RESEARCH REVIEW

Biotic disturbances in Northern Hemisphere forests – a synthesis of recent data, uncertainties and implications for forest monitoring and modelling

Markus Kautz[1]*, Arjan J. H. Meddens[2], Ronald J. Hall[3] and Almut Arneth[1]

[1]*Institute of Meteorology and Climate Research – Atmospheric Environmental Research (IMK-IFU), Karlsruhe Institute of Technology (KIT), Garmisch-Partenkirchen 82467, Germany,* [2]*College of Natural Resources, University of Idaho, Moscow, ID 83844-1133, USA,* [3]*Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre, Edmonton, AB T6H 3S5, Canada*

ABSTRACT

Aim Biotic disturbances (BD, including insects, pathogens and wildlife herbivory) can alter forest structure and the capability of forests to deliver ecosystem services. Impact assessments, however, are limited by the lack of reliable and timely disturbance data at large spatial scales. This review synthesizes empirical data on the magnitude and distribution of spatio-temporal impacts of BD.

Location Northern Hemisphere.

Methods Based on large-scale, multi-year BD data sets, covering *c.* 46% of the global forest, we calculated annual disturbance fractions D_f (percentage of forest area affected) and their inter-annual variability at a grid cell resolution of 1°. The impact of BD on forest carbon pools was determined by overlaying D_f with data on forest cover and carbon density.

Results Overall, 43.9 million hectares (Mha) ($D_f = 2.6\%$) of forests were affected annually by BD, particularly by insects (36.5 Mha, $D_f = 2.2\%$). Our synthesis demonstrates that fractions affected by BD (1) vary greatly over space and time, mainly in response to ephemeral bark beetle and defoliator outbreaks, (2) show temporal trends that are inconsistent across regions, yet are largely increasing over recent decades, and (3) are substantially higher than D_f caused by fire and other abiotic disturbances. Tree mortality was estimated over an area of 3.3 Mha year^{-1} (medium estimate which assumed mortality at 7.5% of the affected area), with associated committed carbon fluxes from living biomass to litter and the atmosphere at 129.9 Mt C year^{-1}.

Main conclusions BD are key drivers of forest dynamics, making a contribution to tree mortality of a similar magnitude to fire. Despite inherent uncertainties, the data reported can be used to improve the representation of BD in global ecosystem models. Our findings call for future forest monitoring approaches to provide accessible, precise and consistent data on the occurrence and severity of BD which are harmonized across jurisdictions.

Keywords
Bark beetle, defoliator, disease, DGVM, forest carbon cycle, insect outbreak, pathogen, pest monitoring, tree mortality.

*Correspondence: Markus Kautz, Institute of Meteorology and Climate Research – Atmospheric Environmental Research (IMK-IFU), Karlsruhe Institute of Technology (KIT), Garmisch-Partenkirchen 82467, Germany.
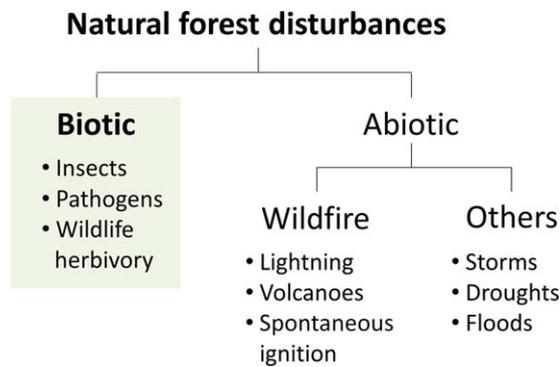E-mail: markus.kautz@kit.edu

Natural forest disturbances

Figure 1 Natural disturbance categories with their main causes of damage; the shaded box indicates biotic disturbances as covered in this study. 'Wildlife herbivory' involves all kinds of biotic damage not specifically caused by insects or pathogens, e.g. by browsing, beaver felling or unspecified/interacting agents (complex decline).

INTRODUCTION

Natural disturbances, including wildfires, other abiotic factors and biotic agents (Fig. 1), are inherent components of global forest ecosystems, affecting their structure, biodiversity and functioning, and hence also important ecosystem services such as timber production and carbon sequestration (Boyd *et al.*, 2013; Thom & Seidl, 2016). These disturbances interact not only with each other (Buma, 2015) but also with recent increases in atmospheric carbon dioxide and related climatic change, which in turn contribute to the dynamics of forest ecosystems (Kurz *et al.*, 2008). This complex interplay challenges our ability to assess present and future forest function in response to disturbance. Currently, about 5% of the world's 4 billion hectares of forest are estimated to be disturbed per year. As a result, more than 60% of global forests are in various states of recovery from a past disturbance at any given time (FAO, 2006; van Lierop *et al.*, 2015). Northern temperate forests have been affected by natural disturbances more frequently and with a higher spatio-temporal variability than by harvesting (Cohen *et al.*, 2016). Further intensification of natural disturbance regimes due to climatic changes are expected, leading to enhanced tree mortality due to drought (Allen *et al.*, 2010; Michaelian *et al.*, 2011; Williams *et al.*, 2013), storms and fire (Seidl *et al.*, 2014), as well as insects and pathogens (Sturrock *et al.*, 2011; Weed *et al.*, 2013; Seidl *et al.*, 2014).

This study addresses biotic disturbances (BD), which include all types of damage to trees induced by living organisms excluding humans. The range of agents causing BD can be classified into three primary groups: (1) insects, (2) pathogens, and (3) wildlife herbivory (Fig. 1). Outbreaks of herbivorous insects are considered the most destructive BD, affecting tens of millions of hectares of global forests annually (van Lierop *et al.*, 2015). While particular disturbance mechanisms depend on the feeding behaviour of the insect herbivore (e.g. leaf chewers, sap suckers, stem borers, root

pruners), all mechanisms interfere with photosynthesis and transpiration, and with the translocation of carbohydrates and nutrients (Edburg *et al.*, 2012; Flower & Gonzales-Meler, 2015). Depending on the severity of an attack, the physiological ability of a tree to function, maintain growth and respond to further stresses can be reduced substantially, which may eventually lead to tree mortality. The most damaging feeding guilds are the xylophagous insects (those that feed on live woody tissues, e.g. bark beetles) and the phyllophagous insects (those that feed on leaf tissues, e.g. defoliators). Tree-killing bark beetles, in particular, can completely devastate forests at the landscape scale within a few years, as recent examples of beetle outbreaks in Canada (Kurz *et al.*, 2008), the USA (Meddens *et al.*, 2012) and central Europe (Kautz *et al.*, 2011) demonstrate. Likewise, repeated attacks by defoliating insects can cause extensive tree mortality (Cooke *et al.*, 2007). Pathogens such as fungi, bacteria or other microorganisms, which sometimes occur in association with an insect infestation, may also cause serious infections to roots, stems or foliage of trees (Santini *et al.*, 2013). Affected trees are typically not immediately killed by these infections; instead, their ability to resist other stresses is reduced, which may ultimately lead to mortality (Desprez-Loustau *et al.*, 2006). The third group of agents, referred to as 'wildlife herbivory' hereafter, includes all biotic damage which is not specifically caused by insects or pathogens. It involves true herbivory, e.g. ungulate browsing, as well as tree damage which is not solely through consumption, e.g. beaver felling. Such wildlife disturbance typically has only relatively marginal impacts on forests, as populations do not exhibit irruptive dynamics. In the context of our study this group may further involve complex forest decline, i.e. damage resulting from the interactions of several biotic agents, or from interactions with abiotic disturbances such as drought (Hicke *et al.*, 2012a).

Recent modelling studies emphasize the sensitivity of forest ecosystem dynamics and of carbon and nutrient cycling to changing disturbance regimes (Edburg *et al.*, 2011; Le Page *et al.*, 2013; Seidl *et al.*, 2014), the sensitivity of disturbance regimes to changes in climate (Jönsson *et al.*, 2007; Bentz *et al.*, 2010), as well as multiple effects caused by interacting disturbance regimes (Jönsson *et al.*, 2012; Temperli *et al.*, 2013). Despite the increasing evidence of substantial impacts of BD on forest ecosystems and on potential global carbon sequestration (Liu *et al.*, 2011; Hicke *et al.*, 2012a; Kurz *et al.*, 2013; Flower & Gonzales-Meler, 2015), quantitative assessments are limited in many regions by the quality and deficiency of available BD data (FAO, 2010; van Lierop *et al.*, 2015). Likewise, today's dynamic global vegetation models (DGVM), considered the state-of-the-art tools for assessing terrestrial carbon cycle dynamics (Le Quéré *et al.*, 2015), have no or only a rudimentary representation of the agents of BD (Arneth & Niinemets, 2010; Quillet *et al.*, 2010; Fisher *et al.*, 2014). The ability to acquire reliable and timely disturbance data and to model disturbance effects is necessary for an accurate assessment of vegetation dynamics and for

quantifying impacts of disturbance in carbon budget models (Kasischke *et al.*, 2013; Anderegg *et al.*, 2015).

To our knowledge, no comprehensive overview has been compiled that quantifies the occurrence of BD in space and time to estimate their ecological impacts at the biome to global scale. While some studies have reported such characteristics for separate regions or agents, e.g. for Europe (Schelhaas *et al.*, 2003a; Seidl *et al.*, 2014) and North America (Hicke *et al.*, 2012a; Flower & Gonzales-Meler, 2015), these results cannot be easily extrapolated to other regions and other disturbance agents without a considerable increase in uncertainty. Overall, this seems challenging but is critical for improving our knowledge from the landscape level of single BD agents and their interactions, in order to develop tools that integrate data and knowledge of ecological processes at the global scale. This review synthesizes recent disturbance data across Northern Hemisphere forests to provide spatially explicit quantitative estimates of the occurrence, variability and potential impacts of BD from which to present the foundation for integrating BD into large-scale ecosystem models, such as DGVM.

MATERIALS AND METHODS

Data sets

Our review focuses on Northern Hemisphere forests, mainly located in boreal and temperate biomes but including some subtropical forests, which together represent approximately 18.6 million km^2 or 46% of total global forest cover (Fig. 2a). We selected data from a number of countries based on two criteria: (1) forests cover a considerable part of the country's land surface and (2) suitable records of BD in these forests, i.e. disturbance by insects, pathogens and/or wildlife herbivory, were available for a time period of more than 10 years. The domain of this study thus includes four major regions: North America (Canada and the USA), Europe (34 countries, excluding Russia), Russia and central-east Asia (China, Mongolia and Japan).

Our analysis builds from national disturbance data sets (see below for disturbance metrics), which were primarily based on aerial surveys and ground inventories. Aerial survey techniques have changed considerably over time, with delineation onto digital tablets with GPS (global positioning systems) being prevalent today (Schrader-Patton, 2003). To avoid strong biases due to sampling techniques, we decided to focus only on a relatively recent time series, beginning in 1980 (where available). Moreover, the availability and quality of BD data also varied across regions due to the different monitoring standards applied. For instance, data for the USA were available at high polygon-level resolution with detailed attributes associated with each damage polygon, e.g. with regard to agent, host and severity (USDA Forest Service, 2005). Canadian forest monitoring provided BD data which were slightly less detailed, and which included insect damage that is mostly representative of managed forests (Canadian Council of Forest Ministers, 2012). By contrast, European

data were not easily available at annual resolution for each country and data quality differed considerably between countries, as each country has its own monitoring standards (Forster *et al.*, 1999; BIO Intelligence Service, 2011). Hence, we used data from the most recent global Forest Resource Assessment (FRA; FAO, 2010) for Europe, which covered *c.* 90% of European forests. The FRA data were based on national enquiries and were limited in their spatial (country), temporal (5-year average) and attributive resolution (lacking information on species level). Likewise, for Russia and central-east Asian countries, available BD data were not as detailed and consistent as the North American data due to less comprehensive monitoring standards (Malysheva *et al.*, 2000; Yang *et al.*, 2015). An overview of the different data sets used for analyses is provided in Table 1, while the data are compiled in the Appendix S1 in Supporting Information. In addition, some information regarding the availability of BD data across global forests outside the study domain is provided in Appendix S2.

