

Mountain pine beetle and forest carbon feedback to climate change

W. A. Kurz¹, C. C. Dymond¹, G. Stinson¹, G. J. Rampley¹, E. T. Neilson¹, A. L. Carroll¹, T. Ebata² & L. Safranyik¹

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins, Coleoptera: Curculionidae, Scolytinae) is a native insect of the pine forests of western North America, and its populations periodically erupt into large-scale outbreaks^{1–3}. During outbreaks, the resulting widespread tree mortality reduces forest carbon uptake and increases future emissions from the decay of killed trees. The impacts of insects on forest carbon dynamics, however, are generally ignored in large-scale modelling analyses. The current outbreak in British Columbia, Canada, is an order of magnitude larger in area and severity than all previous recorded outbreaks⁴. Here we estimate that the cumulative impact of the beetle outbreak in the affected region during 2000–2020 will be 270 megatonnes (Mt) carbon (or 36 g carbon m⁻² yr⁻¹ on average over 374,000 km² of forest). This impact converted the forest from a small net carbon sink to a large net carbon source both during and immediately after the outbreak. In the worst year, the impacts resulting from the beetle outbreak in British Columbia were equivalent to ~75% of the average annual direct forest fire emissions from all of Canada during 1959–1999. The resulting reduction in net primary production was of similar magnitude to increases observed during the 1980s and 1990s as a result of global change⁵. Climate change has contributed to the unprecedented extent and severity of this outbreak⁶. Insect outbreaks such as this represent an important mechanism by which climate change may undermine the ability of northern forests to take up and store atmospheric carbon, and such impacts should be accounted for in large-scale modelling analyses.

Forest insect epidemics can have severe impacts on ecosystem dynamics by causing mortality and reducing the growth of millions of trees over extensive areas⁷. Native insects and alien invasive species affect both managed and natural forests. Beyond the ecological impacts are the associated economic (for example, disrupted timber supply to mills) and social (for example, unemployment, crime rates) effects⁸. The impact of insects on carbon (C) dynamics and global climate are not well documented⁹.

The current outbreak of mountain pine beetle in western Canada is an order of magnitude greater in area than previous outbreaks owing to the increased area of susceptible host (mature pine stands) and favourable climate⁴ (see also Supplementary Fig. 3). An expansion in climatically suitable habitat for the mountain pine beetle, including reduced minimum winter temperature, increased summer temperatures and reduced summer precipitation, during recent decades has facilitated expansion of the outbreak northward and into higher elevation forests^{4,10}. This range expansion, combined with an increase in the extent of the host, has resulted in an outbreak of unprecedented scale and severity. By the end of 2006, the cumulative outbreak area was 130,000 km² (many stands being attacked in multiple years), with tree mortality ranging from single trees to most of a

stand in a single year¹¹. Timber losses are estimated to be more than 435 million m³, with additional losses outside the commercial forest¹². The forest sector has responded by increasing harvest rates and reallocating some harvest, increasing the pine portion of the provincial total volume harvested from 31% to 45% over four years (2001–2004).

We estimated the combined impact of the beetle, forest fires and harvesting on forest productivity and carbon balance from 2000 until 2020 for the south-central region of British Columbia (Fig. 1). This area includes 374,000 km² of productive forest, largely dominated by pine (*Pinus*) and spruce (*Picea*) species. We used a Monte Carlo design for simulating future net biome production (NBP) using a forest ecosystem model (the Carbon Budget Model of the Canadian Forest Sector, CBM-CFS3). This model accounts for annual tree growth, litterfall, turnover and decay, and it explicitly simulates harvest, beetle-caused mortality, and fire-caused mortality and fuel consumption. We developed regional probability distribution functions of the annual area burned and projected future beetle dynamics on the basis of the characteristics of the remaining host (that is, pine stands of suitable age) and the judgement of regional entomologists. We conducted 100 Monte Carlo simulations with different random draws from the probability distributions for the annual area of beetle outbreak and the annual area burned.

