REVIEW

Boreal forest health and global change

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The boreal forest, one of the largest biomes on Earth, provides ecosystem services that benefit society at levels ranging from local to global. Currently, about two-thirds of the area covered by this biome is under some form of management, mostly for wood production. Services such as climate regulation are also provided by both the unmanaged and managed boreal forests. Although most of the boreal forests have retained the resilience to cope with current disturbances, projected environmental changes of unprecedented speed and amplitude pose a substantial threat to their health. Management options to reduce these threats are available and could be implemented, but economic incentives and a greater focus on the boreal biome in international fora are needed to support further adaptation and mitigation actions.

The boreal forest encompasses ~30% of the global forest area (*1*), contains more surface freshwater than any other biome (*2*), and has large tracts of unmanaged forests, mostly in lower-productivity, high-latitude regions of Canada, Russia, and Alaska (*3*) (Fig. 1, A and B). Spread across only a few countries, the biome is characterized by a very low population density and generally low human impacts, although extraction of natural resources is also taking place regionally (Fig. 1C).

Boreal forests provide critical services to local, regional, and global populations. Communities, including those of indigenous people, benefit from ecosystem services provided by the forest for fishing, hunting, leisure, spiritual activities, and economic opportunities (*2*). Countries such as Canada, Finland, Sweden, and Russia (*2*) extract wood from boreal regions for their forest industries. More than 33% of the lumber and 25% of the paper on the export market originate from boreal regions (*2*). Globally, boreal forests help regulate climate through the exchange of energy and water (*4*). They are also a large reservoir of biogenic carbon—on a level comparable to, if not greater than, that of tropical forests—with a likely underestimated 32% of global terrestrial carbon (C) stocks mostly in climate-sensitive peat, soils, and permafrost deposits (*5*, *6*). The boreal forest is estimated to sequester ~20% of the total C sink generated by the world's forests (*5*). Because of these multiple roles, the fate of boreal forests should be a global concern (*4*, *7*).

Global change, which is the combination of climate change and other changes linked to human activities, is rapidly altering the boreal forest environment (*4*, *8*). The rate of these alterations and their cumulative impacts will determine the future health of this biome, including its potential to shift to new undesirable equilibrium states (*9*). In this Review, we evaluate the current status of boreal forest health and discuss the increasing threats these forests face under global change. Based on (*1*), we define forest health as the capacity of forest ecosystems to adjust to changing environmental conditions and to maintain the generation of a wide range of goods and services for society. We assess forest health as a function of two related ecosystem properties: (i) biodiversity at scales from genes to landscapes and (ii) resilience, or the ability to recover from disturbances. We focus our assessment on services linked to wood production and climate regulation, and on forest dynamics and productivity. Finally, we provide examples of the potential impacts of global change and propose options for the long-term maintenance of boreal forest health.

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The character of boreal forests

Boreal forests are defined as forests growing in high-latitude environments where freezing temperatures occur for 6 to 8 months (*2*) and in which trees are capable of reaching a minimum height of 5 m and a canopy cover of 10% (*10*). Boreal forest ecosystems have evolved under the constraints imposed by a short growing season and severe winters during which snow cover may last for several months (*2*, *11*). About one-third of their extent is underlain by permafrost (Fig. 1A) (*12*, *13*). Boreal forests have a low diversity of tree species, of which gymnosperms such as *Abies*, *Larix*, *Pinus*, and *Picea* species usually dominate, with varying proportions of angiosperm *Populus*, *Betula*, and *Alnus* species (*2*, *11*, *14*) in stands that may nevertheless support thousands of species of living organisms (*15*).

Different types of disturbances (fire, insects, wind, etc.) have been an essential part of the dynamics of boreal forest landscapes, with events that affect several square meters to millions of hectares (*14*, *16*). Severe stand-replacing crown fires have historically been common in North America and parts of Russia, whereas nonlethal surface fires have been prevalent in Eurasia (*11*, *14*, *17*). Insect outbreaks have also been recurrent in North America and eastern Russia, but windstorms may have been a more important disturbance type in Fennoscandia and western Russia (*14*). Despite these regional differences, the combination of large- and small-scale disturbances over millennia has shaped the biodiversity of all boreal forests through the maintenance of a high landscape-level diversity of stands varying in size, age, structure, and composition, whose proximity creates a large array of habitats for native species (*15*, *18*).

