Journal of Applied Ecology

British Ecological Society

Journal of Applied Ecology 2016 doi: 10.1111/1365-2664.12782

REVIEW

Managing bark beetle impacts on ecosystems and society: priority questions to motivate future research

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Summary

1. Recent bark beetle outbreaks in North America and Europe have impacted forested landscapes and the provisioning of critical ecosystem services. The scale and intensity of many recent outbreaks are widely believed to be unprecedented.

2. The effects of bark beetle outbreaks on ecosystems are often measured in terms of area affected, host tree mortality rates, and alterations to forest structure and composition.

3. Impacts to human systems focus on changes in property valuation, infrastructure damage from falling trees, landscape aesthetics, and the quality and quantity of timber and water resources.

4. To advance our understanding of bark beetle impacts, we assembled a team of ecologists, land managers and social scientists to participate in a research prioritization workshop.

5. *Synthesis and applications*. We identified 25 key questions by using an established methodology to identify priorities for research into the impacts of bark beetles. Our efforts emphasize the need to improve outbreak monitoring and detection, educate the public on the ecological role of bark beetles, and develop integrated metrics that facilitate comparison of ecosystem services across sites.

Key-words: bark beetles, conifer forests, *Dendroctonus*, ecosystem services, forest disturbance, horizon scanning, *Ips*, outbreaks, resilience, social–ecological systems

Introduction

Native bark beetles (Coleoptera: Curculionidae, Scolytinae) are important disturbance agents in conifer forests. Since the late 1970s, irruptive outbreaks of these insects have affected millions of hectares of trees in North America and Europe, with cascading consequences for ecological systems (Bentz *et al*. 2010; Seidl *et al*. 2014). Changes to landscapes can strongly impact societal groups who value affected forests and/or experience a disruption in ecosystem services (Müller & Job 2009). Important feedbacks occur when people affected by bark beetle outbreaks react and respond to altered forest conditions, which can produce additional changes to forests and

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society. A holistic understanding of the consequences of bark beetle outbreaks requires an integrated social–ecological perspective that accounts for both the direct and indirect impacts of bark beetles on ecosystems as well as the outcomes experienced by society.

World-wide there are approximately 6000 described species of bark and ambrosia beetles (Wood & Bright 1992), and less than 1% are known to cause widespread tree mortality. In the Northern Hemisphere, the genera *Dendroctonus*, *Ips* and *Scolytus* have long been recognized as primary agents that cause tree mortality (Table 1). For example, in western North America (WNA) recent outbreaks of mountain pine beetle *Dendroctonus ponderosae* Hopkins (MPB) have been severe, long-lasting and well-documented (Meddens, Hicke & Ferguson 2012). In British Columbia, Canada, 710 Mm^3 of lodgepole pine *Pinus contorta* Douglas, roughly the volumetric equivalent of 100 times the amount of concrete used to construct New York City, have been killed by MPB over the last decade representing a loss of >50% of the total merchantable pine in that province (British Columbia Ministry of Forests 2012). Outbreaks of similar magnitude have never been documented in WNA for any bark beetle species (Bentz *et al.* 2009).

In Europe, the Eurasian spruce bark beetle *Ips typographus* L. (ESBB) is regarded as the most important mortality agent of Norway spruce *Picea abies* L. Karst, an indigenous tree species that has been planted widely for commercial timber production beyond its native range (Christiansen & Bakke 1988). It is estimated that ESBB caused 8% of all tree mortality that occurred between 1850 and 2000 (Schelhaas, Nabuurs & Schuck 2003). Outbreaks of ESBB are frequently triggered in the aftermath of severe wind events, and in recent decades following several notable storms, wind-damaged Norway spruce were later colonized by ESBB (Komonen, Schroeder & Weslien 2011). These outbreaks include well-studied epidemics in Scandinavia during the 1970s (Eidmann 1992); Germany's Bavarian Forest National Park (Müller, Job & Mayer 2008) and adjacent Šumava Mountains in Czech Republic (Jonášová & Prach 2004) during the 1990s; and the Tatra Mountains of Slovakia and Poland during the 1990s and 2000s (Grodzki *et al.* 2010). Model simulations (Seidl *et al.* 2008) indicate that ESBB will cause extensive damage to spruce forests during the next 100 years in response to warm and dry climate conditions, which accelerates ESBB voltinism (Jönsson *et al.* 2009) and decreases tree vigour in response to ESBB attack, respectively (Marini *et al.* 2012).

Forests provide many goods and services that have ecological, economic and social value, often referred to as

Table 1. Some notable bark beetles capable of causing substantial levels of tree mortality in conifer forests within their native ranges as catalogued by Wood & Bright (1992)