For the period 2000–2020, the average annual NBP was -15.8 ± 7.9 Mt C yr⁻¹ (or -42.4 ± 21 g C m⁻² yr⁻¹; Fig. 2). Carbon losses result from emissions from decomposition and fires and from the transfer of timber to the forest product sector. In a separate analysis¹³, we estimated that the study area was a net sink from 1990 to 2002. The first two years of this study also reported a net sink (0.59 Mt C yr⁻¹), but with increasing beetle impact (Fig. 3), the forest converted to a source of 17.6 Mt C yr⁻¹ from 2003 to 2020. With decreasing beetle impact (Fig. 3), NBP began to recover, but by 2020, the estimated NBP had not yet returned to pre-outbreak levels. Although we can expect that forests will eventually recover from the beetle outbreak, we are reluctant to extend projections beyond 2020 or to speculate on the rate of recovery beyond 2020 given uncertainties about non-host responses, rates of regeneration, and future fires in a region in which major climate change impacts are forecast¹⁴.

One component of the uncertainty in future NBP is that we do not know the future area that will be infested by the beetle. We projected the area infested during 2007–2020 using random draws from regionally calibrated probability distributions of outbreak area and duration that were based on: the 2000–2006 area; mortality and host statistics; historical, spatial and temporal dynamics; remaining host population; and judgment from entomologists. The outbreak was projected to peak between 2006 and 2008, with the maximum area infested ranging from 74,000 km² to 94,000 km² (Fig. 3).

¹Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia, V8Z 1M5, Canada. ²British Columbia Ministry of Forests and Range, Victoria, British Columbia, V8W 9C2, Canada.

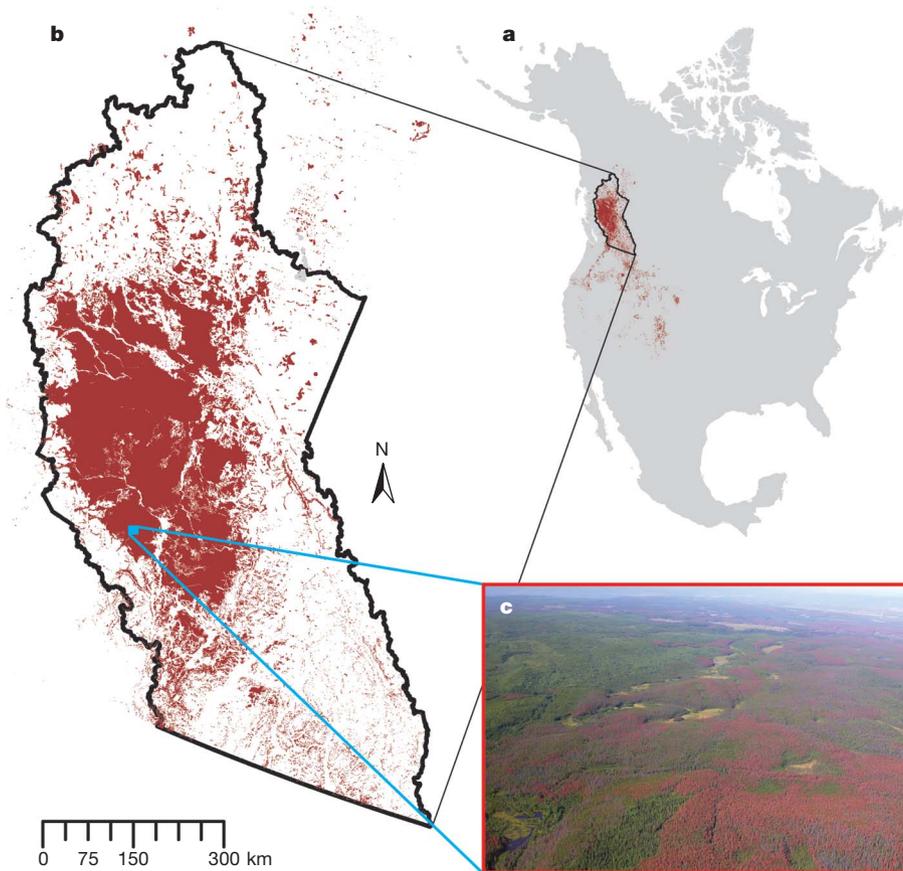


Figure 1 | Geographic extent of mountain pine beetle outbreak in North America. **a**, Extent (dark red) of mountain pine beetle. **b**, The study area includes 98% of the current outbreak area. **c**, A photograph taken in 2006

showing an example of recent mortality: pine trees turn red in the first year after beetle kill, and grey in subsequent years. Photo credit: Joan Westfall, Entopath Management Ltd.