Because of the recurrent nature of disturbances, boreal plant species are generally less affected by fragmentation than tropical forest species (*19*), although specialized species from other groups can be sensitive to fragmentation or change in habitat representation (*15*, *18*). Boreal tree species in particular have evolved mechanisms to survive or recover from disturbances, although the recovery process can be slow (*20*). They also have a generally high adaptive capacity expressed through large environmental tolerance ranges, large population sizes, and high population-level genetic diversity (*21*, *22*). The resilience of these systems is well illustrated in the boreal forest of eastern North America, where the regional tree species pool has remained mostly unchanged over the past 8000 years despite large fluctuations in climate and regional disturbance regimes (*23*).

Is boreal forest health compromised by forest management?

Nearly two-thirds of boreal forests are considered to be managed (*24*), largely for industrial wood production [35 to 40% in Canada (*2*, *25*), 58% in Russia (*26*), and 90% in Fennoscandia (*2*)]. Management intensity ranges from low-input extensive in Canada and Russia to high-input intensive in Fennoscandian forests that represent ~5% of the global boreal forest (*2*). It is estimated that more than 60% of the stands within the managed forest have been harvested at least once (*25*, *27*), although this percentage varies regionally.

Managed forests in Sweden and Finland have been heavily homogenized as a result of long-term use and increasingly intensive silviculture for timber production (*15*, *27*), together with fire suppression (Fig. 1D). Forest productivity and growing stock is increasing, and the aim is to further augment timber extraction (*28*). Lower-yielding managed boreal forests in Canada have retained higher stand and landscape-level diversities through the presence of natural regeneration in postharvest stands and the occurrence of natural disturbances across landscapes (*25*) (Fig. 1D). In boreal Russia, harvest levels, along with investments in forest protection and management, have dropped substantially since the collapse of the Soviet Union (*8*, *29*). Additionally, in spite of existing laws and regulations, up to 20% of current logging is carried out illegally (*8*), with practices that include overharvesting of high-value stems or tree species in the most productive or accessible stands (*30*).

Harvesting has decreased the extent of older forests as compared with natural conditions in all regions with forest management (*14*, *16*). The resulting decline in structural attributes such as large trees for cavity shelters and coarse woody debris associated with older forests has negatively affected biodiversity (*31*). Harvesting has also increased the proportion of early-successional, regenerating stands, but these retain less biological and structural diversity than those originating from natural disturbances in which rapidly changing habitats and high species turnover enhance the adaptation potential to new environmental conditions (*25*). Postharvest stands may be further homogenized through tree plantation with varying degrees of genetic selection and through the control of forest structure and competing vegetation, thereby further reducing their potential for adaptation to a changing environment (*25*). Recently, demand for biomass as a renewable energy feedstock has increased, especially in Nordic countries, with a risk of removing nutrients needed for tree growth (*28*). However, negative effects of harvest residue removal on site fertility have been demonstrated only for specific site types (*32*, *33*).

Although past management practices have been shown to decrease species and landscape diversity, it appears that most boreal forest landscapes have at least partially retained their resilience to disturbance (*25*). However, current evidence suggests that the intensification of forest management to enhance wood production has reduced forest biodiversity and resilience (*15*). With intensified forest management, the maintenance of a productive forest increasingly shifts from a natural process to one whose costs and risks must be borne by the forest sector (*34*). For example, in the Swedish province of Götaland, the 2005 windstorm felled 75 Mm^3 of intensively managed wind-prone conifer stands, increasing unit wood costs by 21% that year for the recovery and storage of the wind-felled trees and the replanting of damaged areas (*35*).

Finally, in addition to forest management, the exploration, development, and extraction of other resources (mining, oil and gas, flooding for hydroelectric projects, etc.) have been taking place in regions spread across both the managed and unmanaged portions of the boreal forest (*1*, *2*, *36*) (Fig. 1C). Cumulatively, these activities across northern territories in recent decades have had negative impacts on the health of forest ecosystems through air pollution, soil and water contamination, changes in hydrological regimes, and the physical alteration and fragmentation of forested landscapes (*1*, *37*)—notably in the permafrost forest ecosystems of Siberia (*36*, *37*).

