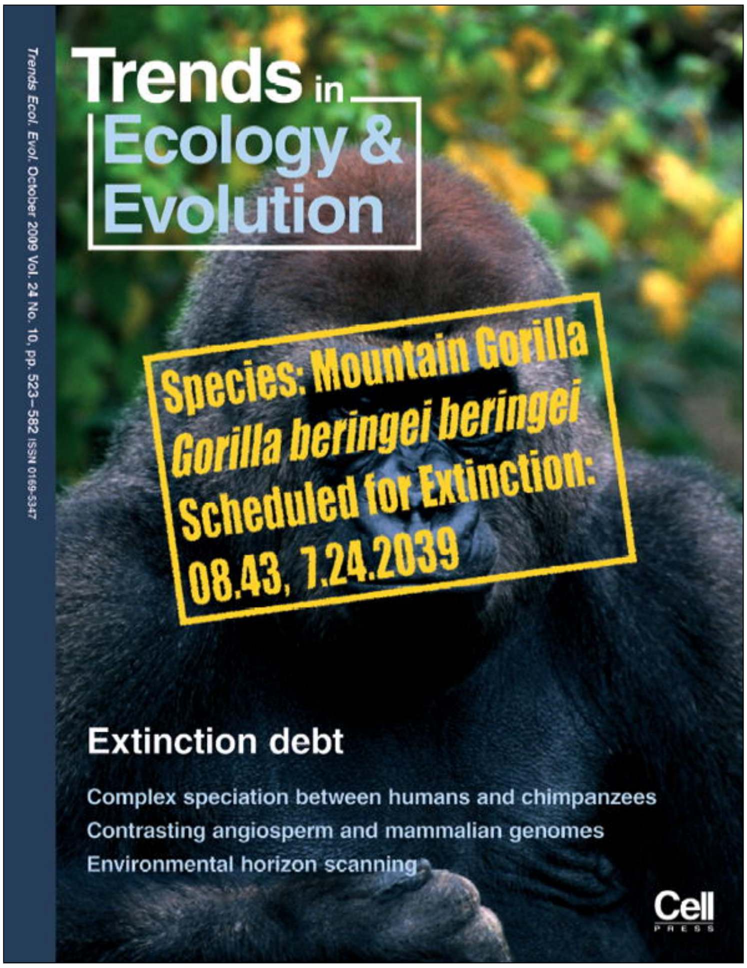
Trends in Ecology & Evolution
Trends Ecol. Evol. October 2009 Vol. 24 No. 10, pp. 523–582 ISSN 0169-5347
Species: Mountain Gorilla
Gorilla beringei beringei
Scheduled for Extinction:
08.43, 7.24.2039
Extinction debt
Complex speciation between humans and chimpanzees
Contrasting angiosperm and mammalian genomes
Environmental horizon scanning
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Opinion

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Urgent preservation of boreal carbon stocks and biodiversity

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Containing approximately one-third of all remaining global forests, the boreal ecosystem is a crucial store of carbon and a haven for diverse biological communities. Historically, fire and insects primarily drove the natural dynamics of this biome. However, human-mediated disturbances have increased in these forests during recent years, resulting in extensive forest loss for some regions, whereas others face heavy forest fragmentation or threat of exploitation. Current management practices are not likely to maintain the attendant boreal forest communities, nor are they adequate to mitigate climate change effects. There is an urgent need to preserve existing boreal forests and restore degraded areas if we are to avoid losing this relatively intact biodiversity haven and major global carbon sink.

Introduction

Much world attention has focused on the loss and degradation of tropical forests over the last three decades [1]. An expansive reservoir for global biodiversity, these forests also contain substantial stores of terrestrial carbon (C) and have an enormous influence on regional and global climates through evaporative cooling processes and the sequestration of C linked to high primary productivity [2]. Although concern rightly persists over continued exploitation of tropical forests [1], a more global perspective on forest loss is necessary so that growing threats to other ecosystems are not ignored [3]. Constituting about one-third of extant forests on Earth and home to nearly half of the remaining large tracts of intact forest, boreal ecosystems support a diverse flora and fauna and likewise harbour a substantial portion of global C stocks [4].

Human populations are typically sparse in boreal zones so there has been relatively limited resource exploitation in these areas, and disturbance dynamics have been largely driven by natural processes such as fire [5]. Consequently, few regions of the boreal forest have been extensively modified compared with their tropical counterparts [6]. However, rising demand for resources (mineral, energy, timber) has increased the extent of perturbation [7], while fire dynamics have been altered due to human encroachment and climate change [8]. Although less immediately threatened by deforestation than the tropics, these remaining havens of the boreal forest could quickly become as threatened as tropical systems [1] while releasing substantial amounts of C into the atmosphere [9].