Common name	Scientific name	Frequently colonized host(s)	Native range
Arizona fivespined ips	*Ips lecontei*	*P. ponderosa*	North America
California fivespined ips	*Ips paraconfusus*	*P. attenuata, P. coulteri, P. lambertiana, P. ponderosa, P. radiata*	North America
Douglas-fir beetle	*Dendroctonus pseudotsugae*	*Pseudotsuga menziesii*	North America
Eastern fivespined ips	*Ips grandicollis*	*P. echinata, P. elliottii, P. taeda, P. virginiana*	North America
Eastern larch beetle	*Dendroctonus simplex*	*Larix laricina*	North America
Six-spined ips	*Ips calligraphus*	*P. echinata, P. elliotti, P. ponderosa, P. taeda, P. virginiana*	North America
Eurasian spruce bark beetle	*Ips typographus*	*Picea abies, Pi. orientalis, Pi. yezoensis, occasionally P. sylvestris*	Eurasia
Fir engraver	*Scolytus ventralis*	*Abies concolor, A. grandis, A. magnifica*	North America
Jeffrey pine beetle	*Dendroctonus jeffreyi*	*P. jeffreyi*	North America
Larger Mexican pine beetle	*Dendroctonus approximatus*	*P. ponderosa*	North America
Mountain pine beetle	*Dendroctonus ponderosae*	*P. albicaulis, P. contorta, P. flexilis, P. lambertiana, P. monticola, P. ponderosa*	North America
Northern spruce engraver	*Ips perturbatus*	*Pi. glauca, Picea x lutzii, Pi. mariana*	North America
Pine engraver	*Ips pini*	*P. contorta, P. jeffreyi, P. lambertiana, P. ponderosa, P. resinosa, P. strobus*	North America
Pinyon ips	*Ips confusus*	*P. edulis, P. monophylla*	North America
Roundheaded pine beetle	*Dendroctonus adjunctus*	*P. arizonica, P. engelmannii, P. flexilis, P. leiophylla, P. ponderosa, P. strobiformis*	North America
Six-toothed bark beetle	*Ips sexdentatus*	*P. heldreichii, P. nigra, P. pinaster, P. sylvestris, Pi. orientalis*	Eurasia
Southern pine beetle	*Dendroctonus frontalis*	*P. echinata, P. engelmannii, P. leiophylla, P. ponderosa, P. rigida, P. taeda, P. virginiana*	North America
Great spruce bark beetle	*Dendroctonus micans* European spruce beetle	*P. sylvestris, Pi. abies*	Eurasia
Spruce beetle	*Dendroctonus rufipennis*	*Pi. engelmannii, Pi. glauca, Pi. pungens, Pi. sitchensis*	North America
Western balsam bark beetle	*Dryocoetes confusus*	*A. lasiocarpa*	North America
Western pine beetle	*Dendroctonus brevicomis*	*P. coulteri, P. ponderosa*	North America

ecosystem services (MA 2005). Ecosystem services from forests include societal provisions such as air purification, control of water run-off and soil erosion, wood and other forest products, and regulation of climate through carbon storage and biophysical processes that affect planetary energy balance. Extensive tree mortality associated with bark beetle outbreaks affects a range of ecosystem services at local to regional scales, including property values, merchantable timber, landscape aesthetics, recreational experiences and tourism (Flint, McFarlane & Muller 2009).

Background

We were motivated by past exercises (Negrón *et al.* 2008) to identify research priorities and our efforts rely on an adapted version of the methodology introduced by Sutherland *et al.* (2006). We modified Sutherland's approach by integrating our exercise within the framework of a professional conference meeting (the Western Forest Insect Work Conference). We present results from a 2-day workshop held in Santa Fe, New Mexico, USA, on 2–3 April 2015 attended by ecologists, land managers and social scientists from North America and Europe. Participants gave 'lightning talks' during an organized symposium. Questions raised during the symposium were pooled and screened to eliminate redundancy and favour those questions that might be applied broadly to research on bark beetles. All workshop participants voted to reduce the list of questions to determine key research frontiers. Though we focused on bark beetles native to North America and Europe, which aligns well with our collective expertise, our methods are likely adaptable to other systems and forest disturbance types (e.g. wildfire).

Results

Below we discuss 25 research questions that our team identified as essential to support advances in academic research and land management efforts. These priority questions are presented in Table 2 and referenced throughout the balance of the manuscript by number (e.g. Q1). Questions were not ranked but organized thematically.

ECOLOGICAL RESPONSES

To monitor the spatial and temporal dynamics of bark beetle infestations, accurate detection and survey methods are required. In many European countries, infested

