13595-017-0663-9>

1413 189. Kovalčík M, Sarvasova Z, Schwarz M, Moravčík M, J. Lásková M, Tutka J. Financial and socio-
1414 economic impacts of nature conservation on forestry in Slovakia. *Journal of Forest Science*.
1415 2012;58:425–35.

1416 190. Sotirov M. *Natura 2000 and forests: Assessing the state of implementation and effectiveness.*
1417 *What Science Can Tell Us* 7. European Forest Institute. 2017.

1418 191. Hagerman SM, Chan KMA. Climate change and biodiversity conservation: impacts, adaptation
1419 strategies and future research directions. *Biology Reports*. 2009;1:1–5.

1420 192. Capinha C, Essl F, Seebens H, Moser D, Pereira HM. The dispersal of alien species redefines
1421 biogeography in the Anthropocene. *Science* [Internet]. American Association for the Advancement of
1422 Science; 2015;348:1248–51. Available from: <https://science.sciencemag.org/content/348/6240/1248>

1423 193. Dukes JS, Pontius J, Orwig D, Garnas JR, Rodgers VL, Brazee N, et al. Responses of insect pests,
1424 pathogens, and invasive plant species to climate change in the forests of northeastern North
1425 America: What can we predict? This article is one of a selection of papers from NE Forests 2100: A
1426 Synthesis of Climate Change Impacts o. *Canadian Journal of Forest Research* [Internet]. 2009;39:231–

1427 48. Available from: <https://doi.org/10.1139/X08-171>

1428 194. Zimová S, Dobor L, Hlásny T, Rammer W, Seidl R. Reducing rotation age to address increasing
1429 disturbances in Central Europe: Potential and limitations. *Forest Ecology and Management*.
1430 2020;475.

1431 195. Colfer C. Adaptive Collaborative Management. In: Gonsalves J, Becker T, Braun A, Campilan D,
1432 De Chvez H, Fajber E, et al., editors. *Participatory Research and Development for Sustainable*
1433 *Agriculture and Natural Resource Management*. International Potato Center-Users' Perspectives with
1434 *Agricultural Research and Development, and International Development Research Centre*; 2005. p.
1435 148–241.

1436 196. Ribot JC. *Waiting for Democracy: The Politics of Choice in Natural Resource Decentralization*
1437 [Internet]. Washington D.C.: World Resources Institute; 2004. Available from:
1438 <https://books.google.cz/books?id=5r0sAQAAMAAJ>

1439 197. Brown K. Integrating Conservation and Development: A Case of Institutional Misfit. *Frontiers in*
1440 *Ecology and The Environment*. 2003;1:479–87.

1441 198. Chen S, Shahi C. Economic and Ecological Trade-Off Analysis of Forest Ecosystems: Options for
1442 Boreal Forests. *Environmental Reviews*. 2016;24.

1443 199. Zeng H, Talkkari A, Peltola H, Kellomäki S. A GIS-Based Decision Support System for Risk
1444 Assessment of Wind Damage in Forest Management. *Environ Model Softw* [Internet]. NLD: Elsevier
1445 Science Publishers B. V.; 2007;22:1240–1249. Available from:
1446 <https://doi.org/10.1016/j.envsoft.2006.07.002>

1447 200. Albrich K, Rammer W, Thom D, Seidl R. Trade-offs between temporal stability and level of forest
1448 ecosystem services provisioning under climate change. *Ecological Applications* [Internet]. John Wiley
1449 & Sons, Ltd; 2018;28:1884–96. Available from: <https://doi.org/10.1002/eap.1785>

1450 201. Kogan M. Integrated Pest Management: Historical Perspectives and Contemporary
1451 Developments. *Annual Review of Entomology* [Internet]. 1998;43:243–70. Available from:
1452 <https://doi.org/10.1146/annurev.ento.43.1.243>