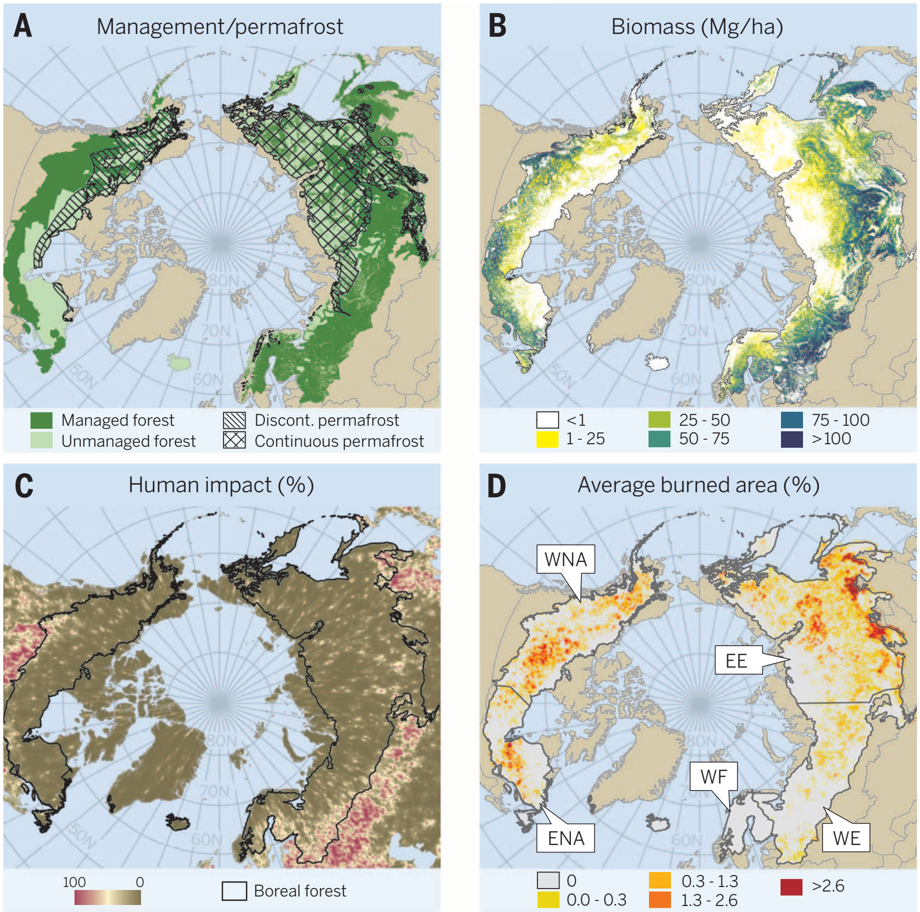

Fig. 1. Characteristics of the circumboreal forest. (**A**) The extent of the managed and unmanaged boreal forests is shown on the map. Forest growing on permafrost covers a large region. (**B**) The current biomass distribution shows the strong south-to-north decrease in forest productivity and the east-to-west increase in the latitude of productive forests across continents. (**C**) The human impact index reflects the overall low but locally important impact due to harvesting, agriculture, human settlements, natural resource exploration and exploitation, mining, or roads, as well as their cumulative importance. (**D**) The mean annual fraction burned (1997–2014) ranges from very low to more than 5% in the drier areas of Eurasian forests. Boreal regions delineated on the map correspond to those considered in Fig. 2B. WNA, western North America; ENA, eastern North America; WF, western Fennoscandia; WE, western Eurasia; EE, eastern Eurasia. See (*70*) for details on data sources.

What risks to boreal forest health are posed by global change?

Over the course of the 21st century, the boreal biome is expected to experience the largest increase in temperatures of all forest biomes (*38*, *39*). In the meantime, the development and extraction of natural resources will likely impose more pressure on boreal forest health (*37*). The expected and unprecedented rate of changes, particularly those of climate and related disturbances, may overwhelm the resilience of species and ecosystems, possibly leading to important biome-level changes (*9*).