Based on our review of data on the changes occurring in boreal forest cover, we propose here that immediate action must be taken to preserve this vital world resource.

A rapidly changing forest

We used the Boreal Forest Monitoring Project's [10] delineation of the region (2000 to 2005) to assess patterns of change over time. They defined the boreal zone based on the Terrestrial Ecoregions map of the World Wildlife Fund [11], with modifications to add ecoregions of temperate coniferous and mixed forests characterized by similar seasonality and presence of winter snow cover. Also included were forested areas of forest-steppe ecoregions within continental North America and Asia and those along forest-tundra transitional ecoregions; excluded due to data limitations were small portions of boreal forest in Iceland and regions $>70^\circ$ N latitude in Siberia.

The second largest biome in the world, the circumpolar boreal forest represents ~32–33% of all the Earth's forests [12], of which 22% is found in Russia alone (78% of this is in Siberia and the remainder in European Russia) (Figure 1a). The other five countries housing the remaining majority of boreal forest are Canada, USA, Sweden, Finland and Norway, although there are some large areas of boreal forest in northern Mongolia and north-eastern China (Figure 1a). In 2005, an estimated 31% of all remaining primary forests ('forests of native species, in which there are no clearly visible indications of human activity and ecological processes are not significantly disturbed') worldwide were found in Russia and Canada alone [13]. An estimated 80% of Canada's boreal forest is thought to be unfragmented by human settlements and roads [7].

Nonetheless, fragmentation in boreal forests is on the rise. The World Intact Forest Landscapes assessment [14] paints a dismal picture of the intactness of this biome (Figure 1b). Using the definition of 'intact' as 'areas $\geq$500 km^2, internally undivided by infrastructure (e.g. roads) and with linear dimensions $\geq$10 km' (see Online

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0169-5347/$ – see front matter doi:10.1016/j.tree.2009.03.019 Available online 11 August 2009