Disturbance metrics

To quantify BD spatially, various metrics can be used, i.e., (1) affected area A_a (area affected by a disturbance agent, typically recorded by aerial or field surveys – this probably also includes unaffected, healthy trees), (2) disturbed area A_d (the truly affected area excluding un-impacted trees), and (3) mortality area A_m (area of trees killed by the disturbance). All of these metrics can be calculated as fractions (%) of a specific forest area unit, in contrast to alternative tree-based measures such as basal area (m^2) or volume (m^3). In our analyses, we consistently used the spatial metric A_a (given in hectares), as it was commonly provided across all countries (Table 1), and it allowed for comparisons among BD agents that may/may not have resulted in mortality, as well as among different natural disturbance categories. Data on A_d (or even A_m) would be a more appropriate measure (cf. Meddens *et al.*, 2012), but these data were unavailable for most of our study area. Since large-scale forest monitoring occurs at a resolution beyond the tree level ($A_a > A_d$), and BD do not necessarily cause tree mortality ($A_d > A_m$), it can be assumed that $A_a > A_m$. The mortality fraction, i.e. the fraction of mortality area A_m in the affected area A_a, varies depending on forest and species characteristics, associated damage severity, the number of consecutive years damage may have occurred and the monitoring resolution. Hence, A_m (and the resulting carbon fluxes) at the scale of our study domain cannot be estimated without considerable uncertainties. Numerous studies have investigated insect-induced tree mortality at the stand scale and found mortality fractions ranging from 0% to almost 100% of the forest area, but typically from 5% to 50% (e.g. Alfaro *et al.*, 1999; MacLean *et al.*, 2001; Orwig *et al.*, 2002; Gray & MacKinnon, 2006; Zhang *et al.*, 2014). Only a few studies, however, have focused on the fraction of A_m in relation to the detected A_a at large spatial scales. Meddens *et al.* (2012) investigated bark
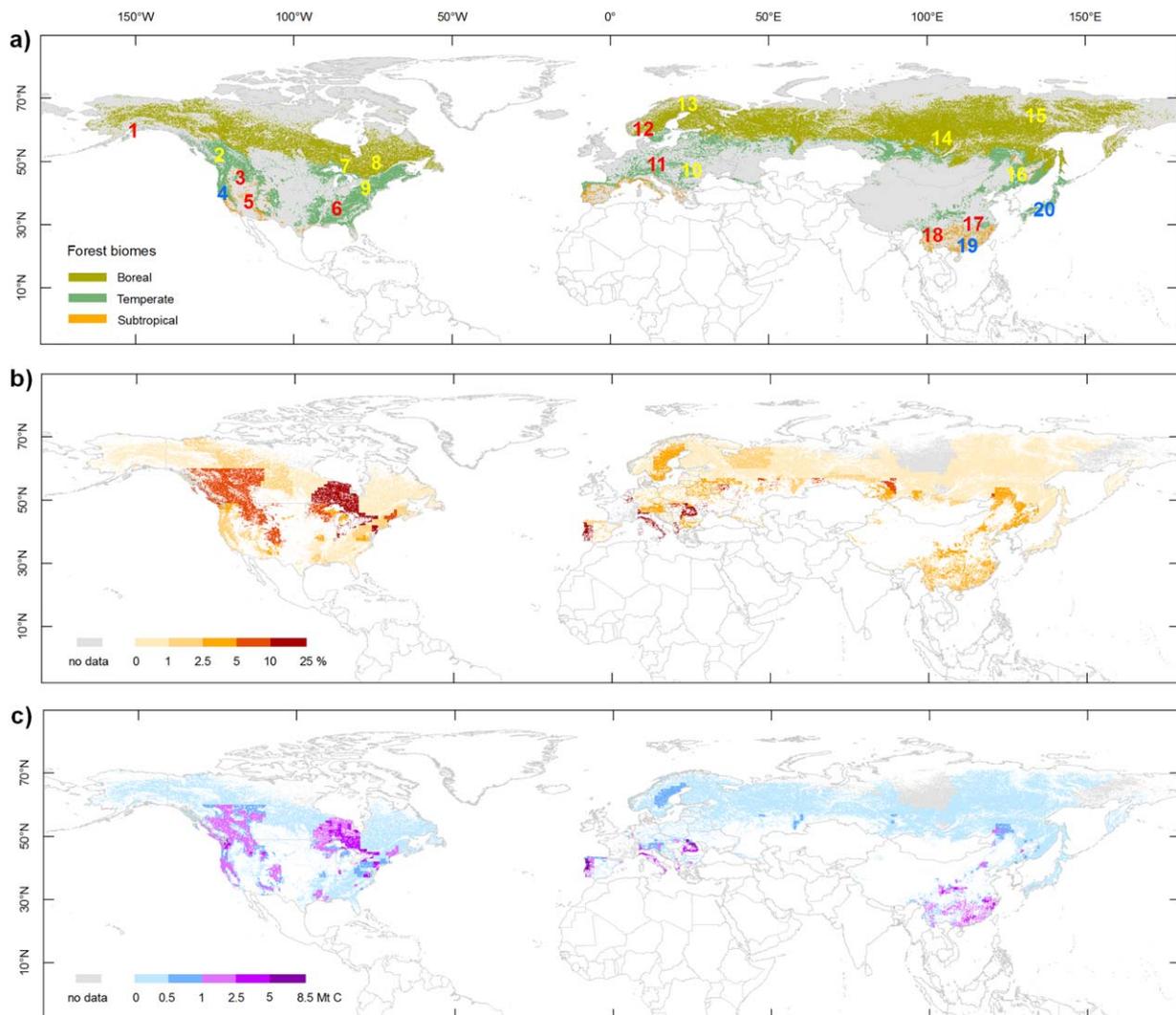
Figure 2 (a) Major biotic disturbance outbreaks during recent decades in Northern Hemisphere forests. Outbreaks are separated into bark beetles (red numbers), defoliators (yellow numbers) and pathogens (blue numbers), and vary in extent, duration and affected host species (see Table 2 for details). The study domain is shaded in grey; the corresponding forest is coloured according to its biome (Bartholomé & Belward, 2005; The Nature Conservancy, 2009). (b) Mean annual biotic disturbance fraction D_f (% forest area affected), derived from multi-year data sets (see Table 1 and Appendix S1 for details). (c) Potential impact of disturbance on vegetation carbon pools (Mt C year^{-1}), estimated by multiplying D_f/100 by the year 2000 state of forest carbon density (t C ha^{-1}; Ruesch & Gibbs, 2008) and forest area (ha; Bartholomé & Belward, 2005) per grid cell. Carbon fluxes due to tree mortality induced by biotic disturbance can be obtained by multiplying these figures with the assumed tree mortality fraction (5%, 7.5% or 10%). For (b) and (c), a grid cell resolution of 1° × 1° is used; sharp colour gradients at borders are due to limitations of biotic disturbance data in different jurisdictions.

beetle-induced mortality for the Canadian province of British Columbia (BC) and the western USA, and revealed average mortality fractions of 8.3% (BC) and $1.7 - 19.4\%$ (western USA, lower and upper estimate) of A_a. For Canada, Kurz & Apps (1999) used mortality fractions of 5% to 15% for five different insect species, including bark beetles and defoliators, in modelling insect-induced carbon fluxes. Similar assumptions were also made in other modelling studies that included one or two main insect species at the regional scale (Kurz *et al.*, 2008; Dymond *et al.*, 2010; Ghimire *et al.*, 2015). While mortality due to pathogens and wildlife herbivory may be assumed to be lower than mortality due to

insects, landscape-scale mortality fractions have been shown to exceed 10% of A_a when severity is high (Meentemeyer *et al.*, 2008; Zhao, 2008) or when these agents interact with insect disturbances (Hicke *et al.*, 2012a). Since we lacked reliable mortality data at the scale of our study, we generated mortality fractions that ranged from 5% to 10% to approximate the effects of BD-induced tree mortality on the vegetation carbon pools. Hence, we defined a medium estimate (ME) based on a 7.5% mortality fraction, i.e. 7.5% of the observed area affected by BD suffered tree mortality ($A_{m(ME)} = A_a \times 0.075$), either directly due to the BD agent or indirectly via a subsequent stressor. This mortality fraction

Table 1 Characteristics of the data sets used for the calculation of biotic disturbance fractions.

Spatial extent	Spatial resolution	Temporal resolution	Time period	Biotic agents	Uncertainty*	Data sources
Canada	Province	1 year	1990 − 2013	Insects (species)	Low (for insects)	Canadian Forest Service (2016)
USA	State[†]	1 year	1997 − 2013	Insects (species), pathogens, wildlife herbivory[‡]	Low	USDA Forest Service (2016)
Europe	Country	5 years[§]	1988 − 92, 1998 − 2007	Insects, pathogens, wildlife herbivory	High	FAO (2010)
Russia	Subject[¶]	1 year	1992 − 2005	Insects/pathogens	High	Federal Service of Forest Management, Russia (2006)
China	Country	1 year	1990 − 2011	Insects, pathogens, wildlife herbivory	High	Fu *et al.* (2011), State Forestry Administration, P.R. China (2013)
Mongolia	Country	1 year	1980 − 2001	Insects	High	Ministry of Nature and Environment, Mongolia (1998, 2002)
Japan	Country	1 year	1980 − 2007	Insects/pathogens, wildlife herbivory	High	Forest Agency, Japan (2009)

See Appendix S1 for further details.
*Estimation of data uncertainty (high–low) is based on spatial, temporal and attributive resolution, and its coverage.
[†]Original polygon data have been aggregated to state level in order to make scales comparable across the study domain.
[‡]Also contains unspecified biotic disturbances closely interacting with abiotic factors (complex decline).
[§]Five-year averages (1988 − 92, 1998 − 2002, 2003 − 07).
[¶]Federal subject is an administrative unit in Russia.

is a generic assumption, averaged over different regions, host species and BD agents. Similarly, we defined a lower-estimate (LE) and an upper-estimate (UE) scenario with 5% and 10% mortality fractions, respectively, in order to account for the uncertainties related to our assumptions.

To make A_a records comparable among aerial units of different sizes, disturbance fractions D_f (%) for each year were derived by dividing A_a by the corresponding total forest area A_f, i.e. $D_f = A_a/A_f \times 100$. This fraction is spatially explicit and integrates single disturbance characteristics, such as extent, magnitude and frequency, into a single metric. When considering a relatively long time period (>10 years), the mean D_f and inter-annual variability (expressed by the standard deviation, SD) are a meaningful measure of the occurrence of BD at a certain location over time. For European countries where FRA data were used, no measure for inter-annual variability was given, as result of the 5-year averaging period.

Analyses

We created a map with a grid at 1°× 1° spatial resolution covering the study domain and overlaid it with the disturbance data (mean D_f, derived from the data sets as listed in Table 1), as well as with forest cover information (Global

Land Cover classes 1–10; Bartholomé & Belward, 2005) and forest carbon density estimates (including above- and below-ground living biomass; Ruesch & Gibbs, 2008). Both forest cover and carbon density data refer to the year 2000, which fits well into the time period of disturbance data employed in this study. As a result, each grid cell contains information about its long-term annual BD fraction D_f (%), its actual forest cover (ha) and its mean carbon density (t C ha^{-1}). To estimate potential carbon impacts due to BD, we multiplied these three values (i.e. D_f/100 × forest cover × carbon density) for each grid cell. By assuming an average tree mortality fraction (as described above), the resulting carbon fluxes from the living biomass pool to the dead organic matter pool and to the atmosphere (t C year^{-1}) could be estimated.

In addition to our analysis of the described data sets, we reviewed the published scientific literature in order to synthesize information regarding recent large outbreaks of BD in Northern Hemisphere forests and on the agent, host, location and extent of each outbreak (Table 2).

RESULTS

Biotic disturbance fractions and outbreak patterns

On average, 43.9 Mha (D_f = 2.6%) of forests were disturbed by BD agents each year in our study domain (Table 3),

Table 2 Major outbreaks of biotic disturbance reported since the 1970s.