Mean annual temperature increases of 1.5°C or more have recently been documented over much of the boreal forest (*38*). Under a globally averaged projection of a warming of 4°C by the end of this century, boreal regions could experience temperature increases from 4° to 11°C, accompanied by a far more modest expected increase in precipitation (*40*) (Fig. 2). In such an extreme scenario, large regions of the boreal forests could, by the end of the century, shift to the drier climate space normally occupied by the woodland/shrubland biome (Fig. 2) (*41*).

Given these changes in climate, biotic and abiotic disturbances are generally predicted to increase in extent, frequency, or severity over the same time frame, although uncertainties in the projections remain (*22*, *39*, *42*–*44*). Fire occurrence, area, and severity are projected to increase considerably, notably for parts of Russia where the share of stand-replacing fires is forecast to increase substantially (*43*–*45*). Warmer temperatures would also lift the climate barriers to population growth or range expansion of native or invasive forest pests, resulting in severe outbreaks similar to those recently experienced in Canada with the mountain pine beetle (*46*) and in Siberia with the Siberian silk moth (*36*). Moreover, the intensification of global trade provides an ever-more efficient vector for the propagation of invasive pests and pathogens to boreal forests (*47*).

Limited evidence suggests a slow northward migration of temperate deciduous tree species

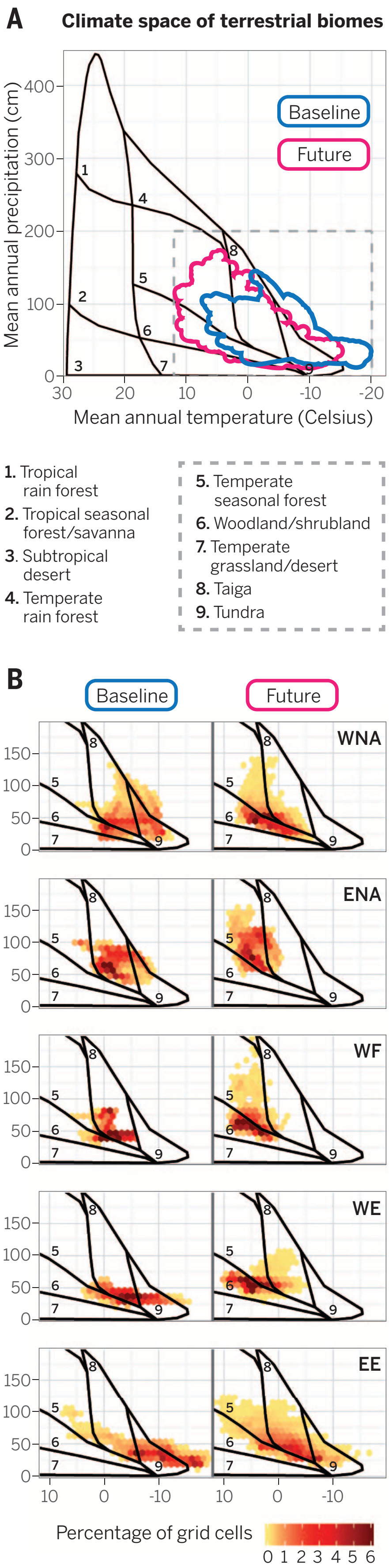

Fig. 2. Mean annual temperature and precipitation in the circumboreal forest represented on the climate space of terrestrial biomes. (**A**) Potential impacts of a changing climate on boreal forests are illustrated by overlaying the climatic envelope of global circumboreal forests on the climate space of terrestrial biomes. Baseline (1975) climate conditions of boreal forests correspond closely to the taiga and tundra climate space. Projections of future climate conditions (2090) under an extreme CO_2 emission scenario (AR4 A2) would also overlap the climate space of the woodland/shrubland (6) and temperate seasonal forest (5) biomes. (**B**) Panels display the frequency of baseline (left) and future (right) climate conditions within a 10-min gridded representation of each region (see Fig. 1D for location). Eastern North America (ENA) is the only region projected to remain within the climate space of forested biomes [either taiga (8) or temperate seasonal forest (5)]. In all other regions, projected precipitation changes appear to be insufficient to fully compensate for the increased evaporative demand generated by warmer temperatures. Large areas of these regions would shift into the climate space of the woodland/shrubland biome. See (*70*) for details on data sources and methods.