1453 202. Matyjaszczyk E, Karmilowicz E, Skrzecz I. How European Union accession and implementation of
1454 obligatory integrated pest management influenced forest protection against harmful insects: A case
1455 study from Poland. *Forest Ecology and Management* [Internet]. 2019;433:146–52. Available from:
1456 <http://www.sciencedirect.com/science/article/pii/S0378112718314968>

1457 203. Nichiforel L, Deuffic P, Thorsen BJ, Weiss G, Hujala T, Keary K, et al. Two decades of forest-
1458 related legislation changes in European countries analysed from a property rights perspective. *Forest*
1459 *Policy and Economics*. 2020;115:1–16.

1460

Appendix A: Spruce distribution and growing stock map: Methodology

We produced a map of Norway spruce growing stock in Europe by combining the live tree volume map of Moreno et al. [1] and the tree species cover map of Brus et al. [2]. The data and code can be found at figshare (<https://dx.doi.org/10.6084/m9.figshare.c.3463902>). The species distribution map is freely available at the European Forest Institute (<http://dataservices.efi.int/tree-species-map/register.php>). We transformed the volume map from a WGS84 projection with a resolution of 0.1333° to the ETRS_1989_LAEA projection of the tree species cover map with a resolution of 1×1km to facilitate further analyses.

We classified the spruce biomass map into the categories ‘low’ (up to 50 m³ ha⁻¹), ‘medium’ (51 to 100 m³ ha⁻¹) and ‘high’ (above 100 m³ ha⁻¹) biomass levels (Fig. 2).

All analyses were performed in ArcMap 10.6.1 [3]. Graphical outputs were produced in R [4] using packages sf [5], ggplot2 [6] and raster [7].

Appendix B: Probability maps of spruce stands being disturbed by bark beetles: Methodology

The annual probability of bark beetle damage (pBB) across Europe was calculated after Seidl et al. [8] on a 25×25 km grid. We used a constant stand age of 100 years, relative stocking density 100%, and spruce share 100%. Climate data was obtained from the Joint Research Centre (<http://agri4cast.jrc.ec.europa.eu/>). We calculated the base map for historical temperature conditions using climate data for the period 1979-1990, and modelled two climate change scenarios by adding 2 °C and 4 °C. This approach focuses on the sensitivities to temperature as it expects a unidirectional change in this parameter for the coming decades, while precipitation changes remain uncertain and will likely differ regionally.

$$pBB = \frac{e^{Z_{ijklm}}}{1 + e^{Z_{ijklm}}}$$

$$Z_{ijklm} = \mu + a_i + b_j + c_k + d_l + e_m + (a \times b)_{ij} + (a \times c)_{ik} + (a \times d)_{il} + (a \times e)_{im} + (b \times c)_{jk} + (b \times d)_{jl} + (b \times e)_{jm} + \varepsilon_{ijklm}$$

pBB	probability of bark beetle damage
Z_{ijklm}	linear combination of predictor variables
μ	intercept
a_i	logarithmic mean annual temperature (i = 2-15°C)
b_j	logarithmic mean annual precipitation (j = 500-2 000 mm)
c_k	stand age (k = 100)
d_l	relative stocking density (l = 1.0)
e_m	host tree share (m = 100 %)
ε_{ijklm}	error term

Class width in the presented maps (Fig. 3) was calculated as the difference between maximum and minimum pBB over all maps divided by the number of classes. The resulting probability categories were: 'very low' (pBB 0.3-1.96), 'low' (pBB 1.97-3.63), 'medium' (pBB 3.64-5.29), 'high' (pBB 5.3-6.95) and 'very high' (pBB 6.96-8.63).