We partitioned the impact of the beetle outbreak on NBP using a single projection of beetle (Fig. 3) and fire area and by simulating three forest carbon dynamics scenarios: without beetle (control), with beetle but no additional harvest, and with beetle and additional harvest. The additional harvest is considered to be part of the beetle impact because it is a management response to the vast quantities of beetle-killed trees. The impact of beetles on NBP was projected to

reach -20 Mt C yr^{-1} ($-53 \text{ g C m}^{-2} \text{ yr}^{-1}$) in 2009 (Fig. 4). Cumulative beetle impact over the 21-yr simulation period was projected to be -270 Mt C , and the additional salvage harvest and removal of both beetle-killed and living trees contributed a further -50 Mt C . Cumulative transfer of beetle-killed timber to the forest product sector was projected to be 31 Mt C (13% of total harvest). Harvesting results in a loss of carbon from the ecosystem, but only some of that carbon is emitted to the atmosphere; the remainder is stored in wood products and landfills.

NBP was reduced in the affected landscape by the beetle and the associated additional harvest response because of reduced net primary production (NPP) and increased heterotrophic respiration. Annual NPP dropped from 440 to 400 g C m^{-2} in 2000–2009. The lowest NPP values (391 g C m^{-2}) were estimated for 2015 to 2018, at which point NPP started to recover. NPP was reduced in the affected landscape during and after the beetle outbreak because of the reduction in photosynthetic capacity caused by widespread tree mortality. Conversely, heterotrophic respiration increased from 408 to 424 g C m^{-2} in the 2003–2007 period because of the large transfers of biomass to dead organic matter pools (471 Mt C transferred by the beetle during the outbreak) and subsequent decomposition.

Impacts of the current beetle outbreak are important because they are of comparable magnitude to other global change factors. Fire emissions vary widely between years, but within the study area the worst year for fires in the simulation period produced direct emissions of 13 Mt C , an amount exceeded by annual beetle-caused impacts from 2005 to 2014. The maximum annual beetle impact (20 Mt C yr^{-1}) for the relatively small study area is of similar magnitude to the direct forest fire emissions from all of Canada during 1959–1999 (27 Mt C yr^{-1})¹⁵. Climate warming, elevated atmospheric CO_2 concentrations, and atmospheric nitrogen deposition may

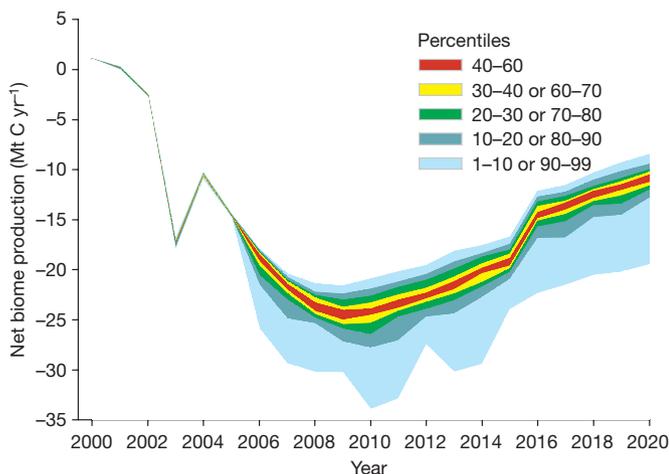


Figure 2 | Annual NBP by percentile from the Monte Carlo simulations. The model results are based on statistics from 2000 to 2006 and projections from 2007 to 2020. Negative values represent fluxes from the forest to the atmosphere (a net source of carbon). Asymmetry of the range of estimates of NBP in any single year is a function of the area burned and the associated direct carbon emissions.