ID no.	Agent species and category*		Primary host species and category*		Location	Affected area (Mha)	Year	Reference
1	Spruce beetle (*Dendroctonus rufipennis*)	B	Spruce (*Picea*) species	c	USA: southern Alaska	1.2	1990 − 2000	Werner *et al.* (2006)
2	Western spruce budworm (*Choristoneura occidentalis*)	D	Coniferous species	c	Canada: southern British Columbia	0.8	2007	Canadian Forest Service (2016)
					USA: north-western states	5.4	1986	USDA Forest Service (2010)
3	Mountain pine beetle (*Dendroctonus ponderosae*)	B	Pine (*Pinus*) species	c	Canada: British Columbia	10.1	2007	Canadian Forest Service (2016)
					USA: western states	9.7	2008 − 10	USDA Forest Service (2016)
4	Sudden oak death (*Phytophthora ramorum*)	P	Oak (*Quercus*) species, tanoak (*Lithocarpus densiflorus*)	b	USA: California, Oregon	0.05	2010 − 13	USDA Forest Service (2016)
5	Pinyon ips beetle (*Ips confusus*)	B	Pinyon pine (*Pinus*) species	c	USA: south-western states	1.4	2003 − 04	USDA Forest Service (2016)
6	Southern pine beetle (*Dendroctonus frontalis*)	B	Pine (*Pinus*) species	c	USA: south-eastern states	0.4	1999 − 2002	Wear & Greis (2013)
7	Forest tent caterpillar (*Malacosoma disstria*)	D	Poplar (*Populus*) species	b	Canada: Ontario, Quebec	14.3	2001	Canadian Forest Service (2016)
8	Eastern spruce budworm (*Choristoneura fumiferana*)	D	Spruce (*Picea*) and fir (*Abies*) species	c	Canada: south-eastern provinces	51.9	1975	Canadian Forest Service (2016)
9	Gypsy moth (*Lymantria dispar*)	D	Broadleaf species	b	USA: north-eastern states	5.2	1981	USDA Forest Service (2010)
10					Romania	0.2	1998 − 99	Lupu *et al.* (1999)
11	European spruce bark beetle (*Ips typographus*)	B	Norway spruce (*Picea abies*)	c	Germany/Czech Republic: Bavarian Forest and Šumava national parks	0.02	1990 − 2012	Kautz *et al.* (2011), Šumava National Park administration, pers. comm.
12					Norway: southern provinces	14	Late 1970s to early 1980s	Bakke (1991)
13	Autumnal moth (*Epirrita autumnata*), winter moth (*Operophtera brumata*)	D	Mountain birch (*Betula pubescens* ssp.)	b	Norway, Sweden: north-ern provinces	0.4	2005	Jepsen *et al.* (2009)

TABLE 2. *Continued*

ID no.	Agent species and category*		Primary host species and category*		Location	Affected area (Mha)	Year	Reference
14	Siberian silk moth	D	Coniferous species	c	Russia: central Siberia	0.7	1994 − 96	Kharuk *et al.* (2007)
15	(*Dendrolimus sibiricus*)				Russia: Sakha Republic	5.9	2000	Gninenko & Orlinskii (2002)
16	Pine caterpillar (*Dendrolimus superans*)	D	Coniferous species	c	China: north-eastern provinces	0.01	2003 − 04	Huang *et al.* (2010)
17	Red turpentine beetle (*Dendroctonus valens*)	B	Pine (*Pinus*) species	c	China: central-eastern provinces	0.5	1999 − 2003	Yan *et al.* (2005), Sun *et al.* (2013)
18	Pine shoot beetle (*Tomicus piniperda*)	B	Yunnan pine (*Pinus yunnanensis*)	c	China: Yunnan	1.5	Late 1970s to early 1990s	Hui & Xue-Song (1999)
19	Pine wood nematode	P	Pine (*Pinus*) species	c	China: central-eastern provinces	0.06	1998 − 2006	Zhao (2008)
20	(*Bursaphelenchus xylophilus*)				Japan: Honshū, Shikoku, Kyūshū	0.65	1979	Mamiya (1988)

ID numbers refer to the map in Fig. 2(a).
*B, bark beetle; D, defoliator; P, pathogen; c, coniferous; b, broadleaf.

although the fraction disturbed varied considerably, both temporally and spatially (Figs 2b & 4). Of the BD agents, insects contributed most to the total observed damage (36.5 Mha, 2.2%), followed by pathogens (4.0 Mha, 0.2%) and wildlife herbivory including complex forest decline (2.9 Mha, 0.2%) (Fig. 3). Over recent decades, D_f showed inconsistent temporal trends between regions: BD have notably intensified in Europe, China and Mongolia, while they remained at a more consistent level in Canada, the USA, Russia and Japan (Fig. 4). Across the observed biomes, average D_f increased from boreal (1.4%), to temperate (3.6%), to subtropical forests (4%) (Fig. 2a, b) − a gradient that is in line with the well-established theory that plant–herbivore interactions are typically enhanced towards lower latitudes (Schemske *et al.*, 2009, and references therein). Overall, the frequency distribution of D_f is distinctly right-skewed; that is, in the majority of forests (63% of the total forest area with disturbance data) the affected area is less than 1%, while in a relatively small proportion of forests the areas are more severely affected (11% of forests had an annual BD fraction >5%). This distribution, however, is also influenced by the size distribution of aerial units used for calculation of D_f.

The area disturbed annually by single outbreak events, primarily involving bark beetles and defoliators, may reach up to several million hectares, well in excess of the long-term average D_f (Table 2). The spatial distribution of outbreaks in the study domain were not random and showed distinctive patterns, probably determined by the presence of BD agents,

environmental factors and the distribution of susceptible host trees. Defoliator outbreaks were located in northern, mainly boreal, coniferous and broadleaf forests, while bark beetle outbreaks principally occurred in coniferous forests in the temperate zone (Fig. 2a). Coniferous forests appear to be more frequently disturbed and killed by insects than broadleaf forests (Table 2), which is probably due to the strong association of tree-killing bark beetles with coniferous hosts (Ohmart, 1989).

North America

BD fractions in Canada (5.4 ± 2.8%) over recent decades were the highest among our study regions, with D_f values more than twice as high as those observed in the USA (2.4 ± 1.0%; Fig. 3). The highest D_f occurred in the Canadian provinces of Ontario (14.5 ± 18.9%), British Columbia (9.3 ± 7.8%) and Alberta (7.2 ± 8.4%), as well as in the US states of Indiana (20.6 ± 82.5%), New Jersey (12.7 ± 26.8%) and Minnesota (8.4 ± 13.5%) (Fig. 2b). While bark beetle outbreaks, sometimes co-occurring with drought (Meddens *et al.*, 2015), affected large extents of western Canada and the USA, defoliator outbreaks have become more prominent in the eastern regions of North America (Fig. 2a, Table 2). Among the western bark beetles, the mountain pine beetle (*Dendroctonus ponderosae*) is by far the most destructive species, affecting millions of hectares since 2000 (Fig. 5a, b, Table 2). This unprecedented outbreak raises particular concern about a further eastward spread of the beetle, which has already spread from British Columbia into Alberta, with the

Table 3 Area affected by biotic disturbances (A_a), calculated disturbance fractions (D_f) and resulting tree mortality area (A_m).

Region	A_a (Mha year^{-1})	D_f (% year^{-1})	A_m (Mha year^{-1}) Lower estimate	Medium estimate	Upper estimate
Canada	16.61	5.37	0.83	1.25	1.66
US	7.38	2.39	0.37	0.55	0.74
Europe	6.16	3.59	0.31	0.46	0.62
Russia	4.19	0.64	0.21	0.31	0.42
China	9.42	4.56	0.47	0.71	0.94
Mongolia	0.14	1.32	0.01	0.01	0.01
Japan	0.01	0.07	0.00	0.00	0.00
Total	43.93	2.60	2.20	3.29	4.39

potential for further host-range expansion into the boreal forest (Cullingham *et al.*, 2011). During the most recent decades, less widespread, yet significant, tree damage has been caused by other bark beetles, such as (1) the pinyon ips beetle (*Ips confusus*) in the south-western USA (Meddens *et al.*, 2015), (2) the spruce beetle (*Dendroctonus rufipennis*) in subalpine forests in southern Alaska, Canada and the western USA (Werner *et al.*, 2006), (3) the southern pine beetle (*Dendroctonus frontalis*) in the southern USA (Wear & Greis, 2013), and (4) the western balsam bark beetle (*Dryocoetes confusus*) in both western Canada and the USA (Meddens *et al.*, 2012; for estimates of area affected by the first three see also Table 2). Defoliators may not necessarily kill trees, yet the extensive disturbances that have occurred in North American forests in recent decades have been found to be comparable to disturbances caused by bark beetles (Fig. 5a, b for the period 1990 − 2013; Table 2). The most prominent examples are the forest tent caterpillar (*Malacosoma disstria*), western spruce budworm (*Choristoneura occidentalis*) and eastern spruce budworm (*Choristoneura fumiferana*), which together have affected more than 100 Mha in Canada and the USA over the past six decades (USDA Forest Service, 2010; Canadian Forest Service, 2016). In addition to insects, invasive pathogens have caused significant tree mortality at smaller scales in recent years, sometimes with drastic consequences for the affected host species, e.g. *Phytophthora ramorum* causing sudden oak death in coastal tanoak forests in the western USA (Meentemeyer *et al.*, 2008) or *Ophiostoma ulmi* causing Dutch elm disease, most visible in urban forests (see review by Loo, 2009).

Europe

Across Europe, the total area of forest affected averaged 3.6% for the study period, which can be separated into the area damaged by insects (1.8%), pathogen-caused diseases (0.9%) and wildlife herbivory (0.9%). The highest total D_f values were reported for Romania (23.4%), Moldova (22.1%) and Albania (20.0%), followed by Portugal (15.0%) and Italy (12.6%), all countries located in the southern or south-

eastern parts of Europe (Fig. 2b). The high fractions in southern Europe are likely to be explained by the large areas of forest plantations, mainly pine or eucalyptus, that have recently been established either for restoration or industrial purposes. These plantations are typically monocultures, even-aged and often poorly adapted to the site, all of which – in combination with the warm and dry climate – increase the risk of insect outbreaks (Branco *et al.*, 2014). In contrast, lower rates were observed in northern Europe, although single outbreak events may have a noticeable, yet local, impact (see Table 2). Disturbance trends increased over the study period (1988 − 2007) in all three BD categories (Fig. 4). By far the most destructive BD agents were bark beetles, especially the European spruce bark beetle (*Ips typographus*) (Grégoire & Evans, 2004; Table 2). For the period 1950 − 2000, the annual damage caused by bark beetles was estimated at 2.9 Mm^3 wood volume, which corresponds to approximately 0.01% of the total growing stock in Europe (Schelhaas *et al.*, 2003a). Recent examples from Slovakia (Økland *et al.*, 2016), Austria (Pasztor *et al.*, 2014) and Switzerland (Stadelmann *et al.*, 2014) underline the causal effect of prior storm damage for subsequent extensive bark beetle infestations. Other important agents included defoliator insects, mainly Lepidoptera, which, although playing a generally more minor role, still severely affected forests at smaller spatial and temporal scales. Examples include the larch budmoth (*Zeiraphera diniana*) (Bjørnstad *et al.*, 2002), the pine processionary (*Thaumetopoea pityocampa*) (Régolini *et al.*, 2014) and geometer moths (Geometridae) (Tenow *et al.*, 2013). There is also a wide variety of pathogens, many of them invasive to European forests (Santini *et al.*, 2013), yet their impact is generally more scattered and less severe at larger scales than that of herbivorous insects (see La Porta *et al.*, 2008).

Russia

Total BD fractions in Russian forests were low (0.6 ± 0.4%; Figs 2b & 3), with a slight increase over time (Fig. 4). The low reported D_f is probably a result of the absence of bark beetles (Gromtsev, 2002; Shorohova *et al.*, 2009) but might
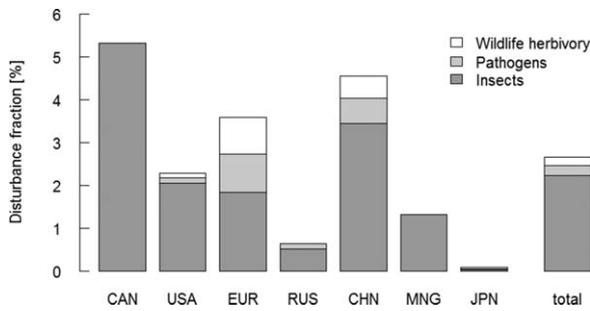
Figure 3 Mean annual biotic disturbance fractions D_f (% forest area affected) in different regions, showing proportions of agent groups: CAN, Canada; USA, United States; EUR, Europe; RUS, Russia; CHN, China; MNG, Mongolia; JPN, Japan. Note that data were not available for all groups in every region, and that complex decline is included in wildlife herbivory for the USA (Table 1).

also be due to incomplete monitoring. Our findings are in accordance with those of Shvidenko *et al.* (2013), who reported an annual A_a of 5.5 Mha (0.7%) for the period $1998 - 2010$ and a peak exceeding 10 Mha in 2001 (Fig. 5c). However, a cross-regional comparison with North America, Europe and China suggests that reported BD fractions are considerably underestimated (Fig. 3). At the sub-national level, D_f varied greatly and was highest in the Southern Federal District ($6.7 \pm 2.1\%$), with the subjects of Volgograd and Rostov showing BD fractions exceeding 20% (Fig. 2b). The neighbouring Central and Privolzhsky districts were also above the national average ($2.2 \pm 0.7\%$ and $1.8 \pm 0.5\%$, respectively), while northern and eastern districts were generally less affected. However, this spatial heterogeneity is probably biased by differing forest monitoring efforts in different regions of the country, with lower estimates in less populated areas. The most destructive agent in Russian forests was the Siberian silk moth (*Dendrolimus sibiricus*), which can defoliate coniferous stands across large spatial extents. Repeated outbreaks of *D. sibiricus* in Siberia have affected a total of >20 Mha since 1880, with exceptional annual damage of >6 Mha in 2000 and 2001 (Gninenko & Orlinskii, 2002; Shorohova *et al.*, 2009; Shvidenko *et al.*, 2013; Fig. 5c). Other significant insect damage was due to several other defoliators, e.g. the European pine sawfly (*Neodiprion sertifer*), the common pine sawfly (*Diprion pini*), the nun moth (*Lymantria monacha*), the green oak moth (*Tortrix viridana*) and the gypsy moth (*Lymantria dispar*) (Mozolevskaya *et al.*, 2003; Fig. 5c).