Appendix C: Biomass of spruce at risk in Europe

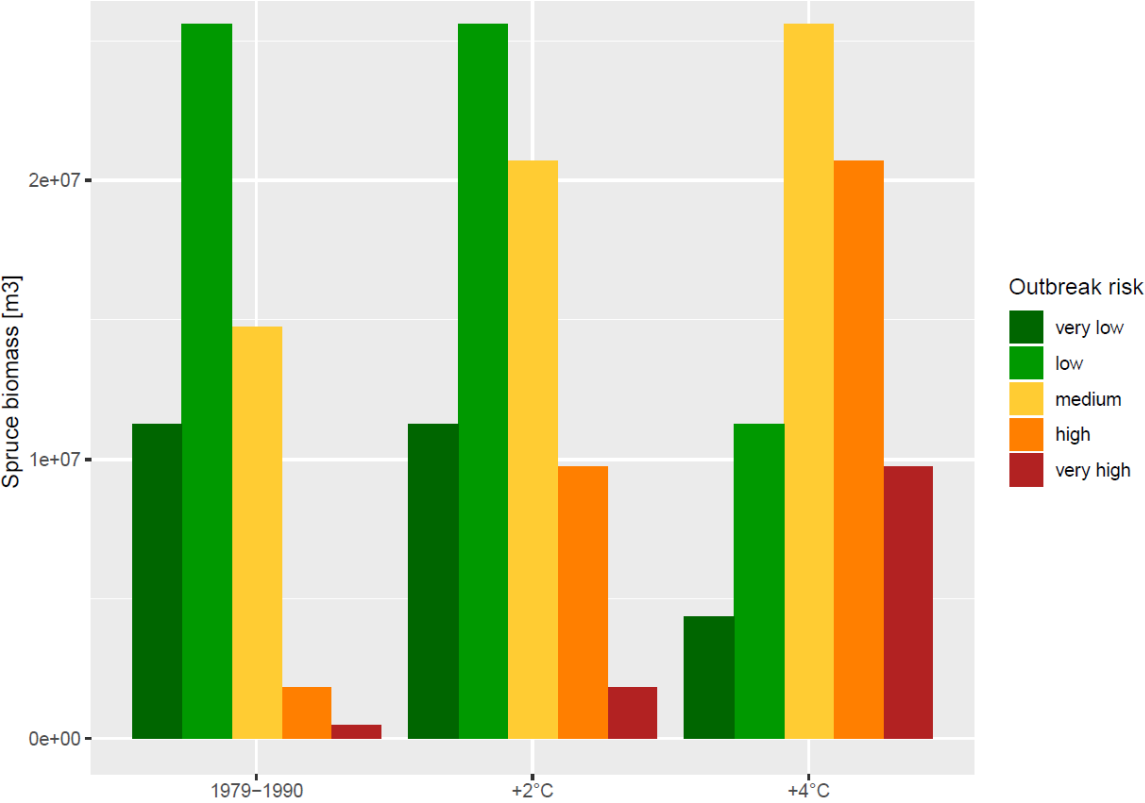


Fig. C1 Absolute volume of Norway spruce in different outbreak risk classes across different temperature conditions. The graph is complementary to Fig. 3 in the main text.

Appendix D: Spruce growing stock in Europe's protected areas

Proportions of spruce growing stock inside and outside protected areas were calculated by overlaying the spruce distribution map (Appendix A) with the World Database on Protected Areas (WDPA) acquired from the Protected Planet network [9]. Protected areas included in the analysis had the following statuses: designated, inscribed, adopted and established. Further, we selected only those areas that were predominantly or entirely terrestrial. We calculated spruce growing stock for two different categories of protected areas:

- 1) Highly protected areas: IUCN categories Ia Strict Nature Reserve, Ib Wilderness area, and II National Park
- 2) Protected areas: IUCN categories Ia Strict Nature Reserve, Ib Wilderness area, II National Park, III Natural Monument or Feature, IV Habitat/Species Management Area, V Protected Landscape/Seascape, VI Protected area with sustainable use of natural resources

Table D1 Spruce growing stock inside and outside protected areas

	Spruce volume (million m ³)	Spruce volume (%)
Total spruce volume	6 987	100
Spruce volume inside protected areas	1 645	23.5
Spruce volume inside highly protected areas	250	3.6
Spruce volume outside protected areas	5 342	76.5

Further, we calculated the number and area of protected areas in Europe falling into the distributional range of spruce in Europe (Appendix A). To identify the distributional range of spruce, we selected areas containing more than 1 m³ha⁻¹ of spruce.