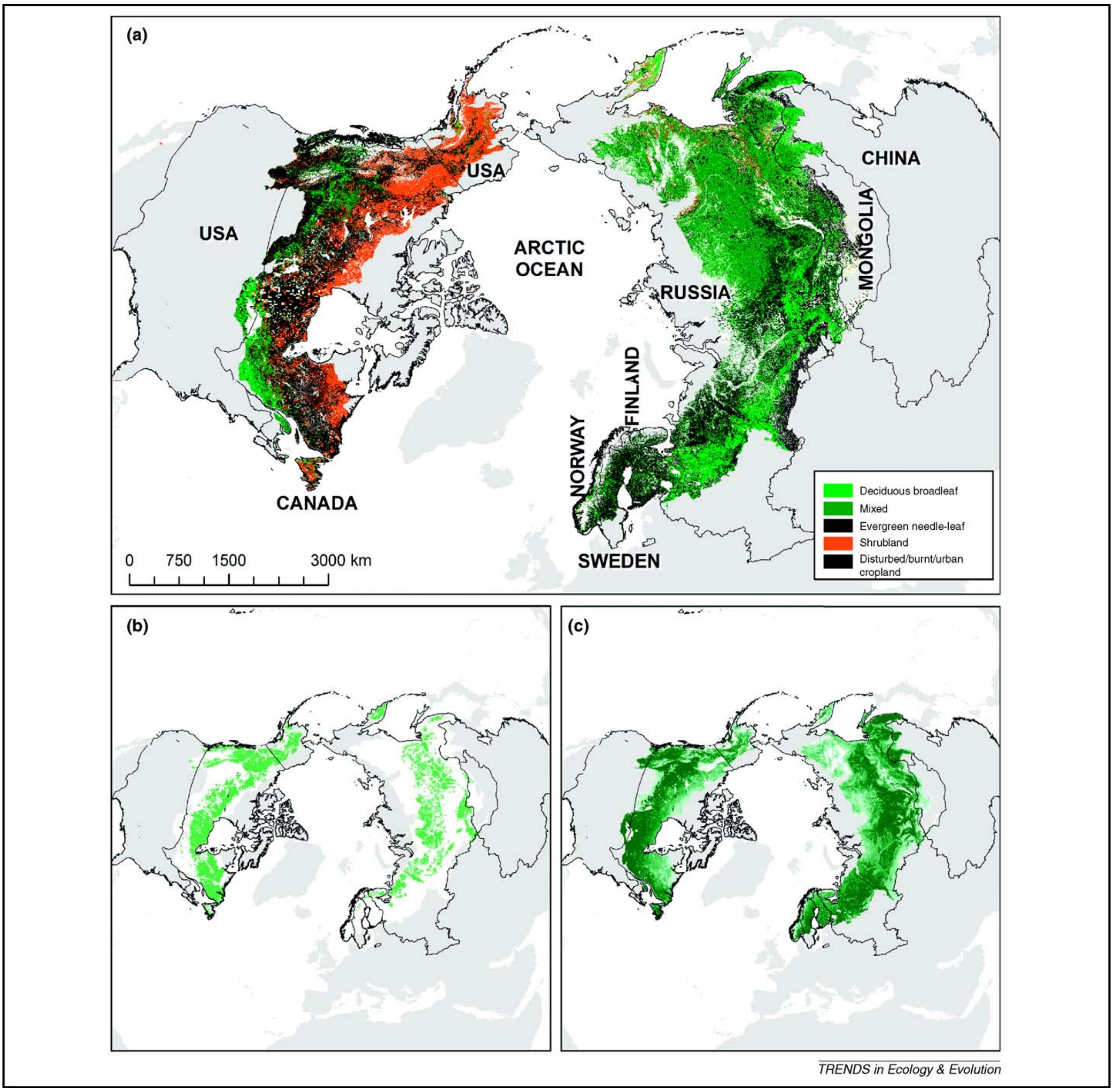

Figure 1. **(a)** Global extent and major classification (deciduous broadleaf, mixed, evergreen needle-leaf, shrubland, and disturbed, burnt, urban or cropland) of boreal forests according to the 2000 Global Landcover dataset (www-tem.jrc.it/glc2000/) [78,79]. The boreal zone limits are taken from the Boreal Forest Monitoring (2000–2005) project [10] (http://globalmonitoring.sdstate.edu/projects/gfm/). The classification 'shrubland' includes broadleaved evergreen, deciduous, needle-leaved and dwarf shrubland, and grassland with sparse tree or shrub layers [78,79]. **(b)** Area of 'intact' boreal forest as defined by the World Intact Forest Landscapes assessment [14]. 'Intact' forest patches are $\geq$500 km^2 in area that are internally undivided by infrastructure (e.g. roads) and with linear dimensions $\geq$10 km. **(c)** Tree canopy density measured as % coverage per pixel (0–100% colour gradient; 500 m resolution) from the 2000 MODIS-based Vegetation Continuous Field layers [80]. This dataset was used to make the World Intact Forest Landscapes assessment [14] shown in (b). The map projection for all panels is *North Pole Lambert Azimuthal Equal Area*.

supplementary material), the ecologically contiguous areas of the boreal forest cover only ~44% of the biome (Figure 1b, c). Although the definition of 'intactness' is arbitrary, the maintenance of large habitat areas is necessary to ensure the persistence of most species in a landscape [15]. The large extent of boreal forests belies the increasing fragmentation occurring there. In our opinion, the decreasing quality of boreal forests should be a cause of concern [1]. The world's most expansive and once contiguous forest in Russia is rapidly turning into a network of smaller fragments [12] due to: (i) increasing threats from logging; (ii) rapid urban development; (iii) deciduous regrowth; (iv) dam construction; (v) peat and other mining; and (vi) increasing frequency of fires.

According to the United Nations Temperate and Boreal Forest Resources Assessment 2000 (TBFRA) [16] and the Food and Agriculture Organization of the United Nations' Global Forest Assessment 2005 (GFA) [13], measures of forest extent in Canada and Fennoscandia have changed little in recent years [12]. However, even though elsewhere there is a perception that boreal forests and temperate forests are increasing in area from past deforestation, the forests are decreasing in 'quality' (see definitions in Online supplementary material) [14,16]. Apart from Russia, the proportion of 'undisturbed' forest in each of the six major boreal countries is <30% (Figure 2), with most (>60%) of forests in the USA and Scandinavia considered 'semi-natural' (see definitions in Online supplementary material) [16]. Another concern is that the total area considered unavailable for wood supply (i.e. 'areas protected in strict nature reserves, wilderness areas, national parks, national monuments, habitat and species management areas, protected landscapes, or managed resource protection areas') [16] does not exceed 2.5×10^7 ha in any country, representing an area <10% of the total forested land in all boreal countries except Sweden (the latter has ~20% protected) (Figure 2).