Table 2. Key research questions identified during our prioritization exercise

Ecological Responses
Q1. What methods can be used to refine current monitoring of outbreaks?
Q2. What palaeoenvironmental methods can be refined and/or merged to reconstruct past outbreaks?
Q3. What are the characteristics of past outbreaks and how do they compare to current outbreaks?
Q4. How do environmental legacies, such as land-use history and antecedent disturbances, influence host susceptibility to outbreaks?
Q5. How do climate dynamics influence past, present and future outbreaks?
Q6. What are the consequences and associated uncertainties of beetle outbreaks on biogeochemistry, future disturbances, biodiversity and hydrology?
Q7. When and where will outbreaks occur, and what are the likely consequences for native beetles on current and novel hosts?
Q8. How can predictive models be used help to forecast where future outbreaks will occur?
Q9. How will genetic adaptations over time modify outbreak behaviour and forest impacts?
Social–Environmental Linkages
Q10. What processes confer or erode resilience of forest ecosystems and the provisioning of ecosystem services to bark beetle outbreaks?
Q11. What are the implications of bark beetle range expansion into new locations, including public and private lands, cities and peri-urban landscapes?
Q12. What actions can land managers, policymakers and stakeholders take to bolster the adaptive capacity of social–ecological systems to bark beetle outbreaks?
Q13. How do we quantitatively measure the effectiveness of management strategies intended to increase resistance and/or resilience?
Q14. How do bark beetles affect ecosystem services and which ecosystems services are most sensitive to outbreaks?
Q15. What ecosystem services are most valued by forest users and are there conflicting interests among user groups that influence management of ecosystem services?
Q16. What are the economic impacts of changed ecosystem services as a result of beetle outbreaks?
Human Perceptions
Q17. How can the apparent disconnect be bridged among science, popular media and public perception about bark beetle disturbances?
Q18. What management practices/tools are (or are not) socially acceptable to reduce future outbreaks and accelerate forest recovery after the disturbance?
Q19. How do we measure the efficacy of knowledge transfer across stakeholders in a manner that is contextually specific, yet applicable to meet local, national and international need?
Q20. How does current science and the communication of that science influence or modify human values or behaviour?
Q21. How do people react to and organize collective responses to bark beetle outbreaks?
Q22. How do different silivicultural treatments influence public sentiment about bark beetle outbreaks?
Q23. How will better information about economic impacts of outbreaks influence public opinion?
Q24. Which developing or emerging economic metrics and methods help to better assess the impacts of bark beetle outbreaks?
Q25. How do public perceptions of outbreak impacts differ among humanized to wilderness landscapes?

trees are detected by trained field observers, called *sawdusters*, who during outbreaks are employed throughout the year to systematically locate infested trees (Fettig & Hilszczański 2015). In WNA, remote sensing technology is often utilized due to the vast landscapes that must be surveilled. For example, aerial detection surveys (ADS) are regularly conducted to detect infestations (Fig. 1a). ADS has several limitations: flights are not always conducted annually; the spatial extent and severity of the infestation are mapped approximately; and considerable variability exists among different technicians (Fettig & Hilszczański 2015). Therefore, measurements of interannual tree mortality, while essential for mitigating outbreaks, are often uncertain. Recently, high-resolution (0·3–1 m) aerial imagery has performed well in classifying MPB attack in low- to moderate-density forests (Gartner *et al.* 2015). In some instances, high-resolution satellite imagery, such as GeoEye-1 (Dennison, Brunelle & Carter 2010), provides detailed information in space and time, but the cost and accessibility of these data are not generally practical for management applications. Some studies have used coarser resolution satellite imagery, such as Landsat, to map outbreak locations and associated tree mortality (Hais *et al.* 2009; Meigs *et al.* 2015), although widespread adoption of these methods has yet to occur. The use of drone aircraft, equipped with high-definition sensors and photographic equipment, offers a new platform for low-cost monitoring over small areas, such as high-value watersheds. However, it is unknown how this rapidly developing approach can be implemented and/or integrated with aerial and satellite imagery to improve detection and mapping (Q1).

A key uncertainty in bark beetle research is whether the synchronous, widespread outbreaks observed in recent decades have any precedence over multicentennial to millennial time-scales (Q2). To understand past outbreaks, ecological records from natural archives, such as tree-ring and lake sediment cores, are used (Fig. 1b,c). Tree-ring records are annually resolved, span decades to centuries and provide information about individual trees. In some ecosystems, tree-ring research has been applied to landscapes to produce estimates of outbreak return intervals. For example, in Rocky Mountain ecosystems dominated by Engelmann spruce *Picea engelmannii* Parry ex. Engelm., the average return interval for spruce beetle *Dendroctonus rufipennis* Kirby (SB) outbreaks is ca. 120 years (Veblen *et al.* 1994). In Alaska, USA Sherriff, Berg & Miller (2011) determined that SB outbreaks recur ca. 50–80 years in white spruce *P. glauca* Moench. In Europe, the return interval for ESBB is estimated to be