into the boreal zone of eastern North America (*48*) and an expansion of evergreen coniferous species into the current habitat of the deciduous larch in Siberia (*49*). However, climate zones are shifting northward at speeds one order of magnitude faster than the trees' ability to migrate (*36*, *50*). Therefore, forests will be affected directly by the changes in their local climatic conditions and indirectly by changes in the local disturbance regimes. Drought-induced mortality has been reported in several boreal regions (*42*) and is predicted to increase regionally (*8*, *39*). Forest productivity has been on the rise in Fennoscandia, in the northern reaches of the North American boreal forest (*51*, *52*), and over major parts of Russia (*53*), partially in response to increased temperature and growing-season length. Additionally, productivity is projected to increase until 2030 in most of Russia's boreal forests (*8*). By contrast, productivity has been shown or predicted to decrease in response to regional drier conditions in parts of the North American boreal forest (*54*, *55*).

The shift to a drier climate and increasingly frequent disturbances may lead to extensive forest cover thinning or loss, as suggested by the projected climate space for large regions of the boreal forest (Fig. 2) (*43*, *56*). Such a change could be accelerated by the documented ability of successive disturbances to rapidly transform closed forests into low-productivity open woodlands (*41*, *56*, *57*). The projected changes from surface to crown fires in Russian forest ecosystems dominated by tree species not adapted to regenerate after stand-replacing fires could also impair regeneration and the return to closed-canopy stands (*43*). The thawing of the permafrost in dry continental Siberia may lead to widespread drought-induced mortality in both the dark coniferous forests (*8*) and in the larch forests that cover 20% of the global boreal forest (*13*).

Projections of forest dynamics under a range of climate scenarios suggest a greater probability that boreal C stocks will decrease rather than increase or stay unchanged (*8*, *58*). Globally, the boreal forest may have started transitioning from a C sink to a C source (*6*), and certain regions [e.g., western Canada (*46*) and Siberia (*59*)] may already be emitting more C than they capture. The characterization and understanding of C stock dynamics vary considerably among different regions of the boreal forest (*58*, *60*), but this biome's numerous peatlands and deep organic deposits encased in permafrost may become highly vulnerable to global warming (*58*). In Russia alone, the release of C from the thawing permafrost by the end of the century could potentially be several times larger than that of current tropical deforestation (*8*). Regionally, such impacts may be exacerbated by industrial development (*36*, *37*). The full consequences of these changes—including long-term geophysical effects on global climate (*61*) and on systems integrity (*4*)—remain to be understood and evaluated.

A way forward

The maintenance of ecosystem services from boreal forests depends on the preservation of forest health, which is threatened by the speed and amplitude of changes in climate projected for these northern latitudes. Considering the importance of the potential impacts these changes may have and the extent over which they may take place, it is imperative that actions be taken to maintain the health of the boreal forest or to enhance its contribution to climate change mitigation. Forest management and economic and global policy considerations represent important avenues to achieve such goals.

Forest management actions to mitigate the effects of climate change can be undertaken (*58*, *62*); these include afforestation and practices to maintain in situ C stocks or to enhance on-site and off-site sequestration (*6*, *62*). Afforestation in the boreal forests should be pursued where possible, but the potential gains are generally small because of low rates of boreal deforestation (*58*, *62*), with a yearly rate of deforestation close to 0.02% (*58*). A notable exception may be the abandonment of 45 Mha of agricultural land in boreal Russia (*63*), of which 18 Mha is already undergoing natural regeneration (*64*). Reforestation could also be used to speed the postdisturbance recovery of forests in the unmanaged boreal region (*8*), across areas that may cover millions of hectares in Russia alone (*36*). In addition, sequestration of C in harvested wood products, the substitution of wood for more energy-intensive building material, and the use of wood as energy feedstock can all be enhanced to provide additional mitigation benefits. However, economic incentives to specifically support afforestation or other carbon-related management actions, such as substitution of energy-intensive building materials, are limited in boreal forests (*7*, *62*).