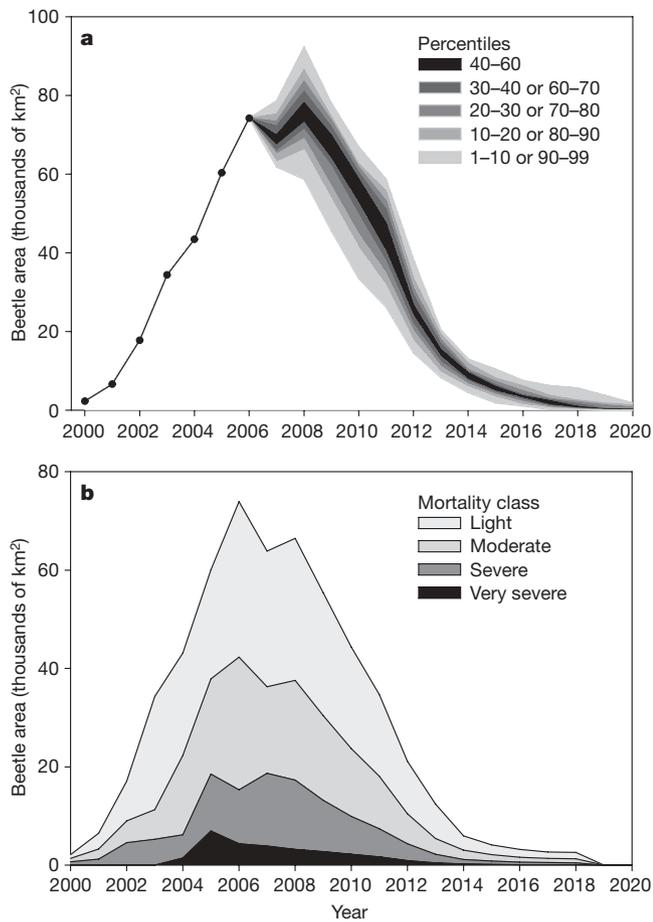


Figure 3 | Area infested with the mountain pine beetle during the simulation period. Statistics are used from 2000 to 2006 and projections are used from 2007 to 2020. **a**, Percentiles describing the parameter space resulting from 100 Monte Carlo projections of the beetle-infested area. Our projections of decreasing area after 2009 are largely based on the decline in available live host (pine) area. **b**, Area statistics for the single Monte Carlo simulation used for scenario analysis broken down by host mortality class.

enhance forest carbon sinks^{16,17}. For example, it was estimated in ref. 5 that NPP increased 6% during the 1980s and 1990s as a result of global change. The impact of the beetle outbreak would negate these gains within the affected region because NPP was reduced by 10% and heterotrophic respiration increased by 6%. Here we examined just one insect outbreak and estimated that its net greenhouse gas impacts over 21 yr (990 Mt carbon dioxide equivalents, CO₂e) are comparable to about 5 yr of emissions from Canada's transportation sector (200 Mt CO₂e in 2005)¹³.

Climate change will have impacts on insect distribution and abundance either directly via effects on their life cycles or indirectly via host-plant defences, the abundance of natural enemies or interactions with competitors¹⁸. For some forest insects, the outcome may be changes in: outbreak frequencies or duration; rates of herbivory and damage; ranges, and associations with host species^{11,19}. Evidence for climate-change-related increases in the extent or severity of forest insect disturbance has begun to accumulate. In north-western North America, warmer temperatures have halved the time required to reproduce for the spruce beetle (*Dendroctonus rufipennis* Kirby, Coleoptera: Curculionidae, Scolytinae) and have contributed to unprecedented damage to spruce forests²⁰. In the western United States, warmer annual temperatures have caused an altitudinal shift in the range of habitats, allowing the mountain pine beetle to invade high-elevation pine forests²¹. Insect impacts have, however, generally been ignored in large-scale carbon budget modelling studies^{22,23} because data on insect impacts covering large areas are expensive