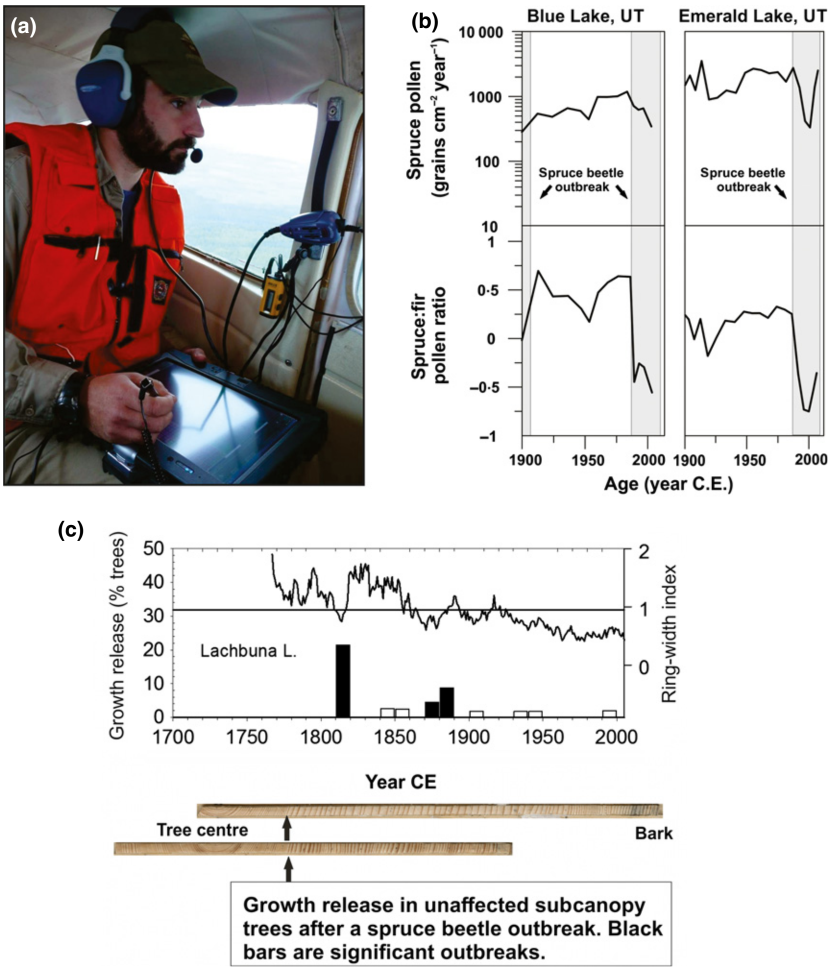

Fig. 1. Depiction of the methods used to monitor, detect and reconstruct bark beetle activity through (a) aerial detection surveys and the analysis of (b) lake sediments (Morris, DeRose & Brunelle 2015) and (c) tree-rings (Sherriff, Berg & Miller 2011).

ca. 70 years in Norway spruce (Trotsiuk *et al.* 2014). Although tree-ring records provide useful information about outbreak return intervals, inferring the severity and extent of past outbreaks is often challenging due to sample size limitations across landscapes (Eisenhart & Veblen 2000). Recent advances in reconstructing outbreak severity have been achieved using intensely gridded spatial sampling networks (Čada *et al.* 2016) and minimum site count thresholds to define severe outbreaks (O'Connor *et al.* 2015). Regional-scale syntheses of tree-ring records can facilitate reconstruction of the spatial dynamics of historic outbreaks to compare to the precedence of recent outbreaks (Jarvis & Kulakowski 2015).

Sediment cores collected from lakes can be used to reconstruct environmental conditions over centennial to millennial time-scales, extending knowledge about historic outbreaks well beyond the temporal range of tree-ring records. The unprecedented nature of recent bark beetle disturbances (Raffa *et al.* 2008) motivated efforts to develop data sets from sedimentary records, using pollen, biogeochemical metrics and the examination of preserved insect remains (Morris, McLauchlan & Higuera 2015). Palaeoenvironmental reconstructions of outbreaks may benefit from investigating newly developed ecological proxies, including ancient DNA, biomarkers, and the remains of beetle obligates, including blue-stain fungi (e.g. *Grosmannia clavigera*), mites and nematodes. Additionally, integrating sedimentary records with other ecological data sets, including tree-ring records, ADS, surface pollen and forest inventories (e.g. Seppä *et al.* 2009), may yield advances in detecting past outbreaks (Q3).

During recent centuries, livestock grazing, logging and fire suppression affected many forest types, especially xeric forests in WNA dominated by ponderosa pine *Pinus ponderosa* Douglas ex C.Lawson and piñon *Pinus edulis* Englm. The complex land-use histories of these forests enhanced fire hazard (Swetnam *et al.* 2016), and may have influenced recent outbreaks of several species of bark beetles, including piñon ips beetle *Ips confusus* LeConte. Research in southern WNA suggests that fire suppression during the 20th century promoted SB outbreaks (O'Connor *et al.* 2015). Recent studies demonstrate that time since disturbance, including stand-replacing fire and logging events, may be important in predicting susceptibility to bark beetle infestation (Bebi, Kulakowski & Veblen 2003; Morris, DeRose & Brunelle 2015) (Fig. 2). In both North America and Europe, stand structure is known to be an important driver of bark beetle infestations (Schmid & Frye 1977; Wermelinger 2004). The degree to which land-use activities, including afforestation, contributes to the severity of outbreaks is poorly understood but has the potential to be useful in budgeting for longer term dynamics in ecosystem services (Jeffers, Nogué & Willis 2015) and associated management strategies (Fettig *et al.* 2007) (Q4).

The role of climate change in recent decades is an important driver of modern outbreaks. Warming air temperatures have created an enlarged spatial footprint of suitable thermal habitat for bark beetles, and in some cases have enhanced reproductive capacity (Wermelinger & Seifert 1999) and facilitated historically novel host interactions (de la Giroday, Carroll & Aukema 2012). Increasing temperatures may also promote drought stress on host trees, thereby reducing their defensive capacity to repel colonizing bark beetles (Faccoli 2009; Kolb *et al.* 2016). Climate interactions with bark beetles that remain inadequately understood include understanding the role of increasing frequency of fire, wind, and drought disturbances on beetle populations as well as interactions with deteriorating air quality, elevated tropospheric ozone and increased atmospheric nitrogen deposition. Models forecast that warming temperatures will promote encroachment of bark beetles