Forest management strategies such as continuous-cover silviculture and the enhancement of tree species diversity and of landscape heterogeneity may aid in the maintenance of forest cover, the conservation of C stocks, and biodiversity (*8*, *65*). Implementation of new management approaches based on the closer emulation of natural processes or on an adaptive systems perspective (*18*) may also alleviate some of the ecological problems associated with past forest management practices while providing economically viable alternatives (*31*, *66*). Large, well-distributed conservation areas, where natural processes are occurring, remain important for the maintenance of biodiversity and the resilience of boreal forest landscapes (*67*). However, considerations for their establishment must now include the changing climate (*67*).

Better control of natural disturbances is often suggested as a means to conserve boreal C stocks (*6*), but achieving this goal—particularly in remote areas—may be economically impossible, especially given future climate conditions. Rather, the incorporation of disturbance risks in timber supply planning can be used to set sustainable management objectives within a changing climate environment (*68*). Managing for multiple objectives may be challenging, but integrated approaches can support the development of strategies that maximize positive outcomes and find trade-offs between possible contradictory objectives such as management for wood production, climate change mitigation, and biodiversity conservation (*6*, *62*).

Monitoring is essential to continuously assess the state of the boreal forests and to improve our understanding of interactions and feedback among processes. The postdisturbance regeneration phase deserves particular attention (*34*), as it may provide early warnings of forest health degradation, such as species invasion, and allow the rapid implementation of remedial actions to prevent, for instance, the loss of forest cover (*36*). Forests on permafrost and in remote areas are also critically linked to climate and should be monitored closely to detect or predict impending signals of permanent shifts from C sinks to C sources (*60*) or from closed to open forest status (*8*). Coupled with modeling, such change-tracking can be used to project the future of this important biome. However, the current models need improvement, as they may not account for regional specificities such as permafrost (*36*) and often fail to converge on similar outcomes [e.g., (*56*, *69*) for central Siberia].

The health of the immense and seemingly timeless boreal forest is presently under threat, together with the vitality of many forest-based communities and economies. On the larger scale, the long-term provisioning of vital ecosystem services such as global climate regulation is at risk. Our vast knowledge of boreal forests can inform solution development, but current international agreements and regional market mechanisms fail to provide incentives or opportunities to fully implement the existing options (*7*, *8*). To support critical and timely action across the boreal forest, global discussions on sustainable development, biodiversity conservation, and climate change mitigation need to place a greater focus on this vast biome.