Table D2 Number and area of protected areas inside and outside spruce distribution range

	Total number	No. within spruce range	Total area (km ²)	Area within spruce range (km ²)	No. %	Area %
Highly protected areas	7 134	6 341	179 345	131 593	88.88	73.37
Protected areas	63 463	47 723	696 816	535 902	75.20	76.91

1528 **Appendix E: Main items of the comprehensive outbreak management**
1529 **framework**

PREPAREDNESS		
#	Tools & Measures	Description
1.1	Improving education	Development of new curricula, and intensive education and training at all levels of forest policy- and decision-making.
1.2	Strengthening international collaboration	The transboundary scale of outbreaks and the potential introduction and spread of invasive pests require strengthened international collaboration on data and knowledge sharing, pest monitoring and crises management.
1.3	Increasing knowledge transfer and evidence-based decision making	Intensifying outbreaks are increasingly questioning the efficiency of traditional approaches to controlling outbreaks. There is a need for improved knowledge transfer from science to policy, legislation and practical management, as well as the development of best practice examples, to improve management of bark beetle populations.
1.4	Developing effective crises management programmes	Outbreaks occurring at national or supranational scales require well-prepared cross-sectoral responses (forestry, environment, finance, transportation, public security, etc.).
1.5	Developing zonation for nature conservation areas	Landscape-level planning in nature conservation areas should include adequate buffer zones to prevent dispersal of beetles into adjacent managed forests.
1.6	Maintaining multi-stakeholder dialogue	Dialogue should be maintained with all stakeholders involved in outbreak management or otherwise concerned with the forest and its development to increase the efficiency of measures, acceptance of the final outcome, and mitigate the risk of societal conflicts.
1.7	Building relationships with local communities	Building relationships with local communities and clearly communicating risks and potential countermeasures prior to outbreaks lends legitimacy to outbreak management and reduces the risk of societal conflicts.
1.8	Improving and/or establishing systems for monitoring forest susceptibility to disturbance and the dynamics of pest populations	Timely and efficient implementation of management actions require early detection of highly susceptible forest conditions, climatic extreme events that could trigger pest outbreaks, quantitative modelling and sampling of pest densities, and detecting the appearance of new pests.
1.9	Maintain sufficient levels of well-trained professionals	Employment levels in forestry are going down, yet challenges - such as dealing with bark beetle outbreaks - are increasing. In order to be prepared to deal with these challenges it is important to have well-trained forestry personnel on site that knows the local conditions.
1.10	Supporting advanced regeneration	Maintaining a vigorous advanced spruce regeneration facilitates a faster recovery of forest cover after a disturbance event.
1.11	Maintain sufficient nursery capacity	Greatly increased demands on reproductive material of suitable species and provenances after large-scale bark beetle

		disturbances may exceed the existing capacity of nurseries and could result in insufficient regeneration of disturbed areas.
1.12	Developing and maintaining an adequate forest road network	A sufficient forest road network is needed for small-scale interventions, resilience-oriented management, as well as efficient detection and removal of infested trees.
1.13	Increasing timber storage capacities	Sufficient facilities for wet storage of timber function as a supply buffer after windthrows and bark beetle outbreaks by preventing large quantities of timber to flood the market.