Data from the TBFRA show that Russia holds the record among the 55 temperate and boreal countries and boreal countries assessed for the greatest annual decline in forest area (1.1 M ha $year^{-1}$ between 1988 and 1993). Despite the decline, Russia still contains nearly 9×10^8 ha (9×10^6 km^2) of 'forest' (defined as having tree crown cover >10% and a minimum patch area >0.5 ha) and 'other wooded land' (OWL; defined as having tree crown cover 5–10%) (Figure 2, see Online supplementary material), of which >80% of forest and OWL combined is considered 'undisturbed' by human activities [16]. Canada has the next largest area of undisturbed forest, but considerably less than Russia (nearly 90% less) at slightly more than 1×10^8 ha that has changed little in extent since 1990 [13]. The USA has $<2 \times 10^7$ ha of boreal forest (mainly in Alaska), and each of the Fennoscandian boreal countries has $<4.5 \times 10^6$ ha (Figure 2).

Fire has been the major disturbance process operating in boreal forests since the last Ice Age, [17] mainly because human population density is relatively low in boreal areas compared with most of the other biomes in the world [4]. However, advancing timber harvest (logging) and other human encroachment has led to an increase in fire frequency in recent years, particularly in Siberia [12]. For example, in Russia, an area of 7.5 M ha burnt in 2002 and 14.5 M ha burnt in 2003 [18], of which most (87% between 2002 and 2005) was started by humans [8]. This is compared with a annual mean burning rate of <4.5 M ha since the 1950s, which is more an index of the long-term natural burning rate [17,19] (Online supplementary material Figure S1). In Russia in particular, most fires occur near roads and other transportation networks, indicating that humans have a constant multiplication effect on fire events (up to eight-times above background rates) [8,17]. Weather anomalies related to human-driven climate change appear to have increased fire susceptibility in recent years [8], but humans are directly responsible for most ignitions in non-intact Russian forests, and from 72% to 78% of ignitions in all boreal forest types combined [8,17].

Biodiversity threats

There are currently about 20300 species found within the boreal forest zone [4], but tree diversity in this zone is relatively low compared with other temperate forests (e.g.