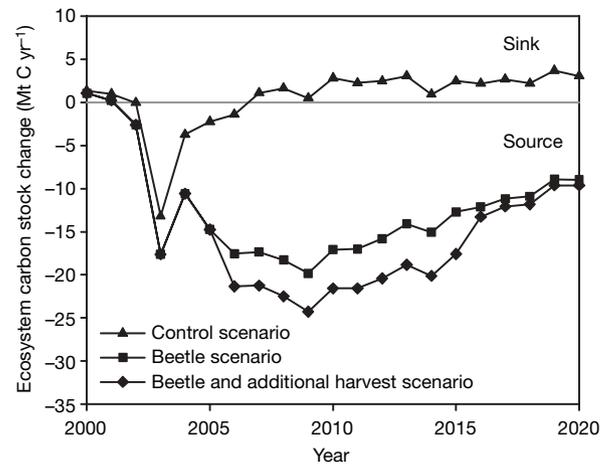


Figure 4 | Total ecosystem carbon stock change for three scenarios. The control simulation was run with no beetle outbreak, and with base harvest and fires. The beetle simulation added insect impacts to the control scenario. The additional harvest simulation added the management response of increased harvest levels from 2006 to 2016 to the beetle simulation. Negative ecosystem carbon stock change values represent fluxes from the forest to the atmosphere (net source of carbon). The source in 2003 was, in part, the result of the large area burned (2,440 km² in the study area) that was included in all three scenarios.

to collect and are therefore not widely available²⁴. Moreover, complex modelling approaches are required to adequately represent the impacts of insects on stand- and landscape-level forest ecosystem dynamics. This failure to account for insect impacts may have resulted in overestimation in previous studies of the potential for forests to offset anthropogenic CO₂.

Other insects, such as eastern spruce budworm (*Choristoneura fumiferana* Clemens, Lepidoptera: Tortricidae) and forest tent caterpillar (*Malacosoma disstria* Hubner, Lepidoptera: Lasiocampidae) also exhibit outbreaks during which they affect forest carbon dynamics by reducing growth and increasing tree mortality over large areas²⁵. Other forms of disturbance, such as fires, also markedly influence terrestrial carbon budgets²⁶. Significant climate warming has already allowed the mountain pine beetle to expand its range into formerly climatically unsuitable habitats^{4,21}. Future projected warming could facilitate further range expansion. Insect outbreaks, together with fires, could put North American forest carbon sinks at risk²⁷. Disturbances are one of the principal drivers of the carbon budget in northern forests²⁶, and this study shows but one example of how climate change can affect disturbance regimes for which impacts on the global carbon cycle then provide strong positive feedback to the global climate system.

METHODS SUMMARY

The CBM-CFS3 uses forest inventory as well as growth and yield data to simulate stand- and landscape-level forest carbon dynamics^{28–30}. It tracks carbon stocks, transfers between pools and emissions. The model accounts for tree growth, litterfall, turnover and decay as annual components of the forest carbon cycle. Fires were simulated as stand-replacing events where a portion of foliage and above-ground dead organic matter pools were consumed; all remaining biomass was killed, and standing snags were transferred to litter and coarse woody debris. Harvests were also simulated as stand-replacing clear-cut events where stemwood carbon was transferred out of the ecosystem to the forest products sector, and the rest of the carbon in biomass pools was transferred to pools of dead organic matter. Beetle infestation areas were simulated as partial-mortality events killing a portion of softwood biomass pools. The remaining stand continues to grow and recover from beetle impacts. The stand mortality classes were 5%, 10%, 30% or 50% per year (see Supplementary Information for more details).

The British Columbia Ministry of Forests and Range supplied forest inventory and growth curve data. Almost 700,000 forest stands were assigned to 86 spatial analysis units that represented the administrative and ecological variability in the study area. Spatially and temporally explicit beetle outbreak area and

area-burned data sets were used for 2000–2006 and projected for 2007–2020 using random draws from historically calibrated probability distributions. Harvest rates for each administrative unit were available for 2000–2005, and forecasts for 2006–2020 were based on local management plans (see Supplementary Information for more details).