Central-east Asia

China had a higher BD fraction ($4.6 \pm 0.9\%$) than its neighbours Mongolia ($1.3 \pm 2.0\%$) and Japan ($0.1 \pm 0.1\%$) (Figs 2b, 3 & 4). On average, nearly 10 Mha were affected annually by BD in China, with an increasing trend over recent years (Fig. 4). Resulting direct and indirect economic losses amounted to 88 billion yuan (approximately US$14 billion) on average each year, which amounts to 10% of China's gross

forestry output (State Forestry Administration, P.R. China, 2013). Insects are the most significant BD agents, damaging Chinese forests by an annual fraction of 3.5% ($\pm$ 0.6%) (Figs 3 & 5d), to which bark beetle and defoliator species contribute equally. The red turpentine beetle (*Dendroctonus valens*), a non-native pest affecting conifers in China since the early 1980s, and the Asian longhorn beetle (*Anoplophora glabripennis*), infesting broadleaf trees, are the most destructive species among the bark beetles (Fig. 5d; Table 2). Forests affected by these species comprised mainly pine and poplar plantations. Further, the Chinese pine caterpillar (*Dendrolimus tabulaeformis*), as well as other *Dendrolimus* species, are important defoliators, damaging around 1.5 Mha annually (Ji *et al.*, 2011; Table 2). In recent years, around 20% of the total D_f in China's forests is attributed to invasive species (Ji *et al.*, 2011), particularly *Dendroctonus valens* and the pine-wood nematode (*Bursaphelenchus xylophilus*), which causes pine-wilt disease. In Mongolia, an insect-induced D_f of 1.3% ($\pm$ 2.0%) for the period $1980 - 2001$ was observed (Ministry of Nature and Environment, Mongolia, 1998, 2002), which is considerably lower than more recent estimates of 5.6% for the period $2003 - 07$, assessed in the FRA (FAO, 2010). Damage was primarily caused by defoliators, and occurred in the northern mountainous regions covered by coniferous forests (Fig. 2b). BD fractions in Japan from 1980 to 2007 were the lowest amongst our study regions, most likely because of its island location and limited species composition. BD in Japan was caused by insects and diseases 0.03% ($\pm$ 0.1%) and by wildlife herbivory 0.04% ($\pm$ 0.01%) (Fig. 3). The most important insect species were oak ambrosia beetle (*Platypus quercivorus*) and Japanese pine sawyer (*Monochamus alternatus*). Major damage, however, was not caused by an insect but by the invasive pine-wood nematode *B. xylophilus*, with *M. alternatus* often serving as a vector. Resulting annual loss of wood volume has ranged from 0.5 to 1 Mm^3 within the past two decades (Forest Agency, Japan, 2009).
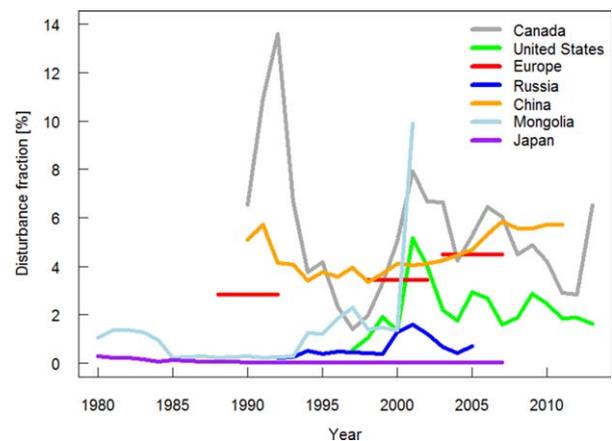

Figure 4 Temporal trends of annual biotic disturbance fractions D_f (% forest area affected) over recent decades. For Europe, available data consist of three 5-year averages (separate horizontal lines). Data sources are given in Table 1.
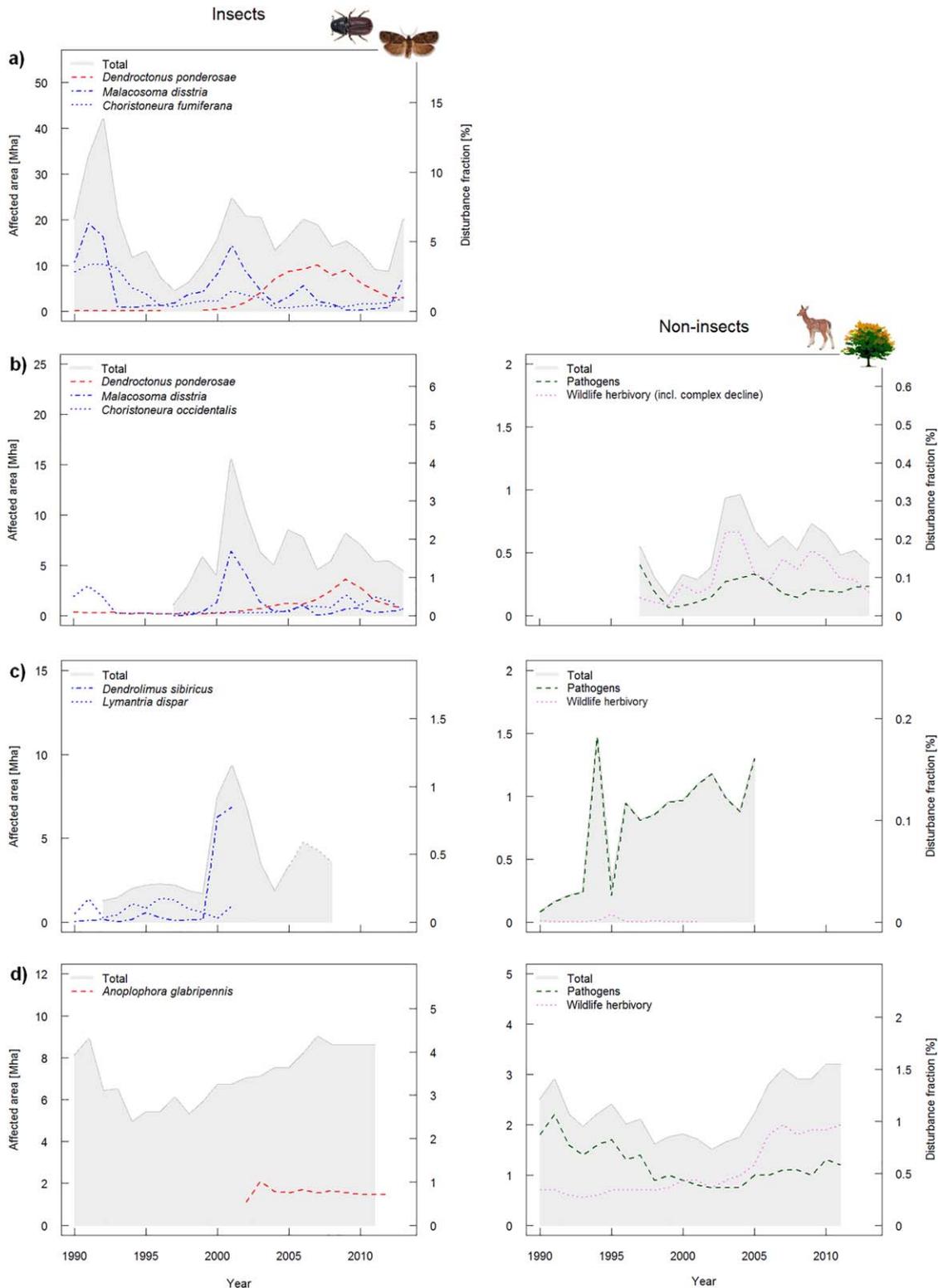
Figure 5 Temporal trends of different biotic disturbance agents for Canada (a), the USA (b), Russia (c) and China (d) over the period 1990 − 2013. Left-hand panels show trends for insects (with main species indicated: bark beetles in red, defoliators in blue), while right-hand panels show trends for non-insect agents (pathogens, wildlife herbivory/complex decline). For each case the annual damage is given by area affected A_a (left *y*-axis) and by the corresponding disturbance fraction D_f (% forest area affected, right *y*-axis). Note that the *y*-axis scale varies among individual panels, and that areas annually disturbed may spatially overlap. Missing panels or values indicate missing data. See Table 1 for data sources for (a), (b) and (d). For (c), single-species data (1990 − 2001; Mozolevskaya *et al.*, 2003) and insect totals for the period 2006 − 08 (dotted lines; Savinov, 2009) are added.

DISCUSSION

Our results revealed BD to be the dominant natural disturbance regime affecting Northern Hemisphere forests: the area affected by biotic agents in the study domain (D_f = 2.6%) exceeded burned forest area by approximately 10 times (D_f = 0.25%, FAO, 2010; see also the Global Fire Emissions Database, Giglio *et al.*, 2013), and the area affected by other abiotic causes by 20 times (D_f = 0.13%, FAO, 2010). Findings further emphasized the high spatio-temporal variability of BD fractions, yet without indicating a consistent temporal trend across different regions (Fig. 4). The reasons for these varying trends include changes in climate and weather patterns (Dale *et al.*, 2001; Bentz *et al.*, 2010), interactions with other natural disturbances such as fire and drought (Buma, 2015), invasion of exotic species (Liebhold *et al.*, 1995) and host connectivity (Seidl *et al.*, 2016), as well as efforts in forest monitoring and management (Schelhaas *et al.*, 2003a), all of which may affect various regions and BD agents individually. Furthermore, trends observed over a limited time period can be strongly influenced by epidemic outbreaks, such as those in Canada in the early 1990s and Mongolia in 2001 (Fig. 4). Among BD, insects were the most damaging agents (Fig. 3), which is in accordance with recent FRA data indicating the area affected by insects to be seven times larger than that affected by pathogens at the global scale (van Lierop *et al.*, 2015). Likewise, for trees in the USA, the risk of infection by insects has been estimated to be 3.6 times higher than that by pathogens (Krist *et al.*, 2007), a trend which is also expected to continue in future years (Krist *et al.*, 2014).

The high spatio-temporal variability in BD frequency and severity, compared with other natural disturbance regimes or harvesting, may complicate the precise prediction of future BD-induced forest impacts. In general, while outbreak periodicity with intervals ranging from few years up to several decades has been documented for many defoliator species globally (Myers & Cory, 2013, and references therein), bark beetle and pathogen populations exhibit less consistent oscillations (Økland *et al.*, 2005; Loo, 2009). Moreover, insect and pathogen outbreaks are highly sensitive to a warming climate, and are thus expected to further intensify in the coming decades (Sturrock *et al.*, 2011; Weed *et al.*, 2013; Seidl *et al.*, 2014). Despite its increasing relevance, to date, the accurate detection of BD across large spatial scales has been limited by the absence of adequate global monitoring approaches. In the following discussion, we demonstrate the significant contribution of BD to tree mortality and on vegetation carbon pools as one example of forest ecosystem services, identify the considerable uncertainties inherent to the analysed BD data, and emphasize the urgent need for improvements to forest monitoring and modelling.

Impacts on tree mortality and forest carbon cycling

Based on the assumption that an average of 7.5% of affected area (A_a) suffered tree mortality, an estimated 3.3 Mha

($A_{m(ME)}$) of trees were killed each year owing to BD in our study domain (for a regional breakdown, and for LE and UE scenarios, see Table 3). By comparison, the forest area affected by fire was only about one-tenth (A_a = 4.6 Mha; FAO, 2010) of that affected by BD, yet tree mortality due to fire was estimated to be significantly higher (40 − 80%; Rogers *et al.*, 2015) than mortality due to BD. These numbers suggest there were at least as many trees killed by BD as by fire (A_m = 1.8 − 3.7 Mha). The more conservative LE scenario resulted in BD-induced mortality comparable to that caused by fire ($A_{m(LE)}$ = 2.2 Mha), while the upper estimate clearly exceeded the fire-killed area ($A_{m(UE)}$ = 4.4 Mha). The latter finding is supported by previous reports that pest-caused timber losses are larger than those due to fire, e.g. in boreal Canada (Volney & Fleming, 2000). Data on the occurrence of abiotic disturbances other than fire were incomplete (FAO, 2010); however, the resulting area of tree mortality was likely to be lower than that caused by either BD or fire (Moore & Allard, 2011). Hence, these results recognize BD as the natural disturbance regime that causes the most frequent tree mortality in Northern Hemisphere forests.