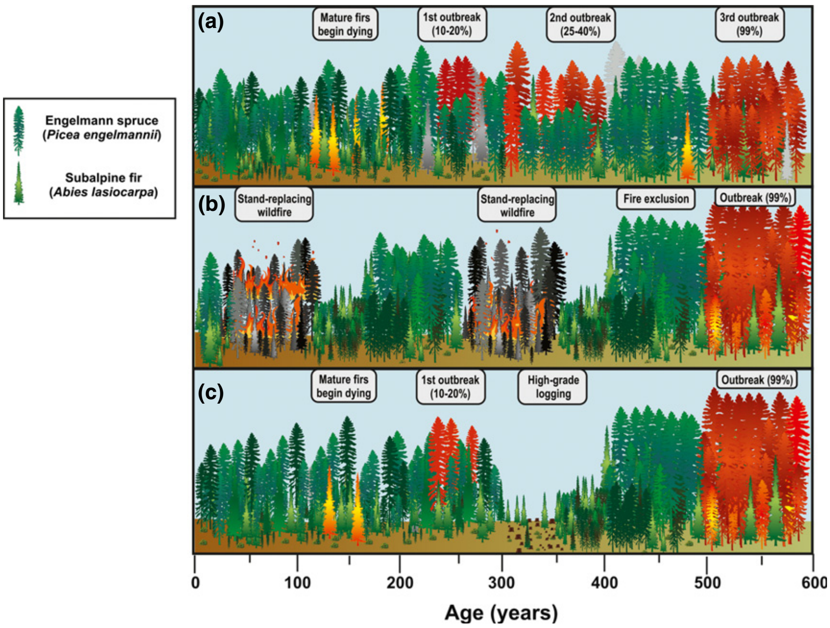

Fig. 2. Hypothetical successional trajectory of a Rocky Mountain subalpine forest composed of Engelmann spruce and subalpine fir to show interactions among disturbances that may lead to severe spruce beetle infestations. Panel a depicts a disturbance regime dominated by spruce beetle where successive, low-severity outbreaks culminate in a high-severity event as understorey spruce eventually achieve canopy dominance (Schmid & Frye 1977). Panel b shows a spruce–fir forest that was once maintained by recurrent, stand-replacing fire, which later became susceptible to a high-severity outbreak under fire suppression (O'Connor *et al.* 2015). Panel c shows how high-grade logging yields even-aged stands that are later at risk for a high-severity outbreak (Morris, DeRose & Brunelle 2015).

into historically novel ecosystems at high elevations and high latitudes (Bentz *et al.* 2010). However, few studies have fully integrated climate effects on beetles and host trees to assess the contribution of drivers to historical outbreaks and estimated the influences of projected climate change on future outbreaks. Furthermore, there is limited understanding of the importance of (potentially different) climate variables across a range of bark beetles, with the exception of a few well-studied species (MPB, ESBB) (Sambaraju *et al.* 2012; Weed *et al.* 2015). Some studies have investigated how subdecadal climate variability has influenced outbreaks (Macias-Fauria & Johnson 2009; Aakala *et al.* 2011), though understanding the impacts of broad-scale climate features on stand-level disturbances is challenging because moisture delivery and temperature fluctuations are often shaped by local topography and weather patterns (Q5).

Beetle-caused tree mortality has the potential to modify globally significant terrestrial carbon pools (Hicke *et al.* 2012a). Some evidence indicates that beetle-impacted forests may switch from net carbon sinks to net carbon sources (Kurz *et al.* 2008), but typically return to sinks within 5–20 years after undergoing an outbreak (Hansen 2014). Recent work suggests that outbreak impacts on other biogeochemical stocks are less than anticipated. For example, under high-severity MPB infestations stream nitrate concentrations were not significantly changed relative to pre-outbreak levels (Rhoades *et al.* 2013), despite elevated levels of total nitrogen and phosphorus in soils from needle fall (Clow *et al.* 2011). In Europe, Huber (2005) found evidence for enhanced nitrate leaching for 5 years after an ESBB outbreak, and Beudert *et al.* (2015) documented significant nitrate concentrations in surface run-off, but only temporarily. In all cases, drinking water quality generally remained below the limit recommended by the World Health Organization. However, the fate of many important nutrients following outbreaks remains largely uninvestigated (Q6).

Process and empirical models have been applied to forecast where future outbreaks might occur (e.g. DeRose *et al.* 2013), while other models predict the interactions of bark beetles with other disturbance types (Temperli, Bugmann & Elkin 2013). Despite the diversity of beetle species and forest types at risk (Table 1), the majority of modelling efforts have centred on a few bark beetles in spruce and pine systems. Therefore, additional studies are necessary for other species, such as the six-toothed bark beetle *Ips sexdentatus* Boerner and great spruce bark beetle *Dendroctonus micans* Kugelann in Europe, which have the potential to heavily impact Norway spruce forests. The great spruce bark beetle expanded its Eurasian range historically, and outbreaks have been observed in recent decades at the margins of its distribution (Grégoire 1988). Research is especially needed in systems where native and invasive beetle species could infest historically novel hosts and habitats (Seybold, Penrose & Graves 2016) (Q7). In management planning, hazard rating systems are used to quantify risk factors for bark beetle outbreaks. Such systems have been developed for some forest types (e.g. Netherer & Nopp-Mayr 2005), but are currently lacking for many others. Developing new hazard rating systems and integrating them with process and empirical models for anticipating future outbreaks are of potential use to management agencies (Q8).