1530

1531

PREVENTION		
#	Tools & Measures	Description
2.1	Developing early-warning systems and integrating them in outbreak management	Development and maintenance of early-warning systems based on near-real time weather data, automated beetle monitoring, and/ or remote sensing data helps to identify areas with a high risk of bark beetle attacks, and to implement targeted prevention measures.
2.2	Coordinating beetle management across the landscape	Effective management of outbreaks is often complicated in multi-owner landscapes. Plans for coordinated management actions across property boundaries is needed to prevent outbreaks to spread.
2.3	Decreasing landscape-scale host connectivity	Aim to reduce the landscape-scale connectivity of susceptible hosts by implementing targeted landscape management measures that contain the spread of beetles from individual attack spots.
2.4	Use pheromone traps to monitor beetle populations and potential invasions	Pheromone traps can be efficiently used to monitor beetle populations and inform management decisions on timing and intensity of control measures.
2.5	Maintaining compositionally and structurally diverse stands	Mixed stands with a complex vertical and horizontal structure tend to be less likely to generate outbreaks and generally exhibit a higher survival rate under compounding disturbances than monospecific stands of homogeneous structure.
2.6	Reducing the rotation period	Tree vulnerability to wind and bark beetle damage increases with age and tree size. Reducing the area of susceptible age classes reduces the overall outbreak risk.
2.7	Increasing host tree resistance by thinning	Silvicultural treatments that reduce competition between trees can increase tree vigour and resistance against bark beetles.
2.8	Early detection of infested trees	A prerequisite for efficient sanitation felling is the ability to detect infested trees early (in the green attack stage) using a range of terrestrial and remote sensing approaches.
2.9	Reducing outbreak risks by sanitation felling	Removing infested trees from the forest while the beetle brood is still inside can reduce beetle populations, maintain forest health, and decrease outbreak risks. Sanitation harvest of windfelled trees to prevent build-up of beetle populations is also effective.
2.10	Preventing beetle spread from felled trees and logs	Mechanical or chemical treatment of infested windfalls and logs can prevent beetles from leaving the trees and infesting live trees. Another option is the timely removal of infested trees from the forest.
2.11	Creating habitats for the natural enemies of bark beetles	Bark beetles have a number of natural enemies (birds, predatory beetles, etc.). Creating diverse stands with favourable habitat conditions for natural enemies can reduce beetle populations and reduce outbreak risks.

RESPONSE		
#	Tools & Measures	Description
3.1	Salvage logging	Salvage logging is the removal of infested, windfelled or otherwise damaged trees with the primary intention to recover economic losses. Salvaging needs to take place before timber quality deteriorates. Potential negative impacts of salvage logging on biodiversity should be considered.
3.2	Reducing planned harvests	A reduction of planned harvests can free up capacities for logging of beetle-killed timber and mitigate adverse effects of a temporary timber surplus on the market.
3.3	Subsidising response measures	Responses to a large-scale bark beetle outbreak may require substantial investments, which could exceed the capacity of forest owners. Subsidizing timber transport, storage, and other components of outbreak management can mitigate economic impacts and increase the efficiency of the response actions.
3.4	Considering “no management” as a possible response option	No management needs to be considered as a possible response option in situations where salvaging is not economically viable and extensive sanitary felling, mass-trapping or other measures do not hold promise of containing the outbreak. In such situations, benefits from the retention of biological legacies should be exploited.
3.5	Sanitation logging	Detection and removal of infested trees can be applied to prevent the spread of infestations, particularly for small infestation spots. Trees damaged by wind or other abiotic factors should be prioritized because they have weakened defences against bark beetles and serve as multipliers for beetle populations. Hazard-rating and other types of models can be used to optimize sanitation felling and reduce the connectivity of host trees and beetle populations.
3.6	Increasing multi-stakeholder dialogue and communicating response strategies to the public	Maintaining a good dialogue with all stakeholders involved in outbreak management will improve the efficiency of control measures and the acceptance of final outcomes. Use of the media to communicate management strategies and progress to the general public will raise awareness and reduce the risk of negative responses towards management actions.