To exemplify the effects of BD on forest functioning, we quantified their potential impacts on forest vegetation carbon pools in the study domain. The total vegetation carbon potentially affected each year by BD (D_f/100 × forest cover × carbon density) summed to 1.73 Gt C. Applying the ME scenario with a 7.5% mortality fraction of A_a resulted in total committed carbon fluxes of 129.9 Mt C year^{-1} (i.e. 0.4 t C ha^{-1} year^{-1}) from biomass to dead organic matter pools, from which carbon will then be gradually released to the atmosphere once the killed trees decay (see Table 4 for LE and UE scenarios). Similar to the distribution of D_f (Fig. 2b), fluxes showed large spatial variability, with the highest vegetation carbon loss (3 − 8 t C ha^{-1} year^{-1}) in certain grid cells in Canada (Ontario, British Columbia and Alberta), the USA (Washington, New Jersey, Indiana and Colorado), southern and south-eastern Europe (Portugal, Italy, Romania and Albania) and southern China (Fig. 2c). For North America (Canada, 43.0 Mt C year^{-1}; USA, 27.8 Mt C year^{-1}) and Europe (23.6 Mt C year^{-1}) our medium-estimate fluxes were consistent with previous studies at the regional scale (Stinson *et al.*, 2011; Hicke *et al.*, 2013; Seidl *et al.*, 2014), while for Russia and China they showed less agreement (Fu *et al.*, 2011; Dolman *et al.*, 2012; Table 4). A likely reason for our relatively low flux estimate for Russia (7.5 Mt C year^{-1}) was an underestimated BD fraction, rather than a higher mortality fraction. In contrast, for China our estimate (27.6 Mt C year^{-1}) – when compared with the results for North America and Europe – was probably more realistic than the very low figure previously reported (4.3 Mt C year^{-1}; Fu *et al.*, 2011). Furthermore, at the regional scale, committed fluxes caused by BD were shown to be widely comparable to (the more instantaneous) fluxes caused by fire (Table 4), yet significantly lower than vegetation carbon loss as a consequence of logging (Fu *et al.*, 2011; Stinson *et al.*, 2011; Williams *et al.*, 2012; Hicke *et al.*, 2013).

Table 4 Forest vegetation carbon loss caused by biotic disturbance- and fire-induced tree mortality.

	This study				Regional studies for comparison			
	Biotic disturbances (Mt C year^{-1})			Time period	Biotic disturbances (Mt C year^{-1})	Fire (Mt C year^{-1})	Time period	Reference
Region	Lower estimate	Medium estimate	Upper estimate					
Canada	28.6	43.0	57.3	1990 − 2013	25 ± 32*	27 ± 19*	1990 − 2008	Stinson *et al.* (2011)
USA	18.5	27.8	37.1	1997 − 2013	1.8 − 24.4[†]	7.2 − 14.1[†]	1997 − 2010	Hicke *et al.* (2013)
					0.9 − 15.4[‡]	−	2000 − 09	Ghimire *et al.* (2015)
					−	14.5[§]	1984 − 2008	Ghimire *et al.* (2012)
Europe	15.7	23.6	31.5	1988 − 92, 1998 − 2007	10.6[¶]	6.1[¶]	2021 − 30	Seidl *et al.* (2014)
Russia	5	7.5	10	1992 − 2005	50.8**	55**	2009	Dolman *et al.* (2012)
China	18.4	27.6	36.8	1990 − 2011	4.3[††]	1.6	1990 − 2009	Fu *et al.* (2011)
Mongolia	0.1	0.2	0.2	1980 − 2001	−	−		
Japan	0.1	0.2	0.2	1980 − 2007	−	−		
Total	86.6	129.9	173.2					

*Insects/fire in managed forests, comprising *c.* 66% of Canada's total forest area.
[†]Bark beetles/fire in the western USA; see also Hicke *et al.* (2012a) for additional examples for the USA.
[‡]Bark beetles in the western USA.
[§]Fire in the western USA.
[¶]Bark beetles in 13 and fire in 29 European countries, future scenario without climate change.
**Insects/fire in Russia, Ukraine, Belarus and Kazakhstan.
[††]Total biotic disturbances, of which *c.* 80% were due to insects.

Although this approach was based on rather simplified assumptions, which also do not account for vegetation dynamics or legacy effects, it is the first to quantify BD-induced carbon fluxes by applying empirical long-term data at a larger spatial scale. Hence, it goes beyond previous work which focused either on regional geographical scales or on single BD agents (Hicke *et al.*, 2012a; Seidl *et al.*, 2014), or which used non-specific disturbance fractions (Le Page *et al.*, 2013). Given the magnitude of the effects we found, future efforts should focus on refining these rough estimates by developing DGVM-based assessments that also include non-lethal BD (defoliators) as well as post-disturbance processes such as management, decay and recovery (Liu *et al.*, 2011).

Data availability and uncertainty

The lack of a coherent and transparent cross-regional monitoring system results in a high spatial variability regarding the availability of BD data and their inherent uncertainties. While data access is mainly public in countries such as Canada and the USA, it is restricted in others (Russia, central-east Asia, some countries in Europe). Likewise, data uncertainty levels depend upon monitoring methods, data sources and geographical coverage. Since we were not able to realistically quantify the uncertainty, we employed qualitative uncertainty levels for different regions based on factors such as spatial, temporal and attributive resolution

(Table 1). Overall, uncertainty was low for North America (with the lowest for the USA), while it increased considerably for Europe, Russia and central-east Asia. For Russia in particular, the quality of BD data has been previously criticized (e.g. Potapov *et al.*, 2012), and the expanse of BD is thought to be considerably underestimated (Selikhovkin, 2005; Shvidenko *et al.*, 2013), since large parts of the country are not surveyed regularly, particularly those in remote, unmanaged Siberian forests (Malysheva *et al.*, 2000).

With regard to the metrics used for analysis, it should be mentioned that D_f is dependent on the size of the aerial units used for its calculation. This scale dependence potentially resulted in higher fractions (and higher variability) in smaller areal units (i.e. smaller provinces or countries), while lower fractions and variability are more likely to be found in larger areas, as a consequence of averaging of local extremes. For example, provinces in China might have fractions that are considerably higher or lower than the country's average; such heterogeneity, however, was not observable with the data available.

Among BD agents, insect damage has been recorded most frequently in all study regions, while pathogen- and/or wildlife herbivory-induced damage has not been recorded, or has been recorded inadequately, in Canada, Russia and Mongolia (for differences in agent-specific data availability outside of the study domain see Appendix S2). Furthermore, we cannot rule out (but also do not have evidence for) the case that

forest damage initiated by pathogens, but with subsequent insect attack leading ultimately to tree mortality, has been assigned erroneously to insects only as these were the more obvious disturbance agents. Such differences in uncertainty across agents and/or regions inevitably limited comparability, and consequently rankings may be biased.

In summary, large-scale BD data – based mainly on aerial surveys and ground inventories – imply considerable uncertainties that should be taken into account in interpreting the presented results:

1. Aerial-survey BD data generally lack information regarding accuracy, which is more difficult to determine than for assessments based on aerial digital images or ground surveys. Some studies, however, have attempted to quantify the accuracy of aerial surveys (c. 70% accuracy; Johnson & Ross, 2008; Backsen & Howell, 2013; Hall et al., 2016). Because affected areas are sketch-mapped using a subjective process during flight, and survey polygons often encompass healthy trees, delineated polygons overestimate the true area of disturbance (Backsen & Howell, 2013; Hall et al., 2016).

2. Agent-specific affected areas may spatially overlap, i.e. an area may suffer damage simultaneously from more than one agent (e.g. from a defoliator and a pathogen). This leads to multiple counting and thus to increased D_f values.

3. Surveys are typically limited in their ability to specify the tree-scale severity caused by BD (e.g. mortality versus dysfunction). In particular, light levels of tree damage (<30% defoliation) can be difficult to detect during aerial surveys, and often cannot be discriminated clearly from areas with no damage (MacLean & MacKinnon, 1996; Hall et al., 2016). Hence, large portions of less severe and dispersed damage, e.g. by pathogens, may not appear in forest health statistics (FAO, 2010; van Lierop et al., 2015).

4. The timing of an annual survey is critical for optimizing detection, thus surveys are typically planned when damage is most visually obvious (Wulder et al., 2006; Hall et al., 2016). Insect defoliation, however, can be missed or underestimated if the tree rapidly recovers foliage before it is surveyed. Furthermore, there may be a time lag between agent occurrence and detectability of disturbances, which may lead to differences between the year of detection and the year of agent occurrence, as demonstrated for bark beetles (Kautz, 2014).

5. Aerial surveys are typically not conducted over the complete forest area, and focus on monitoring those areas where outbreaks are known to have occurred. While thereby recording most of the large-scale mortality, surveys may miss damage in remote, non-managed forests and in urban forests. BD data are often reported without indicating the associated surveyed area, which may ultimately lead to biased disturbance distributions and underestimated fractions.

Implications for forest disturbance monitoring and global vegetation modelling

Knowledge of the spatio-temporal patterns of disturbances and associated processes is essential not only for developing appropriate mitigation strategies through forest management (Millar et al., 2007; Seidl et al., 2008) but also for improving large-scale ecosystem modelling approaches (McDowell et al., 2011; Hartig et al., 2012). Our review provides spatially explicit data on BD at national- or province-level resolution, covering nearly half of the global forest, and can be used to better inform large-scale ecosystem models. However, our findings also underline that existing disturbance data often do not match the needs for comprehensive representation by those models. Hence, based on current limitations, here we identify challenges for future efforts in monitoring and modelling of BD.

Disturbance regimes are related to the ecosystem and act across administrative boundaries, whereas data quality often changes abruptly at borders because of different monitoring efforts across jurisdictions (BIO Intelligence Service, 2011; Canadian Council of Forest Ministers, 2012). Until recently, there have only been a few attempts at compiling and harmonizing disturbance data consistently across national borders, e.g. at the regional (western USA/Canada: Meddens et al., 2012), continental (Europe: Database on Forest Disturbances in Europe, Schelhaas et al., 2003b; International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests, Eichhorn et al., 2010) or biome to global scale (boreal and temperate forests: Montréal Process, 2003; global: FRA, FAO, 2010; van Lierop et al., 2015). Unfortunately, most of these data are fragmentary either in their spatial, temporal or attributive dimensions, thus largely limiting their potential for integration into global models (see Appendix S2 for details on the FRA data set). Hence, we suggest a further intensification of national and international efforts towards globally standardized (i.e. accurate, repeatable and transparent) BD assessments. According to McDowell et al. (2015), a global disturbance monitoring system should fulfil the following criteria: (1) distinguish among different disturbance types, (2) integrate over spatial scales with a global coverage, and (3) incorporate ecological principles in order to detect causes and effects of disturbances. Moreover, quantifying BD-induced mortality (A_m) in addition to the reported affected area (A_a) would be particularly useful for model applications. Recent advances on global-scale monitoring of forest disturbances by remote sensing seem promising (Hansen et al., 2013; McDowell et al., 2015), as satellite-based approaches would provide continuous data, and thereby overcome the limitations of unstandardized data from different sources. However, the detection of BD still remains challenging compared with other larger-scale and often more abrupt forest cover changes such as those caused by fire or harvesting (Guindon et al., 2014; Neigh et al., 2014; Cohen et al., 2016). Higher spatio-temporal resolution, combined with field observations, is required to relate remotely detected damage to the agent and severity (Hall et al., 2016). In addition, further studies are needed to more accurately link disturbance severity and resulting ecosystem impacts (e.g. carbon sequestration) under different environmental conditions. The call for future monitoring to provide more

accurate estimates of area and severity of forest pests for car-
bon policy in Canada is but one example of the need for
more consistent pest monitoring data (Bernier *et al.*, 2012;
Hall *et al.*, 2016). Both detection and impact assessment
seem particularly challenging for disturbances that do not
immediately cause mortality, such as defoliation or top-kill,
yet significantly reduce stand physiological health and pro-
ductivity, consequently affecting the stand's capability to pro-
vide certain ecosystem services. Complementary to forest
monitoring, palaeo-ecological approaches, e.g. using tree-ring
or sedimentary records, can be particularly useful to recon-
struct past disturbance events and to detect changes in natu-
ral disturbance regimes and their biogeochemical
consequences over centennial to millennial time-scales (see
review by McLauchlan *et al.*, 2014).

While today's DGVM mostly include fire as a disturbance
factor (Arneth *et al.*, 2012; Fisher *et al.*, 2014), BD are poorly
represented to date, although they are gaining increasing
attention (Arneth & Niinemets, 2010; Quillet *et al.*, 2010;
McDowell *et al.*, 2011; Fisher *et al.*, 2014). Typically, a con-
stant annual rate (e.g. 1%) is used as a proxy for 'back-
ground' tree mortality, which summarizes mortality due to
all non-fire natural disturbances without specifying various
causes and processes (McDowell *et al.*, 2011). As yet, DGVM
consider neither specific BD agents nor their spatial and tem-
poral variability. Only few represent forest structure (height,
age classes), which would allow the models to account for
disturbance-related mortality and ensuing regrowth. Our
findings highlight the relevance of adequately capturing BD,
in addition to the well-implemented fire disturbances, in
DGVM. Moreover, interactions between different natural dis-
turbances (biotic, abiotic and fire) and their complex inter-
play with changing environmental conditions need to be
considered when studying and modelling forest ecosystem
functioning and dynamics (Seidl *et al.*, 2011; Temperli *et al.*,
2015). Despite the absence of data on these interactions in
most disturbance data sets, evidence based on recent case
studies (see reviews by Desprez-Loustau *et al.*, 2006; Hicke
et al., 2012b) may facilitate their implementation in next-
generation ecosystem models (Anderegg *et al.*, 2015). A par-
ticular challenge arises from the need to model disturbances,
their occurrence and impacts in a process-based way that is
feasible for global-scale models (in contrast to stand- or
landscape-scale approaches, which allow a more detailed con-
sideration; see Seidl *et al.*, 2011; Keane *et al.*, 2015, and refer-
ences therein). As a way forward, we suggest improving the
representation of BD in such models primarily by (1)
accounting for spatio-temporal variability of disturbance-
related mortality rather than using a constant rate, and (2)
separating different BD agents and their specific disturbance
mechanisms, which account for varying degrees of severity
(BD functional types; cf. Dietze & Hatala Matthes, 2014;
Landry *et al.*, 2016).