Bark beetles carry an array of phoretic organisms, many of which exhibit complex interactions that can contribute to the success of beetle populations. For example, upon invading a potential host tree, MPB inoculates the phloem tissue with fungi, *Grosmannia clavigera* Rob.-Jeffr. & R.W. Davidson, and *Ophiostoma montium* Syd & P.Syd., which provide vital nutrients to feed larvae. While both fungi are important, *G. clavigera* supports higher levels of brood production (Bleiker & Six 2007). Each fungus has different thermal ranges for optimal growth (Rice, Thormann & Langor 2008), and seasonal temperature dictates which fungal species are ultimately vectored by dispersing beetles (Six & Bentz 2007). Shifts in temperature could indirectly affect MPB population success through changes in the presence of these fungi as well as that of other symbionts, but the dynamics between most bark beetles and their phoretic assemblages are not yet well understood (Q9).

SOCIAL–ENVIRONMENTAL LINKAGES

Resilience is an important concept for assessing the influence of bark beetle disturbances on environmental conditions, resource management policies and economic markets (Seidl 2014). In ecology, resilience is often defined as the capacity for a system to absorb perturbation while maintaining fundamentally similar structure and function to its pre-disturbed condition (Gunderson 2000). We modify this definition to encompass the capability of a coupled social–ecological system to recuperate the environmental, economic and aesthetic properties that sustained the system prior to bark beetle outbreak. How social and ecological factors, feedbacks and processes operate individually and in combination with promote or erode resilience is currently not well understood. Therefore, the degree to which management policies and market forces can help to mitigate undesirable social and ecological outcomes, and presumably promote a return to pre-disturbed conditions, requires new research (Q10).

In a warming climate, bark beetles are likely to encroach into new habitats (Bentz *et al.* 2010) to affect human populations and challenge management paradigms in novel systems. For example, MPB has expanded eastwards and northwards into the Canadian boreal forest, successfully colonizing and reproducing in the naïve host jack pine *Pinus banksiana* Lamb., potentially providing a conduit for other novel host interactions in eastern North America (de la Giroday, Carroll & Aukema 2012). The interaction of outbreaks with social values in naïve communities is a critical knowledge gap in bark beetle research (Q11). Currently, pre-emptive management strategies tend to favour silivicultural treatments that focus on increasing forest resilience (or resistance) to beetle infestation (DeRose & Long 2014) and studies investigating the outcomes of treatment versus no-treatment strategies are of general interest to managers (Grodzki *et al*. 2006; Trzcinski & Reid 2008). Following outbreaks, societal expectations, policy and management strategies guide a variety of responses which may (or may not) be effective at reaching the intended goals of local, regional and nationwide mandates. Management responses can be influenced by public sentiment, which may include removal of dead trees to reduce perceived wildfire risk and to improve public safety from treefalls (Q12). Developing management strategies sensitive to social and ecological resilience requires an empirical evaluation of current management strategies, the efficacy of those strategies, the capacity of an agency to adopt new strategies, and the real and perceived barriers that constrain implementation of these adaptive strategies (Q13).

Tree mortality caused by bark beetle outbreaks modifies the ecosystem services provided by forests and future research may benefit from considering ecosystem response as a function of time since disturbance. For example, post-outbreak forests can be more (or less) fire-prone compared with unaffected forests, which depends on how recently an outbreak occurred and the resulting forest structure (Hicke *et al*. 2012b). In addition, heterogeneous tree mortality across landscapes suggests that outbreak severity is important when assessing changes in ecosystem services. Controlling for and reporting variability in ecosystem services over space and longer temporal scales are critical for interpreting results and for comparing the impacts of bark beetles across systems and studies. There is a growing need to fully document and monetize the impacts of outbreaks on ecosystem services, especially to include decay functions that account for time since disturbance (Q14).

Societal impacts of bark beetle outbreaks can be positive or negative. For example, outbreaks can increase water yield (Bearup *et al*. 2014), which is generally perceived as a net positive for society. Other benefits to society include improved livestock forage, wildlife viewing and hunting due to population increases of some big game species (Saab *et al*. 2014). Yet, bark beetles can also cause deleterious effects to human health (Embrey, Remais & Hess 2012), including diminished air quality (Amin *et al*. 2012) and increased nutrient levels in surface water (Mikkelson *et al*. 2013), though elevated nutrient concentrations after outbreaks may not necessarily exceed drinking water standards (Huber *et al*. 2004). Other negative impacts include real or perceived increases in wildfire risk, perhaps leading to modification of wildfire management strategies (Jenkins *et al*. 2014). Additionally, increased potential for infrastructure damage from falling trees may adversely impact society. Improved understanding of the social value of ecosystem services affected by bark beetle outbreaks is also necessary (Q15). The monetary and social value of most ecosystem services impacted by bark beetles remains unquantified, though a recent synthesis provides a framework to direct future research (Maguire *et al*. 2015) (Q16).