1533

1534

RECOVERY		
#	Tools & Measures	Description
4.1	Fostering diverse stands	During the recovery phase there are excellent opportunities to influence the tree species composition of the regeneration, thereby reducing the vulnerability to future outbreaks.
4.2	Supporting advanced regeneration	Advanced regeneration present on site should be spared during logging operations, as it facilitates a faster recovery of the forest canopy and restores the microclimate.
4.3	Harnessing early-successional species	Regeneration of early-successional species such as birch, poplar, and larch can swiftly establish a new canopy. Commercially more important species can later be planted under this canopy.
4.4	Considering natural recovery processes	Forests have a high capacity to naturally recover from disturbances. Low-cost natural stand recovery options can be considered in areas where a speedy recovery of spruce forests is not of paramount importance and where locally relevant ecosystem services are also provided by naturally regenerating tree species.
4.5	Planting seedlings on disturbed sites	Planting seedlings leads to a quicker recovery of tree cover and gives more control over the future tree species composition.
4.6	Protecting the regeneration against adverse effects	Protection of seedlings against animal browsing and competing vegetation improves the growth rate and quality (shape) of the trees.
4.7	Integrating disturbance legacies into the recovering forest	Disturbance legacies, such as remaining live trees and standing and downed deadwood, can be integrated into the recovering forest rather than being completely removed. Such legacies support the regenerating tree cohort and increase the structural diversity of the recovering stand.
4.8	Reducing browsing by ungulates	Browsing by ungulates is a key limiting factor for regeneration of disturbed forests in many parts of Europe. Ungulate densities should thus be regulated to levels where they do not hamper a successful and swift regeneration of desired tree species.
4.9	Maintaining multi-stakeholder dialogue	Maintaining the dialogue with all stakeholders involved in outbreak management makes it possible to track changing risk perceptions and responses.
4.10	Forest insurance	Forest owners can be insured against certain kinds of forest damage and loss of future income in some countries (e.g. Finland and Norway). This provides an effective distribution of economic risks from disturbances among forest owners.
4.11	Subsidising recovery measures	Recovery from large-scale bark beetle outbreaks may require substantial investments, which may exceed the capacity of forest owners. Recovery actions can be made more efficient by subsidizing afforestation with tree species mixtures, tree species that are well adapted to local climates, protection measures against browsing, etc.

1535

1536

Appendix references

1. Moreno A, Neumann M, Hasenauer H. Forest structures across Europe. *Geoscience Data Journal*. 2017;4:17–28.
2. Brus DJ, Hengeveld GM, Walvoort DJJ, Goedhart PW, Heidema AH, Nabuurs GJ, et al. Statistical mapping of tree species over Europe. *European Journal of Forest Research*. 2012;131:145–57.
3. ESRI. ArcGIS Desktop. Redlands, CA: Environmental System research Institute; 2011.
4. R Core Team. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing; 2019.
5. Pebesma E. sf: Simple features for R [Internet]. 2018. p. 436. Available from: <https://cran.r-project.org/package=sf>. R packageversion 0.6-1.
6. Wickham H. Ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag; 2016. p. 439.
7. Hijmans RJ. Raster: Geographic Data Analysis and Modeling [Internet]. 2016. p. 444. Available from: <https://cran.r-project.org/package=raster>
8. Seidl R, Schelhaas MJ, Lindner M, Lexer MJ. Modelling bark beetle disturbances in a large scale forest scenario model to assess climate change impacts and evaluate adaptive management strategies. *Regional Environmental Change*. 2009;9:101–19.
9. UNEP-WCMC, IUCN. Protected Planet: [WDPA_Jun2020-shapefile.zip; The World Database on Protected Areas (WDPA)/The Global Database on Protected Areas Management Effectiveness (GD-PAME)] [On-line]. Cambridge, UK: UNEP-WCMC and IUCN. Available at: www.protectedplanet.net. 2020.