Based on our findings, we suggest prioritizing high-impact
agents affecting large forest fractions at high severity levels,
i.e. tree-killing bark beetles and defoliators, when

implementing BD in global models, while medium- (other
insects, pathogens) and low-impact agents (wildlife herbi-
vory) become more relevant at finer spatial scales, e.g. at
landscape to regional scales. We suggest that a hierarchical
implementation, applying the concept of BD functional
types, will best account for the particular characteristics of
different BD agents (cf. Kasischke *et al.*, 2013) and will also
reflect the nonlinear relationship between disturbance severity
and ecosystem impacts (Flower & Gonzales-Meler, 2015;
Stuart-Haëntjens *et al.*, 2015).

CONCLUSIONS

By synthesizing recent disturbance data we reveal, for the
first time, large-scale patterns of BD occurrence and impacts
across Northern Hemisphere forests. Our results indicate that
BD make a significant contribution to forest dynamics and
that BD-induced tree mortality and that the resulting forest
carbon fluxes are important processes which may require
particular attention when modelling forests at the biome to
global scale. At these scales, the magnitude of impacts due to
BD is shown to be comparable to fire impacts. BD trends are
characterized by a large temporal and spatial variability,
mainly as a result of ephemeral insect outbreaks. Hence, vari-
ability of BD, in both time and space, needs to be considered
when disturbance impacts on forests are analysed or pre-
dicted. Among the various BD agents, insects are considered
high-impact agents severely affecting Northern Hemisphere
forests, hierarchically followed by pathogens and wildlife her-
bivory, which cause less severe damage at larger scales. The
compiled spatially explicit, multi-year data set on BD frac-
tions in Northern Hemisphere forests may eventually facili-
tate a better integration of BD into future large-scale
ecosystem models such as DGVM, thereby leading to more
precise knowledge about global forest dynamics, carbon
budgets and climate feedbacks. Our review also stresses cur-
rent limitations due to varying data uncertainty across the
globe. For future work, we recommend: (1) a more sophisti-
cated representation of BD in global ecosystem models that
better considers spatio-temporal variability and disturbances
not resulting in immediate mortality, and (2) an improved
forest monitoring system to provide accessible, precise and
consistent data on BD occurrence and severity which are
harmonized across jurisdictions.

ACKNOWLEDGEMENTS

Technology Enterprise Team. Finally, we thank the two anonymous referees who provided comments that were helpful in improving the manuscript.

REFERENCES

Alfaro, R.I., Taylor, S., Brown, G. & Wegwitz, E. (1999) Tree mortality caused by the western hemlock looper in landscapes of central British Columbia. *Forest Ecology and Management*, **124**, 285–291.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A. & Cobb, N. (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, **259**, 660–684.

Anderegg, W.R.L., Hicke, J.A., Fisher, R.A., Allen, C.D., Aukema, J., Bentz, B., Hood, S., Lichstein, J.W., Macalady, A.K., McDowell, N., Pan, Y., Raffa, K., Sala, A., Shaw, J.D., Stephenson, N.L., Tague, C. & Zeppel, M. (2015) Tree mortality from drought, insects, and their interactions in a changing climate. *New Phytologist*, **208**, 674–683.

Arneth, A. & Niinemets, U. (2010) Induced BVOCs: how to bug our models? *Trends in Plant Science*, **15**, 118–125.

Arneth, A., Mercado, L., Kattge, J. & Booth, B.B.B. (2012) Future challenges of representing land-processes in studies on land–atmosphere interactions. *Biogeosciences*, **9**, 3587–3599.

Backsen, J.C. & Howell, B. (2013) Comparing aerial detection and photo interpretation for conducting forest health surveys. *Western Journal of Applied Forestry*, **28**, 3–8.

Bakke, A. (1991) Using pheromones in the management of bark beetle outbreaks. *Forest insects guilds: patterns of interaction with host trees* (ed. by Y.N. Baranchikov, W.J. Mattson, F.P. Hain and T.L. Payne), pp. 371–377. USDA Forest Service General Technical Report NE-153.

Bartholomé, E. & Belward, A.S. (2005) GLC2000: a new approach to global land cover mapping from Earth observation data. *International Journal of Remote Sensing*, **26**, 1959–1977.

Bentz, B.J., Régnière, J., Fettig, C.J., Hansen, E.M., Hayes, J.L., Hicke, J.A., Kelsey, R.G., Negrón, J.F. & Seybold, S.J. (2010) Climate change and bark beetles of the western United States and Canada: direct and indirect effects. *BioScience*, **60**, 602–613.

Bernier, P., Kurz, W.A., Lemprière, T. & Ste-Marie, C. (2012) *A blueprint for forest carbon science in Canada 2012 − 2020*. Natural Resources Canada, Canadian Forest Service, Ottawa. Available at: http://cfs.nrcan.gc.ca/pubwarehouse/pdfs/34222.pdf (accessed 20 February 2016).

BIO Intelligence Service (2011) *Disturbances of EU forests caused by biotic agents*. Final report, prepared for European Commission (DG ENV).

Bjørnstad, O.N., Peltonen, M., Liebhold, A.M. & Baltensweiler, W. (2002) Waves of larch budmoth outbreaks in the European Alps. *Science*, **298**, 1020–1023.

Boyd, I.L., Freer-Smith, P.H., Gilligan, C.A. & Godfray, H.C.J. (2013) The consequences of tree pests and diseases for ecosystem services. *Science*, **342**, 1235773.

Branco, M., Bragança, H., Sousa, E. & Phillips, A.J.L. (2014) Pests and diseases in Portuguese forestry: current and new threats. *Forest context and policies in Portugal* (ed. by F. Reboredo), pp. 117–154. Springer, Cham, Switzerland.

Buma, B. (2015) Disturbance interactions: characterization, prediction, and the potential for cascading effects. *Ecosphere*, **6(4)**, art. 70.

Canadian Council of Forest Ministers (2012) *Forest pest monitoring in Canada: current situation, compatibilities, gaps and proposed enhanced monitoring program*. Canadian Forest Service, Ottawa. Available at: http://www.ccfm.org/pdf/PestMonitoring_2012_en.pdf (accessed 30 November 2016).

Canadian Forest Service (2016) *National forestry database*. Available at: http://nfdp.ccfm.org (accessed 20 February 2016).

Cohen, W.B., Yang, Z., Stehman, S.V., Schroeder, T.A., Bell, D.M., Masek, J.G., Huang, C. & Meigs, G.W. (2016) Forest disturbances across the conterminous United States from 1985 − 2012: the emerging dominance of forest decline. *Forest Ecology and Management*, **360**, 242–252.

Cooke, B.J., Nealis, V.G. & Régnière, J. (2007) Insect defoliators as periodic disturbances in northern forest ecosystems. *Plant disturbance ecology* (ed. by E.A. Johnson and K. Miyanishi), pp. 487–525. Academic Press, New York

Cullingham, C.I., Cooke, J.E.K., Dang, S., Davis, C.S., Cooke, B.J. & Coltman, D.W. (2011) Mountain pine beetle host-range expansion threatens the boreal forest. *Molecular Ecology*, **20**, 2157–2171.

Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R.P., Ayres, M.P., Flannigan, M.D., Hanson, P.J., Irland, L.C., Lugo, A.E., Peterson, C.J., Simberloff, D., Swanson, F.J., Stocks, B.J. & Wotton, B.M. (2001) Climate change and forest disturbances. *BioScience*, **51**, 723–734.

Desprez-Loustau, M.L., Marçais, B., Nageleisen, L.M., Piou, D. & Vannini, A. (2006) Interactive effects of drought and pathogens in forest trees. *Annals of Forest Science*, **63**, 597–612.

Dietze, M.C. & Hatala Matthes, J. (2014) A general ecophysiological framework for modelling the impact of pests and pathogens on forest ecosystems. *Ecological Letters*, **17**, 1418–1426.

Dolman, A.J., Shvidenko, A., Schepaschenko, D., Ciais, P., Tchebakova, N., Chen, T., van der Molen, M.K., Belelli Marchesini, L., Maximov, T.C., Maksyutov, S. & Schulze, E.D. (2012) An estimate of the terrestrial carbon budget of Russia using inventory-based, eddy covariance and inversion methods. *Biogeosciences*, **9**, 5323–5340.

Dymond, C.C., Neilson, E.T., Stinson, G., Porter, K., MacLean, D.A., Gray, D.R., Campagna, M. & Kurz, W.A. (2010) Future spruce budworm outbreak may create a

carbon source in eastern Canadian forests. *Ecosystems*, **13**, 917–931.

Edburg, S.L., Hicke, J.A., Lawrence, D.M. & Thornton, P.E. (2011) Simulating coupled carbon and nitrogen dynamics following mountain pine beetle outbreaks in the western United States. *Journal of Geophysical Research: Biogeosciences*, **116**, G04033.

Edburg, S.L., Hicke, J.A., Brooks, P.D., Pendall, E.G., Ewers, B.E., Norton, U., Gochis, D., Gutmann, E.D. & Meddens, A.J.H. (2012) Cascading impacts of bark beetle-caused tree mortality on coupled biogeophysical and biogeochemical processes. *Frontiers in Ecology and the Environment*, **10**, 416–424.

Eichhorn, J., Roskamp, P., Ferretti, M., Mues, V., Szepesi, A. & Durrant, D. (2010) Visual assessment of crown condition and damaging agents. Manual part IV. UNECE ICP Forest Programme Co-ordinating Centre, Hamburg. Available at http://icp-forests.net/page/icp-forests-manual (accessed 30 November 2016).

FAO (2006) *Global forest resources assessment 2005*. FAO Forestry Paper 147. Food and Agriculture Organization of the United Nations, Rome, Italy.

FAO (2010) *Global forest resources assessment 2010*. FAO Forestry Paper 163. Food and Agriculture Organization of the United Nations, Rome, Italy. Available at http://countrystat.org/home.aspx?c=FOR&tr=5 (accessed 20 February 2016).

Federal Service of Forest Management, Russia (2006) *Major indicators of forest management activities for 1988, 1992–2005*. Roslesinforg, Moscow, Russia (in Russian).

Fisher, J.B., Huntzinger, D.N., Schwalm, C.R. & Sitch, S. (2014) Modeling the terrestrial biosphere. *Annual Review of Environment and Resources*, **39**, 91–123.

Flower, C.E. & Gonzales-Meler, M.A. (2015) Responses of temperate forest productivity to insect and pathogen disturbances. *Annual Review of Plant Biology*, **66**, 547–569.

Forest Agency, Japan (2009) *State of Japan's forests and forest management*. 2nd country report of Japan to the Montreal Process. Forestry Agency, Japan, Tokyo.

Forster, B., Knížek, M. & Grodzki, W. (eds) (1999) *Methodology of forest insect and disease survey in Central Europe. Proceedings of the 2nd workshop of the IUFRO WP 7.03.10, April 20–23, 1999, Sion-Châteauneuf, Switzerland*. Swiss Federal Institute for Forest, Snow and Landscape Research, Birmensdorf.

Fu, C., Fang, H. & Yu, G. (2011) Carbon emissions from forest vegetation caused by three major disturbances in China. *Journal of Resources and Ecology*, **2**, 202–209.

Ghimire, B., Williams, C.A., Collatz, G.J. & Vanderhoof, M. (2012) Fire-induced carbon emissions and regrowth uptake in western U.S. forests: documenting variation across forest types, fire severity, and climate regions. *Journal of Geophysical Research: Biogeosciences*, **117**, G03036.

Ghimire, B., Williams, C.A., Collatz, G.J., Vanderhoof, M., Rogan, J., Kulakowski, D. & Masek, J.G. (2015) Large carbon release legacy from bark beetle outbreaks across western United States. *Global Change Biology*, **21**, 3087–3101.

Giglio, L., Randerson, J.T. & van der Werf, G.R. (2013) Analysis of daily, monthly, and annual burned area using the fourth-generation global fire emissions database (GFED4). *Journal of Geophysical Research: Biogeosciences*, **118**, 317–328.