REFERENCES AND NOTES

1. J. P. Brandt, M. D. Flannigan, D. G. Maynard, I. D. Thompson, W. J. A. Volney, *Environ. Rev.* **21**, 207–226 (2013).
2. P. J. Burton *et al.*, in *Forests and Society – Responding to Global Drivers of Change*, G. Mery *et al.*, Eds. (International Union of Forest Research Organizations, Vienna, Austria, 2010), pp. 249–282.
3. P. Potapov *et al.*, *Ecol. Soc.* **13**, 51 (2008).
4. W. Steffen *et al.*, *Science* **347**, 1259855 (2015).
5. Y. Pan *et al.*, *Science* **333**, 988–993 (2011).
6. C. J. A. Bradshaw, I. G. Warkentin, *Global Planet. Change* **128**, 24–30 (2015).
7. J. Moen *et al.*, *Conserv. Lett.* **7**, 408–418 (2014).
8. Food and Agriculture Organization of the United Nations (FAO), "The Russian Federation forest sector. Outlook study to 2030" (FAO, Rome, 2012); www.fao.org/docrep/016/i3020e/i3020e00.pdf
9. C. P. O. Reyer *et al.*, *J. Ecol.* **103**, 5–15 (2015).
10. FAO, "Global forest resources assessment 2010. Terms and definitions," Working paper 144/E, FAO, Rome, 2010; www.fao.org/docrep/014/am665e/am665e00.pdf.
11. D. Kneeshaw, Y. Bergeron, T. Kuuluvainen, in *The Sage Handbook of Biogeography*, A. Millington, M. Blumler, U. Schickhoff, Eds. (Sage, London, 2011), pp. 261–278.
12. S. A. Zimov, E. A. G. Schuur, F. S. Chapin III, *Science* **312**, 1612–1613 (2006).
13. A. Osawa, Y. Matsuura, T. Kajimoto, in *Permafrost Ecosystems. Siberian Larch Forests*, A. Osawa, O. A. Zyryanova, Y. Matsuura, T. Kajimoto, R. W. Wein, Eds. (Springer, Netherlands, 2010), pp. 459–481.
14. E. Shorohova, D. Kneeshaw, T. Kuuluvainen, S. Gauthier, *Silva Fenn.* **45**, 785–806 (2011).
15. T. Kuuluvainen, J. Siitonen, in *Managing Forests as Complex Adaptive Systems - Building Resilience to the Challenge of Global Change*, C. Messier, K. J. Puettmaan, K. D. Coates, Eds. (Routledge, New York, 2013), pp. 244–268.
16. T. Kuuluvainen, T. Aakala, *Silva Fenn.* **45**, 823–839 (2011).
17. B. M. Rogers, A. J. Soja, M. L. Goulden, J. T. Randerson, *Nat. Geosci.* **8**, 228–234 (2015).
18. P. J. Burton, in *Managing Forests as Complex Adaptive Systems - Building Resilience to the Challenge of Global Change*, C. Messier, K. J. Puettmaan, K. D. Coates, Eds. (Routledge, New York, 2013), pp. 79–108.
19. K. A. Harper *et al.*, *J. Ecol.* **103**, 550–562 (2015).
20. D. K. Bolton, N. C. Coops, M. A. Wulder, *Remote Sens. Environ.* **163**, 48–60 (2015).
21. S. N. Aitken, S. Yeaman, J. A. Holliday, T. Wang, S. Curtis-McLane, *Evol. Appl.* **1**, 95–111 (2008).
22. M. Lindner *et al.*, *For. Ecol. Manage.* **259**, 698–709 (2010).
23. O. Blarquez, C. Carcaillet, T. Frejaville, Y. Bergeron, *Front. Ecol. Evol.* **2**, 1–8 (2014).
24. A forest is considered to be managed when it is included within a forest management plan for purposes such as conservation, fire protection, or wood production. A managed forest may not be accessible or may not yet have been subjected to active management activities.
25. L. A. Venier *et al.*, *Environ. Rev.* **22**, 457–490 (2014).
26. Federal Agency of Forest Service, *Forest Fund of the Russian Federation (state by 1 January 2009)* (Federal Agency of Forest Service, Moscow, 2009) [in Russian].
27. P. J. Burton *et al.*, in *Towards Sustainable Management of the Boreal Forest*, P. J. Burton, C. Messier, D. W. Smith, W. L. Adamowicz, Eds. (NRC Research Press, Ottawa, Canada, 2003), pp. 1–40.
28. H.-S. Helmisaari, L. Kaarakka, B. A. Olsson, *Scand. J. For. Res.* **29**, 312–322 (2014).
29. State Program of the Russian Federation, *Development of Forest Management for 2013-2020* [in Russian]; www.mnr.gov.ru/upload/iblock/e82/GP_2013-2020.pdf.
30. J. P. Newell, J. Simeone, *Eurasian Geogr. Econ.* **55**, 37–70 (2014).
31. T. Kuuluvainen, O. Tahvonen, T. Aakala, *Ambio* **41**, 720–737 (2012).
32. D. G. Maynard *et al.*, *Environ. Rev.* **22**, 161–178 (2014).