HUMAN PERCEPTIONS

The conspicuous changes to landscape aesthetics following severe outbreaks are arguably the primary point of interaction with society. In survey research conducted on three National Forests affected by MPB in Colorado and Wyoming, value orientations were explored by Clement & Cheng (2011) who asked respondents to rank the importance of aesthetic and recreation values related to forests. Respondents in all three National Forests gave their highest rating for 'life-sustaining value', defined as 'I value these forests because they help produce, preserve, clean, and renew air, soil, and water'. Examining the same study area, Czaja *et al*. (2012) reported that the majority of respondents were generally supportive of management practices and indicated that they held an attitude of 'do what you need to save the forest'. Considering public perceptions in advance of bark beetle outbreaks will help to understand how management strategies in novel systems may be perceived (Q17).

It is important for land managers to have access to information that provides insight into how the public evaluates and responds to outbreak policies and actions (Q18). For example, public educational level helps to shape perceptions of forest recovery and expectations for management policy. In a survey of landowners in Virginia, USA, college-educated residents were more willing than non-college-educated residents to participate in the state's Southern Pine Beetle Prevention Program (Watson *et al*. 2013). This programme concentrates on pre-commercial thinning to reduce forest susceptibility to southern pine beetle *Dendroctonus frontalis* Zimmerman infestation. If prevention measures fail to subdue the beetle infestation, affected forests are often perceived as degraded ecosystems that will require restoration strategies. However, in most cases a forest can be expected to eventually recover from an outbreak in the absence of human intervention (Burton 2006). Flint, McFarlane & Muller (2009) emphasize the importance of understanding how the communication of science and management strategies influences public perceptions of bark beetles and associated management efforts (Q19). It is vital to prioritize research that investigates how media and communication of science and management influence human perceptions (Q20).

Public attitudes and values influence behaviours, including support for management actions and policies aimed to address bark beetle disturbance. Although public opinion is an important factor in shaping policy (Wellstead, Davidson & Stedman 2006), few studies have evaluated the social acceptance of various management strategies in response to outbreaks (Q21). For example, McFarlane, Stumpf-Allen

& Watson (2006) examined public attitudes towards MPB infestations in two national parks in western Canada. Most visitors reported ‘allowing the outbreak to follow its course without intervention’ was an unacceptable option. However, this perspective differs from attitudes in Germany in reaction to an ESBB outbreak in Bavarian Forest National Park, where respondents reported a neutral attitude towards the disturbance, and were disinclined to support control measures (Müller & Job 2009). In Colorado and Wyoming, a majority of respondents favoured fuel reduction programmes, treatments to benefit wildlife habitat via salvage logging, but were less supportive of salvage logging conducted purely for economic benefit (Clement & Cheng 2011). Future studies should explore how perceptions of various treatments differ among communities and user groups (Q22).

Ecosystem change is generally considered to have a negative impact on property values (Price, McCollum & Berrens 2010). Following outbreaks, reductions in property values are a significant concern in communities that experienced a change in surroundings from living to dead forest. Homeowners are often concerned about treefalls, loss of privacy from neighbours and increased risk of wildfire. However, an emerging paradigm suggests that trade-offs occur between the ecosystem services that are either enhanced or degraded by the disturbance. For example, homeowners in some settings have realized net increases in real estate values due to enhanced viewsheds or successional transitions towards more appealing dominant tree species (Hansen & Naughton 2013; Cohen *et al.* 2014). Fluctuations in property values and other economic indices from outbreaks are likely regionally and culturally specific, and quantifying these impacts also requires evaluating the ecosystem services affected by outbreaks and their dynamics over time, including time since disturbance (Q23). In California, bark beetle outbreaks not only changed the value of properties, but also affected the advertised sale prices of homes where properties were listed with (and without) dead tree removal (Lundquist *et al.* 2015), suggesting that emerging marketplace metrics may help to quantify the impacts of bark beetles (Q24).

It is important to understand the factors that influence changes to public perception of bark beetle outbreaks (McGrady *et al.* 2016). Landscape aesthetics are of particular concern among recreationists and tourism concessionaires as landscape appearance influences visitor experience and the frequency of subsequent visitation (Sheppard & Picard 2006). Viewing and experiencing iconic, ‘high-quality’ landscapes are significant motivations for nature-based tourism. As such, aesthetics and perceptions of the ‘natural’ environment are important, but are currently unquantified in the context of bark beetle outbreaks (Q25).

Discussion

SYNTHESIS

The 25 questions we highlight and discuss in this manuscript are a mix of applied and theoretical research topics pertinent to bark beetle disturbances. Many of these questions have obvious connectivity with management applications and planning, include bark beetle population monitoring (Q1) and tools to predict where future outbreaks might occur (Q8). Model forecasts suggest that climate warming will promote bark beetle outbreaks in North America and Europe during the