Gninenko, Y.I. & Orlinskii, A.D. (2002) *Dendrolimus sibiricus* in the coniferous forests of European Russia at the beginning of the twenty-first century. *OEPP/EPPO Bulletin*, **32**, 481–483.

Gray, D.R. & MacKinnon, W.E. (2006) Outbreak patterns of the spruce budworm and their impacts in Canada. *The Forestry Chronicle*, **82**, 550–561.

Grégoire, J.C. & Evans, H.F. (2004) Damage and control of BAWBILT organisms, an overview. *Bark and wood boring insects in living trees in Europe, a synthesis* (ed. by F. Lieutier, K.R. Day, A. Battisti, J.-C. Grégoire and H.F. Evans), pp. 19–37. Kluwer Academic Publishers, Dordrecht.

Gromtsev, A. (2002) Natural disturbance dynamics in the boreal forests of European Russia: a review. *Silva Fennica*, **36**, 41–55.

Guindon, L., Bernier, P.Y., Beaudoin, A., Pouliot, D., Villemaire, P., Hall, R.J., Latifovic, R. & St-Amant, R. (2014) Annual mapping of large forest disturbances across Canada's forests using 250 m MODIS imagery from 2000 to 2011. *Canadian Journal of Forest Resources*, **44**, 1545–1554.

Hall, R.J., Castilla, G., White, J.C., Cooke, B.J. & Skakun, R.S. (2016) Remote sensing of forest pest damage: a review and lessons learned from a Canadian perspective. *The Canadian Entomologist*, **148**. doi:10.4039/tce.2016.11.

Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O. & Townshend, J.R.G. (2013) High-resolution global maps of 21st-century forest cover change. *Science*, **342**, 850–853.

Hartig, F., Dyke, J., Hickler, T., Higgins, S.I., OHara, R., Scheiter, S. & Huth, A. (2012) Connecting dynamic vegetation models to data – an inverse perspective. *Journal of Biogeography*, **39**, 2240–2252.

Hicke, J.A., Allen, C.D., Desai, A.R., Dietze, M.C., Hall, R.J., Hogg, E.H., Kashian, D.M., Moore, D., Raffa, K.F., Sturrock, R.N. & Vogelmann, J. (2012a) Effects of biotic disturbances on forest carbon cycling in the United States and Canada. *Global Change Biology*, **18**, 7–34.

Hicke, J.A., Johnson, M.C., Hayes, J.L. & Preisler, H.K. (2012b) Effects of bark beetle-caused tree mortality on wildfire. *Forest Ecology and Management*, **271**, 81–90.

Hicke, J.A., Meddens, A.J.H., Allen, C.D. & Kolden, C.A. (2013) Carbon stocks of trees killed by bark beetles and wildfire in the western United States. *Environmental Research Letters*, **8**, 035032.

Huang, L., Ning, Z. & Zhang, X. (2010) Impacts of caterpillar disturbance on forest net primary production estimation in China. *Ecological Indicators*, **10**, 1144–1151.

Hui, Y. & Xue-Song, D. (1999) Impacts of *Tomicus minor* on distribution and reproduction of *Tomicus piniperda* (Col., Scolytidae) on the trunk of the living *Pinus yunnanensis* trees. *Journal of Applied Entomology*, **123**, 329–333.

Jepsen, J.U., Hagen, S.B., Høgda, K.A., Ims, R.A., Karlsen, S.R., Tømmervik, H. & Yoccoz, N.G. (2009) Monitoring the spatio-temporal dynamics of geometrid moth outbreaks in birch forest using MODIS-NDVI data. *Remote Sensing of Environment*, **113**, 1939–1947.

Ji, L., Wang, Z., Wang, X. & An, L. (2011) Forest insect pest management and forest management in China: an overview. *Environmental Management*, **48**, 1107–1121.

Johnson, E.W. & Ross, J. (2008) Quantifying error in aerial survey data. *Australian Forestry*, **71**, 216–222.

Jönsson, A.M., Harding, S., Barring, L. & Ravn, H.P. (2007) Impact of climate change on the population dynamics of *Ips typographus* in southern Sweden. *Agricultural and Forest Meteorology*, **146**, 70–81.

Jönsson, A.M., Schroeder, L.M., Lagergren, F., Anderbrant, O. & Smith, B. (2012) Guess the impact of *Ips typographus* – an ecosystem modelling approach for simulating spruce bark beetle outbreaks. *Agricultural and Forest Meteorology*, **166**, 188–200.

Kasischke, E.S., Amiro, B.D., Barger, N.N., French, N.H.F., Goetz, S.J., Grosse, G., Harmon, M.E., Hicke, J.A., Liu, S. & Masek, J.G. (2013) Impacts of disturbance on the terrestrial carbon budget of North America. *Journal of Geophysical Research: Biogeosciences*, **118**, 303–316.

Kautz, M. (2014) On correcting the time-lag bias in aerial-surveyed bark beetle infestation data. *Forest Ecology and Management*, **326**, 157–162.

Kautz, M., Dworschak, K., Gruppe, A. & Schopf, R. (2011) Quantifying spatio-temporal dispersion of bark beetle infestations in epidemic and non-epidemic conditions. *Forest Ecology and Management*, **262**, 598–608.

Keane, R.E., McKenzie, D., Falk, D.E., Smithwick, E.A.H., Miller, C. & Kellogg, L.K.B. (2015) Representing climate, disturbance, and vegetation interactions in landscape models. *Ecological Modelling*, **309–310**, 33–47.

Kharuk, V.I., Ranson, K.J. & Fedotova, E.V. (2007) Spatial pattern of Siberian silk moth outbreak and taiga mortality. *Scandinavian Journal of Forest Research*, **22**, 531–536.

Krist, F.J., Jr, Sapio, F.J. & Tkacz, B.M. (2007) *Mapping risk from forest insects and diseases*. FHTET 2007-06. United States Department of Agriculture, Washington, DC.

Krist, F.J., Jr, Ellenwood, J.R., Woods, M.E., McMahan, A.J., Cowardin, J.P., Ryerson, D.E., Sapio, F.J., Zweifler, M.O. & Romero, S.A. (2014) *2013–2027 National insect and disease forest risk assessment*. FHTET 14-01. United States Department of Agriculture, Washington, DC.

Kurz, W.A. & Apps, M.J. (1999) A 70-year retrospective analysis of carbon fluxes in the Canadian forest sector. *Ecological Applications*, **9**, 526–547.

Kurz, W.A., Dymond, C.C., Stinson, G., Rampley, G.J., Neilson, E.T., Carroll, A.L., Ebata, T. & Safranyik, L. (2008) Mountain pine beetle and forest carbon feedback to climate change. *Nature*, **452**, 987–990.

Kurz, W.A., Shaw, C.H., Boisvenue, C., Stinson, G., Metsaranta, J., Leckie, D., Dyk, A., Smyth, C. & Neilson, E.T. (2013) Carbon in Canada's boreal forest – a synthesis. *Environmental Reviews*, **21**, 260–292.

Landry, J.S., Price, D.T., Ramankutty, N., Parrott, L. & Matthews, H.D. (2016) Implementation of a marauding insect module (MIM, version 1.0) in the integrated biosphere simulator (IBIS, version 2.6b4) dynamic vegetation–land surface model. *Geoscientific Model Development*, **9**, 1243–1261.

La Porta, N., Capretti, P., Thomsen, I.M., Kasanen, R., Hietala, A.M. & Von Weissenberg, K. (2008) Forest pathogens with higher damage potential due to climate change in Europe. *Canadian Journal of Plant Pathology*, **30**, 177–195.

Le Page, Y., Hurtt, G., Thomson, A.M., Bond-Lamberty, B., Patel, P., Wise, M., Calvin, K., Kyle, P., Clarke, L., Edmonds, J. & Janetos, A. (2013) Sensitivity of climate mitigation strategies to natural disturbances. *Environmental Research Letters*, **8**, 015018.

Le Quéré, C., Moriarty, R., Andrew, R.M. *et al.* (2015) Global carbon budget 2014. *Earth System Science Data*, **7**, 47–85.

Liebhold, A.M., Macdonald, W.L., Bergdahl, D. & Mastro, V.C. (1995) Invasion by exotic forest pests: a threat to forest ecosystems. *Forest Science Monograph*, **30**, 1–49.

van Lierop, P., Lindquist, E., Sathyapala, S. & Franceschini, G. (2015) Global forest area disturbance from fire, insect pests, diseases and severe weather events. *Forest Ecology and Management*, **352**, 78–88.

Liu, S.G., Bond-Lamberty, B., Hicke, J.A., Vargas, R., Zhao, S.Q., Chen, J., Edburg, S.L., Hu, Y.M., Liu, J.X., McGuire, A.D., Xiao, J.F., Keane, R., Yuan, W.P., Tang, J.W., Luo, Y.Q., Potter, C. & Oeding, J. (2011) Simulating the impacts of disturbances on forest carbon cycling in North America: processes, data, models, and challenges. *Journal of Geophysical Research: Biogeosciences*, **116**, G00k08.

Loo, J.A. (2009) Ecological impacts of non-indigenous invasive fungi as forest pathogens. *Biological Invasions*, **11**, 81–96.

Lupu, D., Mihalache, G. & Ciorne, C. (1999) Aspects regarding the phytosanitary state of broad-leaved forests in Romania in 1998. *Methodology of forest insect and disease survey in Central Europe. Proceedings of the 2nd workshop of the IUFRO WP 7.03.10, April 20–23, 1999, Sion-Châteauneuf, Switzerland* (ed. by B. Forster, M. Knížek and W. Grodzki), pp. 42–47. Swiss Federal Institute for Forest, Snow and Landscape Research, Birmensdorf.

McDowell, N.G., Beerling, D.J., Breshears, D.D., Fisher, R.A., Raffa, K.F. & Stitt, M. (2011) The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends in Ecology and Evolution*, **26**, 523–532.

McDowell, N.G., Coops, N.C., Beck, P.S.A. *et al.* (2015) Global satellite monitoring of climate-induced vegetation disturbances. *Trends in Plant Science*, **20**, 114–123.

McLauchlan, K.K., Higuera, P.E. *et al.* (2014) Reconstructing disturbances and their biogeochemical consequences over multiple timescales. *BioScience*, **64**, 105–116.

MacLean, D.A. & MacKinnon, W.E. (1996) Accuracy of aerial sketch-mapping estimates of spruce budworm defoliation in New Brunswick. *Canadian Journal of Forest Research*, **26**, 2099–2108.

MacLean, D.A., Erdle, T.A., MacKinnon, W.E., Porter, K.B., Beaton, K.P., Cormier, G., Morehouse, S. & Budd, M. (2001) The spruce budworm decision support system: forest protection planning to sustain long-term wood supply. *Canadian Journal of Forest Research*, **31**, 1742–1757.

Malysheva, N., Shvidenko, A., Nilsson, S., Petelina, S. & Öskog, A. (2000) *An overview of remote sensing in Russian forestry*. IR-00-034. International Institute for Applied Systems Analysis, Laxenburg, Austria.

Mamiya, Y. (1988) History of pine wilt disease in Japan. *Journal of Nematology*, **20**, 219–226.

Meddens, A.J.H., Hicke, J.A. & Ferguson, C.A. (2012) Spatio-temporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States. *Ecological Applications*, **22**, 1876–1891.

Meddens, A.J.H., Hicke, J.A., Macalady, A.K., Buotte, P.C., Cowles, T.R. & Allen, C.D. (2015) Patterns and causes of observed piñon pine mortality in the southwestern United States. *New Phytologist*, **206**, 91–97.

Meentemeyer, R.K., Rank, N.E., Shoemaker, D.A., Oneal, C.B., Wickland, A.C., Frangioso, K.M. & Rizzo, D.M. (2008) Impact of sudden oak death on tree mortality in the Big Sur ecoregion of California. *Biological Invasions*, **10**, 1243–1255.

Michaelian, M., Hogg, E.H., Hall, R.J. & Arsenault, E. (2011) Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest. *Global Change Biology*, **17**, 2084–2094.

Millar, C.I., Stephenson, N.L. & Stephens, S.L. (2007) Climate change and forests of the future: managing in the face of uncertainty. *Ecological Applications*, **17**, 2145–2151.

Ministry of Nature and Environment, Mongolia (1998) *Biological diversity in Mongolia. 1st national report*. Ministry of Nature and Environment, Ulaanbaatar, Mongolia.

Ministry of Nature and Environment, Mongolia (2002) *Report on national forest and water policy of Mongolia*. Ministry of Nature and Environment, Ulaanbaatar, Mongolia.

Montréal Process (2003) *First forest overview report 2003*. Available at: http://www.montrealprocess.org (accessed 20 February 2016).

Moore, B.A. & Allard, G. (2011) *Abiotic disturbances and their influence on forest health. FAO Working Paper FBS/35E*. Food and Agriculture Organization of the United Nations, Rome, Italy.