Received 9 December 2007; accepted 29 January 2008.

- Amman, G. D. & Cole, W. E. in *Mountain Pine Beetle Dynamics in Lodgepole Pine Forests Part II: Population Dynamics*. General Technical Report No. GTR-INT-145 (United States Department of Agriculture Forest Service, Intermountain Forest and Range Experiment Station, Ogden, 1983).
- Safranyik, L., Shrimpton, D. & Whitney, H. in *Management of Lodgepole Pine to Reduce Losses from the Mountain Pine Beetle. Technical Report 1* (Environment Canada, Canadian Forestry Service, Victoria, 1974).
- Taylor, S. W. & Carroll, A. L. in *Mountain Pine Beetle Symposium: Challenges and Solutions BC-X-399* (eds Shore, T. L., Brooks, J. E. & Stone, J. E.) 41–51 (Natural Resources Canada, Canadian Forest Service, Victoria, 2004).
- Taylor, S. W., Carroll, A. L., Alfaro, R. I. & Safranyik, L. in *The Mountain Pine Beetle: A Synthesis of Biology, Management and Impacts in Lodgepole Pine* (eds Safranyik, L. & Wilson, B.) 67–94 (Natural Resources Canada, Canadian Forest Service, Victoria, 2006).
- Nemani, R. R. et al. Climate-driven increases in global terrestrial net primary production from 1982 to 1999. *Science* **300**, 1560–1563 (2003).
- Carroll, A. L., Taylor, S. W., Regniere, J. & Safranyik, L. in *Mountain Pine Beetle Symposium: Challenges and Solutions*. Report number BC-X-399 (eds Shore, T. L., Brooks, J. E. & Stone, J. E.) 223–232 (Natural Resources Canada, Canadian Forest Service, Victoria, 2004).
- Mattson, W. J. & Addy, N. D. Phytophagous insects as regulators of forest primary productivity. *Science* **190**, 515–522 (1975).
- Parkins, J. R. & McKendrick, N. A. Assessing community vulnerability: a study of the mountain pine beetle outbreak in British Columbia, Canada. *Glob. Environ. Chang.* **17**, 460–471 (2007).
- Volney, W. J. A. & Fleming, R. A. Climate change and impacts of boreal forest insects. *Agr. Ecosys. Env.* **82**, 283–294 (2000).
- Williams, D. W. & Liebhold, A. M. Climate change and the outbreak ranges of two North American bark beetles. *Agr. For. Ent.* **4**, 87–99 (2002).
- Westfall, J. *2006 Summary of Forest Health Conditions in British Columbia* (British Columbia Ministry of Forests and Range, Victoria, 2007).
- Walton, A. et al. *Provincial-Level Projection of the Current Mountain Pine Beetle Outbreak* (<http://www.for.gov.bc.ca/hre/bcmapb/Year4.htm>) (British Columbia, Ministry of Forest and Range, Victoria, 2007).
- Environment Canada. *National Inventory Report, 1990–2005: Greenhouse Gas Sources and Sinks in Canada*. (http://www.ec.gc.ca/pdb/ghg/inventory_report/2005_report/tm-toc_eng.cfm). (Environment Canada, Gatineau, 2007).
- Hamann, A. & Wang, T. Potential effects of climate change on ecosystem and tree species distribution in British Columbia. *Ecology* **87**, 2773–2786 (2006).
- Amiro, B. D. et al. Direct carbon emissions from Canadian forest fires, 1959–1999. *Can. J. For. Res.* **31**, 512–525 (2001).
- Canadell, J. G. et al. in *Terrestrial Ecosystems in a Changing World* (eds Canadell, J. G., Pataki, D. E. & Pitelka, L. F.) 59–78 (Springer, Berlin, 2007).
- Denman, K. L. et al. in *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Solomon, S. et al.) 499–587 (Cambridge Univ. Press, Cambridge, 2007).
- Ayres, M. P. & Lombardero, M. J. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *Sci. Total Environ.* **262**, 263–286 (2000).
- Kurz, W. A., Apps, M. J., Stocks, B. J. & Volney, W. J. A. in *Biotic Feedbacks in the Global Climatic System: Will the Warming Feed the Warming?* (eds Woodwell, G. M. & Mackenzie, F. T.) 119–133 (Oxford Univ. Press, Oxford, 1995).
- Berg, E. E., Henry, J. D., Fastie, C. L., De Volder, A. D. & Matsuoka, S. M. Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Klauane National Park and Reserve, Yukon Territory: relationship to summer temperatures and regional differences in disturbance regimes. *For. Ecol. Manage.* **227**, 219–232 (2006).
- Logan, J. A. & Powell, J. A. Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). *Am. Ent.* **47**, 160–173 (2001).
- McGuire, A. D. et al. Carbon balance of the terrestrial biosphere in the twentieth century: analyses of CO₂, climate and land use effects with four process-based ecosystem models. *G. Biogeochem. Cycles* **15**, 183–206 (2001).
- Myneni, R. B. et al. A large carbon sink in the woody biomass of northern forests. *Proc. Nat. Acad. Sci.* **98**, 14784–14789 (2001).
- Wulder, M. A., Dymond, C. C., White, J. C., Leckie, D. G. & Carroll, A. L. Surveying mountain pine beetle damage of forests: a review of remote sensing opportunities. *For. Ecol. Manage.* **221**, 27–41 (2001).
- Berryman, A. A. *Dynamics of Forest Insect Populations: Patterns, Causes, Implications* (Plenum, New York, 1988).
- Bond-Lamberty, B., Peckham, S. D., Ahl, D. E. & Gower, S. T. Fire as the dominant driver of central Canadian boreal forest carbon balance. *Nature* **450**, 89–92 (2007).
- Kurz, W. A., Stinson, G. & Rampley, G. Could increased boreal forest ecosystem productivity offset carbon losses from increased disturbances? *Phil. Trans. R. Soc. B.* doi:10.1098/rstb.2007.2198 (2007).
- Kurz, W. A., Apps, M. J., Webb, T. M. & McNamee, P. J. *The Carbon Budget of the Canadian Forest Sector: Phase I*. Information Report NOR-X-326 (Forestry Canada, Northwest Region, Northern Forestry Centre, Edmonton, 1992).
- Kurz, W. A. & Apps, M. J. A 70-year retrospective analysis of carbon fluxes in the Canadian forest sector. *Ecol. Appl.* **9**, 526–547 (1999).
- Kull, S. et al. *Operational-Scale Carbon Budget Model of the Canadian Forest Sector (CBM-CFS3) Version 1.0: User's Guide* (Natural Resources Canada, Canadian Forest Service, Edmonton, 2006).

Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

Acknowledgements Funding for this study was provided by Canada's Climate Change Action Plan. We thank British Columbia Ministry of Forests and Range (MoFR) collaborators for providing data and detailed reviews: D. Draper, G. Lawrence, M. Boyce and D. Spittlehouse. S. Beukema provided assistance in formatting MoFR data for use in CBM-CFS3. Fire and beetle projection methodologies were developed with the assistance of J. Metsaranta, S. Beukema, B. Stocks, B. Amiro, M. Flannigan, R. Landry, B. de Groot, K. Anderson, S. Taylor and T. Shore. Climate data were provided by D. McKenney. CBM-CFS3 model development was assisted by T. White, G. Zhang, M. Magnan, E. Banfield, C. Shaw and B. Simpson. Finally, we thank V. Nealis, D. Draper, D. Spittlehouse and A. Nussbaum for comments on an earlier draft.

Author Contributions All authors contributed to study design, model parameterizations, and development of future projections; C.C.D., G.J.R., G.S. and E.T.N. conducted model simulations; W.A.K., C.C.D., G.S. and E.T.N. analysed results; and all authors contributed to the manuscript.

Author Information Reprints and permissions information is available at www.nature.com/reprints. Correspondence and requests for materials should be addressed to W.A.K. (wkurz@nrcan.gc.ca).