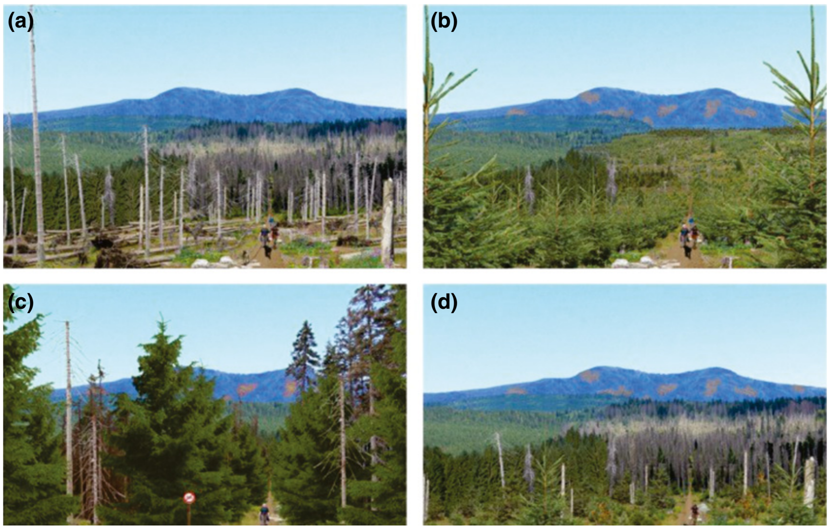

Fig. 3. Example of a stated choice model to assess how visitors respond to landscape management scenarios. Each panel is shown to a forest user to assess their preference for landscape aesthetics with various preventative and salvage logging treatments in response to bark beetles. Panel a depicts logging of beetle-killed timber in the foreground with unharvested stands in the background. Panel b shows complete removal of beetle-killed timber with a manually reseeded forest in the foreground and active timber harvests on distance mountains. Panel c shows an unmanaged forest in the foreground with a matrix of live and dead mature trees. In the distance, several timber harvests are visible. Panel d shows a mix of salvage harvesting and manual reseeding with active harvests on the distance mountains. Using these depictions, the acceptance of management strategies and disturbance attributes can be assessed to understand the preferences among forest user groups (Arnberger *et al.* 2016).

current century (e.g. Seidl *et al.* 2008), and accordingly, a number of questions reflect the likelihood of outbreaks moving into novel ecosystems and communities (Q7, Q11). The seemingly unprecedented scale and severity of recent outbreaks motivated several questions designed to improve the fidelity of retrospective studies to inform this topic (Q2), and to help constrain the climate and land-use drivers that promote high-severity infestations over a range of spatial and temporal scales (Q4).

In general, many of the priority questions that we identified centred on establishing common metrics to facilitate comparison of changes to landscapes and adjacent communities across regions and among forest types (Q13). This need could be potentially addressed by explicitly monetizing ecosystem services (Q16, Q23). Other questions presumably would require detailed evaluations of stakeholders, including idealized representations of landscape aesthetics (Fig. 3) to better characterize why specific user groups prefer some landscape qualities over others (Q15, Q25). Several questions emphasized the emerging utility of alternative landscape appearances (Q21) and land-use history (Q3). Together these topics suggest that agencies must weigh trade-offs among managing landscapes to be reflective of past environmental conditions, resource production, and the aesthetic expectations of recreationists and adjacent communities. However, landscape treatments to achieve these mixed purposes will undergo scrutiny from the public based on the type of silvicultural methods and the proximity of the affected landscape to residential areas (Q18, Q22, Q25). A key aspect of approaching divergent public opinion is to facilitate timely dissemination of scientific results through various media channels, as well as providing a platform to educate and engage the concerns of a diversity of user groups (Q15, Q17).

A main challenge in managing bark beetle outbreaks is to stabilize the provisioning of ecosystem services. To achieve advances in this area, a priority is to bridge mismatches in the spatial and temporal scaling of data with low-cost, technologically advanced detection and monitoring systems (Q1, Q13). It is also necessary to improve proxy-based reconstructions to better understand baseline variability in beetle affected forests (Q3, Q14). The sensitivity and resilience of ecosystem services to disturbance are likely regionally specific and dependent upon the ability of various public and private agencies to adapt to and manage beetle-impacted landscapes. For example, managing fluctuations in the resale value of homes likely require the costly removal of standing dead trees to prevent treefalls, though the proximity of neighbours and/or emerging viewsheds can further modify home prices both positively and negatively (Q25). However, educating private landowners and the general population on the ecological role and expected recurrence interval of outbreaks, should those data be available, may aid in the acceptance of preventative landscape treatments as well as augment popular misconceptions about bark beetle outbreaks, including perceived increased risk of fire and ecosystem degradation (Q22, Q24). Effectively communicating the role of bark beetle disturbances in promoting forest rejuvenation is also an important aspect of educating forest user groups and the general public.

Conclusion

In summary, the 25 questions discussed in this manuscript leverage the recent proliferation of bark beetle research in North America and Europe to establish where critical knowledge gaps exist. Our effort to assess priority research questions on social–ecological impacts of bark beetle outbreaks follows a growing body of research prioritization in ecology. We aim for this effort to be useful for motivating future research, and for fostering collaboration among scientists of disparate expertise to address the complex and interdisciplinary nature of bark beetle impacts to social–ecological systems.

Acknowledgements

Our workshop was funded by the Mountain Social-Ecological Observatory Network (DEB-1231233) and IGBP: Past Global Changes through the Forest Dynamics Working Group. We thank Andrew D. Graves and the organizers and participants of the Western Forest Insect Work Conference for their efforts. Participation of C.J.F. and S.J.S. was coordinated through the USDA Forest Service R&D Western Bark Beetle Research Group. We are grateful to Lorenzo Marini and two anonymous reviewers whose suggestions led to improvements our manuscript.

Data accessibility

Data have not been archived because this article does not contain data.

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Received 2 June 2016; accepted 7 September 2016
Handling Editor: Lorenzo Marini