Mozolevskaya, E.G., Utkina, I.A. & Matusevich, L.S. (2003) Dynamics of foci of forest pest insects in Russia over the last decade. *Proceedings. Ecology, survey and management of forest insects* (ed. by M.L. McManus and A.M. Liebhold), pp. 61–67. USDA Forest Service General Technical Report NE-311. USDA Forest Service, Newtown Square, PA.

Myers, J.H. & Cory, J.S. (2013) Population cycles in forest Lepidoptera revisited. *Annual Review of Ecology, Evolution, and Systematics*, **44**, 565–592.

Neigh, C.S.R., Bolton, D.K., Diabate, M., Williams, J.J. & Carvalhais, N. (2014) An automated approach to map the history of forest disturbance from insect mortality and harvest with Landsat time-series data. *Remote Sensing*, **6**, 2782–2808.

Ohmart, C.P. (1989) Why are there so few tree-killing bark beetles associated with angiosperms? *Oikos*, **54**, 242–245.

Orwig, D.A., Foster, D.R. & Mausel, D.L. (2002) Landscape patterns of hemlock decline in New England due to the introduced hemlock woolly adelgid. *Journal of Biogeography*, **29**, 1475–1487.

Økland, B., Liebhold, A.M., Bjørnstad, O.N., Erbilgin, N. & Krokene, P. (2005) Are bark beetle outbreaks less synchronous than forest Lepidoptera outbreaks? *Oecologia*, **146**, 365–372.

Økland, B., Nikolov, C., Krokene, P. & Vakula, J. (2016) Transition from windfall- to patch-driven outbreak dynamics of the spruce bark beetle *Ips typographus*. *Forest Ecology and Management*, **363**, 63–73.

Pasztor, F., Matulla, C., Rammer, W. & Lexer, M.J. (2014) Drivers of the bark beetle disturbance regime in Alpine forests in Austria. *Forest Ecology and Management*, **318**, 349–358.

Potapov, P., Turubanova, S., Zhuravleva, I., Hansen, M., Yaroshenko, A. & Manisha, A. (2012) Forest cover change within the Russian European north after the breakdown of Soviet Union (1990–2005). *International Journal of Forestry Research*, **2012**, doi:10.1155/2012/729614.

Quillet, A., Peng, C. & Garneau, M. (2010) Toward dynamic global vegetation models for simulating vegetation-climate interactions and feedbacks: recent developments, limitations, and future challenges. *Environmental Reviews*, **18**, 333–353.

Régolini, M., Castagneyrol, B., Dulaurent-Mercadal, A.M., Piou, D., Samalens, J.C. & Jactel, H. (2014) Effect of host tree density and apparency on the probability of attack by the pine processionary moth. *Forest Ecology and Management*, **334**, 185–192.

Rogers, B.M., Soja, A.J., Goulden, M.L. & Randerson, J.T. (2015) Influence of tree species on continental differences in boreal fires and climate feedbacks. *Nature Geoscience*, **8**, 228–234.

Ruesch, A. & Gibbs, H.K. (2008) *New IPCC Tier1 global biomass carbon map for the year 2000*. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, TN. Available at: http://cdiac.ornl.gov/epubs/ndp/global_carbon/carbon_documentation.html (accessed 20 February 2016).

Santini, A., Ghelardini, L., De Pace, C. et al. (2013) Biogeographical patterns and determinants of invasion by forest pathogens in Europe. *New Phytologist*, **197**, 238–250.

Savinov, A.I. (2009) *Criteria and indicators for the conservation and sustainable management of temperate and boreal forests (Montreal Process): Russian Federation's national report.* Moscow, Russia. Available at http://www.rinya.maff.go.jp/j/kaigai/pdf/2009r_3.pdf (accessed 30 November 2016)

Schelhaas, M.J., Nabuurs, G.J. & Schuck, A. (2003a) Natural disturbances in the European forests in the 19th and 20th centuries. *Global Change Biology*, **9**, 1620–1633.

Schelhaas, M.J., Schuck, A. & Varis, S. (2003b) *Database on forest disturbances in Europe (DFDE) – technical description.* EFI Internal Report 14. European Forest Institute, Joensuu, Finland. Available at http://www.efi.int/files/attachments/publications/ir_14.pdf (accessed 30 November 2016)

Schemske, D.W., Mittelbach, G.G., Cornell, H.V., Sobel, J.M. & Kaustuv, R. (2009) Is there a latitudinal gradient in the importance of biotic interactions? *Annual Review of Ecology, Evolution, and Systematics*, **40**, 245–269.

Schrader-Patton, C. (2003) *Digital aerial sketchmapping.* USDA Forest Service Report RSAC-1202-RPT2. USDA Forest Service, Remote Sensing Applications Center, Fort Collins, CO.

Seidl, R., Rammer, W., Jäger, D. & Lexer, M.J. (2008) Impact of bark beetle (*Ips typographus* L.) disturbance on timber production and carbon sequestration in different management strategies under climate change. *Forest Ecology and Management*, **256**, 209–220.

Seidl, R., Fernandes, P.M., Fonseca, T.F., Gillet, F., Jönsson, A.M., Merganičová, K., Netherer, S., Arpaci, A., Bontemps, J.D., Bugmann, H., González-Olabarria, J.R., Lasch, P., Meredieu, C., Moreira, F., Schelhaas, M.J. & Mohren, F. (2011) Modelling natural disturbances in forest ecosystems: a review. *Ecological Modelling*, **222**, 903–924.

Seidl, R., Schelhaas, M.J., Rammer, W. & Verkerk, P.J. (2014) Increasing forest disturbances in Europe and their impact on carbon storage. *Nature Climate Change*, **4**, 806–810.

Seidl, R., Müller, J., Hothorn, T., Bässler, C., Heurich, M. & Kautz, M. (2016) Small beetle, large-scale drivers: how regional and landscape factors affect outbreaks of the European spruce bark beetle. *Journal of Applied Ecology*, **53**, 530–540.

Selikhovkin, A.V. (2005) Main disturbance factors in northwest Russian forests: structure and databases. *Scandinavian Journal of Forest Research*, **20**, 27–32.

Shorohova, E., Kuuluvainen, T., Kangur, A. & Jõgiste, K. (2009) Natural stand structures, disturbance regimes and successional dynamics in the Eurasian boreal forests: a review with special reference to Russian studies. *Annals of Forest Science*, **66**, 1–20.

Shvidenko, A.Z., Gustafson, E., McGuire, A.D., Kharuk, V.I., Schepaschenko, D.G., Shugart, H.H., Tchebakova, N.M., Vygodskaya, N.N., Onuchin, A.A., Hayes, D.J., McCallum, I., Maksyutov, S., Mukhortova, L.V., Soja, A.J., Belelli-Marchesini, L., Kurbatova, J.A., Oltchev, A.V., Parfenova, E.I. & Shuman, J.K. (2013) Terrestrial ecosystems and their change. *Regional environmental changes in Siberia and their global consequences* (ed. by P.Y. Groisman, and G. Gutman), pp. 172–249. Springer, Heidelberg.

Stadelmann, G., Bugmann, H., Wermelinger, B. & Bigler, C. (2014) Spatial interactions between storm damage and subsequent infestations by the European spruce bark beetle. *Forest Ecology and Management*, **318**, 167–174.

State Forestry Administration, P.R. China (2013) *National report on sustainable forest management.* China Forestry Publishing House, Beijing.

Stinson, G., Kurz, W.A., Smyth, C.E., Neilson, E.T., Dymond, C.C., Metsaranta, J.M., Boisvenue, C., Rampley, G.J., Li, Q., White, T.M. & Blain, D. (2011) An inventory-based analysis of Canada's managed forest carbon dynamics, 1990 to 2008. *Global Change Biology*, **17**, 2227–2244.

Stuart-Haëntjens, E., Curtis, P.S., Fahey, R.T., Vogel, C.S. & Gough, C.M. (2015) Net primary production of a temperate deciduous forest exhibits a threshold response to increasing disturbance severity. *Ecology*, **96**, 2478–2487.

Sturrock, R.N., Frankel, S.J., Brown, A.V., Hennon, P.E., Kliejunas, J.T., Lewis, K.J., Worrall, J.J. & Woods, A.J. (2011) Climate change and forest diseases. *Plant Pathology*, **60**, 133–149.

Sun, J., Lu, M., Gillette, N.E. & Wingfield, M.J. (2013) Red turpentine beetle: innocuous native becomes invasive tree killer in China. *Annual Review of Entomology*, **58**, 293–311.

Temperli, C., Bugmann, H. & Elkin, C. (2013) Cross-scale interactions among bark beetles, climate change, and wind disturbances: a landscape modeling approach. *Ecological Monographs*, **83**, 383–402.

Temperli, C., Veblen, T.T., Hart, S.J., Kulakowski, D. & Tepley, A.J. (2015) Interactions among spruce bark beetle disturbances, climate change and forest dynamics captured by a forest landscape model. *Ecosphere*, **6**, 231.

Tenow, O., Nilssen, A.C., Bylund, H. et al. (2013) Geometrid outbreak waves travel across Europe. *Journal of Animal Ecology*, **82**, 84–95.

The Nature Conservancy (2009) *Global terrestrial ecoregions.* The Nature Conservancy, Arlington, VA. Available at: http://maps.tnc.org/gis_data.html (accessed 20 February 2016).

Thom, D. & Seidl, R. (2016) Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. *Biological Reviews*, **91**, 760–781.

USDA Forest Service (2005) *Aerial survey geographic information system handbook.* United States Department of Agriculture, Washington, DC.

USDA Forest Service (2010) *Major forest insect and disease conditions in the United States: 2009 update.* FS-952. United States Department of Agriculture, Washington, DC.

USDA Forest Service (2016) *Insect and disease survey data base.* Available at: http://foresthealth.fs.usda.gov (accessed 20 February 2016).

Volney, W.J.A. & Fleming, R.A. (2000) Climate change and impacts of boreal forest insects. *Agriculture, Ecosystems and Environment*, **82**, 283–294.

Wear, D.N. & Greis, J.G. (2013) *The southern forest futures project: technical report*. SRS-GTR-178. USDA Forest Service, Asheville, NC.

Weed, A.S., Ayres, M.P. & Hicke, J.A. (2013) Consequences of climate change for biotic disturbances in North American forests. *Ecological Monographs*, **83**, 441–470.

Werner, R.A., Holsten, E.H., Matsuoka, S.M. & Burnside, R.E. (2006) Spruce beetles and forest ecosystems in south-central Alaska: a review of 30 years of research. *Forest Ecology and Management*, **227**, 195–206.

Williams, A.P., Allen, C.D., Macalady, A.K., Griffin, D., Woodhouse, C.A., Meko, D.M., Swetnam, T.W., Rauscher, S.A., Seager, R., Grissino-Mayer, H.D., Dean, J.S., Cook, E.R., Gangodagamage, C., Cai, M. & McDowell, N.G. (2013) Temperature as a potent driver of regional forest drought stress and tree mortality. *Nature Climate Change*, **3**, 292–297.

Williams, C.A., Collatz, G.J., Masek, J. & Goward, S.N. (2012) Carbon consequences of forest disturbance and recovery across the conterminous United States. *Global Biogeochemical Cycles*, **26**, GB1005.

Wulder, M.A., Dymond, C.C., White, J.C., Leckie, D.G. & Carroll, A.L. (2006) Surveying mountain pine beetle damage of forests: a review of remote sensing opportunities. *Forest Ecology and Management*, **221**, 27–41.

Yan, Z., Sun, J., Don, O. & Zhang, Z. (2005) The red turpentine beetle, *Dendroctonus valens* LeConte (Scolytidae): an exotic invasive pest of pine in China. *Biodiversity and Conservation*, **14**, 1735–1760.

Yang, J., Dai, G. & Wang, S. (2015) China's national monitoring program on ecological functions of forests: an analysis of the protocol and initial results. *Forests*, **6**, 809–826.

Zhang, X., Lei, Y., Zhihai, M., Kneeshaw, D. & Peng, C. (2014) Insect-induced tree mortality of boreal forests in eastern Canada under a changing climate. *Ecology and Evolution*, **4**, 2384–2394.

Zhao, B.G. (2008) Pine wilt disease in China. *Pine wilt disease* (ed. by B.G. Zhao, K. Futai, J.R. Sutherland and Y. Takeuchi), pp. 18–25. Springer, Tokyo.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site:

Appendix S1 Biotic disturbance data sets as listed in Table 1.
Appendix S2 Availability of biotic disturbance data across global forests.

BIOSKETCH

Markus Kautz is a physical geographer interested in quantifying the impact of forest disturbances on ecological processes and ecosystem services, and how climatic changes may alter these impacts. He applies approaches of remote sensing, GIS and modelling across spatio-temporal scales, ranging from the single tree to global biomes.

Editor: Ben Poulter