33. E. Thiffault *et al.*, *Environ. Rev.* **19**, 278–309 (2011).
34. S. Gauthier *et al.*, *Environ. Rev.* **22**, 256–285 (2014).
35. Skogsstyrelsen, Swedish Forest Agency, www.skogsstyrelsen.se/en/AUTHORITY/Statistics/Subject-Areas/Economy/Tables-and-figures/.
36. A. Z. Shvidenko *et al.*, in *Regional Environmental Changes in Siberia and Their Global Consequences*, P. Y. Groisman, G. Gutman, Eds. (Springer, New York, 2013), pp. 171–249.
37. A. A. Baklanov *et al.*, in *Regional Environmental Changes in Siberia and Their Global Consequences*, P. Y. Groisman, G. Gutman, Eds. (Springer, New York, 2013), pp. 303–346.
38. Intergovernmental Panel on Climate Change (IPCC), *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, T. F. Stocker *et al.*, Eds. (Cambridge Univ. Press, Cambridge, 2013).
39. D. T. Price *et al.*, *Environ. Rev.* **21**, 322–365 (2013).
40. World Bank, "Turn down the heat: Confronting the new climate normal" (World Bank, Washington, DC, 2014); https://openknowledge.worldbank.org/handle/10986/20595.
41. M. Scheffer, M. Hirota, M. Holmgren, E. H. Van Nes, F. S. Chapin III, *Proc. Natl. Acad. Sci. U.S.A.* **109**, 21384–21389 (2012).
42. C. D. Allen *et al.*, *For. Ecol. Manage.* **259**, 660–684 (2010).
43. A. Z. Shvidenko, D. G. Schepaschenko, *Contemp. Probl. Ecol.* **6**, 683–692 (2013).
44. Y. Boulanger, S. Gauthier, P. J. Burton, *Can. J. For. Res.* **44**, 365–376 (2014).
45. W. J. de Groot, M. D. Flannigan, A. S. Cantin, *For. Ecol. Manage.* **294**, 35–44 (2013).
46. W. A. Kurz *et al.*, *Nature* **452**, 987–990 (2008).
47. D. W. Langor *et al.*, *Environ. Rev.* **22**, 372–420 (2014).
48. L. Boisvert-Marsh, C. Périé, S. de Blois, *Ecosphere* **5**, 83 (2014).
49. V. Kharuk, K. J. Ranson, M. L. Dvinskaya, *Eurasian J. For. Res.* **10**, 163–171 (2007).
50. D. W. McKenney, J. H. Pedlar, K. Lawrence, K. Campbell, M. F. Hutchinson, *Bioscience* **57**, 939–948 (2007).
51. P. E. Kauppi, M. Posch, P. Pirinen, *PLOS ONE* **9**, e111340 (2014).
52. K. Zhang *et al.*, *J. Geophys. Res.* **113**, G03033 (2008).
53. A. Lapenis, A. Shvidenko, D. Shepaschenko, S. Nilsson, A. Aiyyer, *Glob. Change Biol.* **11**, 2090–2102 (2005).
54. P. S. A. Beck *et al.*, *Ecol. Lett.* **14**, 373–379 (2011).
55. M. P. Girardin, F. Raulier, P. Y. Bernier, J. C. Tardif, *Ecol. Model.* **213**, 209–228 (2008).
56. N. M. Tchebakova, E. I. Parfenova, A. J. Soja, *Reg. Environ. Change* **11**, 817–827 (2011).
57. J. P. P. Jasinski, S. Payette, *Ecol. Monogr.* **75**, 561–583 (2005).
58. W. A. Kurz *et al.*, *Environ. Rev.* **21**, 260–292 (2013).
59. A. J. Dolman *et al.*, *Biogeosciences* **9**, 5323–5340 (2012).
60. C. S. R. Neigh *et al.*, *Remote Sens. Environ.* **137**, 274–287 (2013).
61. G. B. Bonan, *Science* **320**, 1444–1449 (2008).
62. T. C. Lemprière *et al.*, *Environ. Rev.* **21**, 293–321 (2013).
63. I. Kurganova, V. Lopes de Gerenyu, J. Six, Y. Kuzyakov, *Global Change Biol.* **20**, 938–947 (2014).
64. A. Z. Shvidenko, D. G. Schepaschenko, *Siberian J. For. Sci.* **1**, 69–92 (2014) [in Russian].
65. T. Pukkala, E. Lähde, O. Laiho, *J. For. Res.* **25**, 627–636 (2014).
66. J. Rämö, O. Tahvonen, *Scand. J. For. Res.* **29**, 777–792 (2014).
67. M. E. Andrew, M. A. Wulder, J. A. Cardille, *Environ. Rev.* **22**, 135–160 (2014).
68. S. Gauthier *et al.*, *Can. J. For. Res.* 10.1139/cjfr-2015-0079 (2015).
69. E. J. Gustafson, A. Z. Shvidenko, B. R. Sturtevant, R. M. Scheller, *Ecol. Appl.* **20**, 700–715 (2010).
70. Supplementary information on data sources and methods on the figures are available on *Science* Online.

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SUPPLEMENTARY MATERIALS

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Figs. S1 and S2
References (*71*–*82*)

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