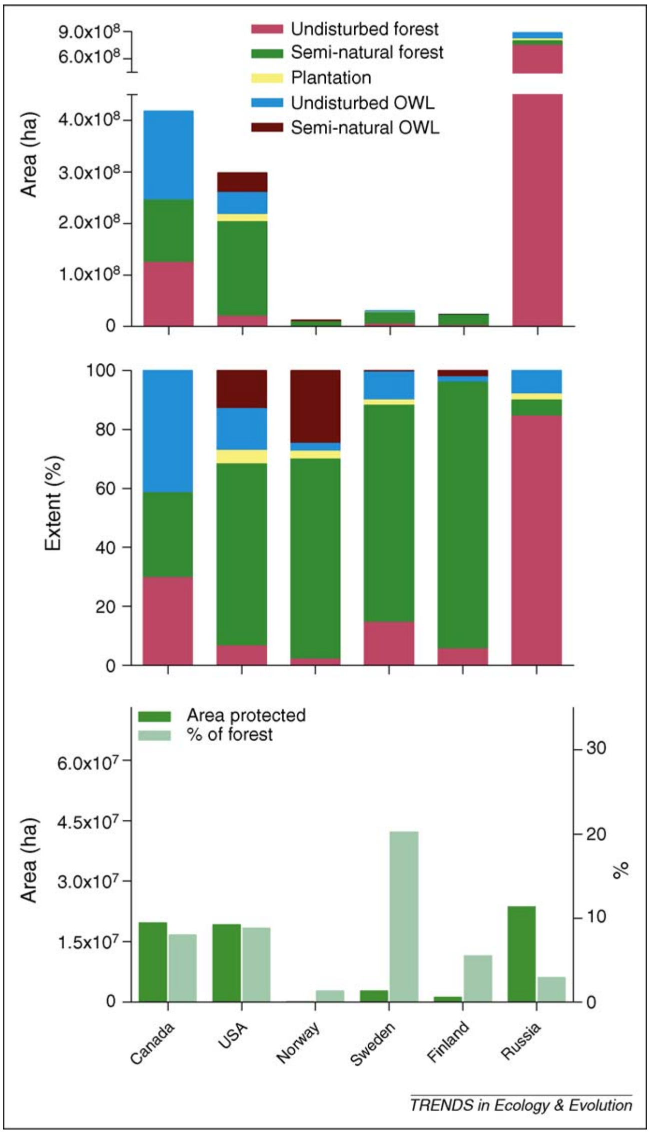

Figure 2. **(a)** Total forest cover in the six main boreal countries categorized as 'forest' (tree crown cover with >10% and area >0.5 ha) and 'other wooded land' (OWL = tree crown cover 5–10%), and whether or not 'undisturbed' by human activities according to the United Nations Temperate and Boreal Forest Resources Assessment 2000 (TBFRA) [16]. **(b)** Values expressed as percentages for each country [16]. See Online Supplementary Material for more detailed definitions of forest types. **(c)** Total area and proportion of total forest (tree crown cover with >10% and area >0.5 ha) not available for wood supply according to the TBFRA 2000 [16] for each of the six main boreal countries. The TBFRA definition of 'unavailable for wood supply' is taken from the IUCN as 'an area of land and/or sea especially dedicated to the protection and maintenance of biological diversity; and of natural and associated cultural resources, and managed through legal or other effective means'.

Pacific Rim) [13,16]. For birds and mammals in the boreal forest zone, the lowest diversity at all taxonomic levels occurs in Europe, and the highest in western North America and east Asia [20]. To examine the degree to which boreal species are threatened, we searched the IUCN's 2008 Red List (www.iucnredlist.org) for species under the 'boreal forest' habitat heading, which listed 367 species. After removing some mistakenly classified non-boreal species and verifying distributions, there were 348 species in the Red List in this category. Of these, >94% were listed as *Least Concern* – the remainder were

Table 1. Taxonomic breakdown (by percentage) of threatened species[a]

Taxon	IUCN Red List 2008[b]	TBFRA 2000[c,d]
Fungi and lichens	5	15.9
Plants	5	–
Ferns	–	1.4
Mosses	–	16.1
Vascular plants[e]		23.0
Trees		1.6
Butterflies and moths	–	20.1
Birds	50	7.6
Mammals	35	5.2
Other vertebrates[f]	5	9.1

[a]See also Online Supplementary Material text and Tables S3 and S5 for more detail.
[b]IUCN 2008 Red List (www.iucnredlist.org). There were 348 entries designated as 'boreal forest' species, of which 328 (94.3%) fall into the *Least Concern* category (not threatened); percentages therefore summarize the remaining 20 threatened species by taxon.
[c]United Nations Temperate and Boreal Forest Resources Assessment 2000 (TBFRA) [16]. The percentages are derived from the among-country (Canada, USA, Norway, Sweden, Finland and Russia) mean number of 'endangered' species (1927 species listed in total; average of 321 endangered species per country) per taxonomic category.
[d]Sum of among-country mean percentages does not equal 100%.
[e]Excluding trees.
[f]Reptiles and amphibians (IUCN); reptiles, amphibians and fish (TBFRA).

considered *Threatened* (taxonomic breakdown in Table 1, and IUCN category breakdown and listed threatened species in Online supplementary material Tables S3 and S4).

We also examined the TBFRA 2000 database [16] for additional data on species endangerment patterns in the six main boreal countries. The TBFRA compiled information based on IUCN Red List data, national compendia and taxonomically specific lists and, although incomplete, now out-of-date, and including some temperate (not strictly 'boreal') species that may bias the number of threatened species upward, the dataset probably represents a more detailed assessment of biodiversity trends in this region compared to the 2008 Red List because the TBFRA includes expert opinion and national listings for many species not adequately assessed by the IUCN [16]. The mean proportions of 'endangered' forest species (i.e. assessed generally as of conservation concern) within nine taxonomic groups are listed in Table 1 (a summary by boreal country is presented in Online supplementary material Table S5). Across all taxa, Fennoscandian countries have the highest proportional endangerment, with Sweden exceeding all other countries for all taxa except trees and 'other vertebrates' (reptiles, amphibians and fish); these last two categories are highest for Finland and Norway, respectively (Online supplementary material Table S5). Even though categorization of 'forest-occurring' species (see Online supplementary material) was not always available, and assessments can be more conservative in some countries, the results generally appear to reflect the distribution of highest human population density and development relative to total forest area. Nonetheless, the boreal forest is a critical habitat for its threatened species, whereas its migratory species also need simultaneous preservation in tropical areas.

Changing patterns of carbon storage and flux

Like its proportional forest coverage, the boreal ecosystem contains roughly 30% of the stored terrestrial C of the Earth, with an estimated 550 Gt C in combined soil and above-ground pools [21]. Although the boreal forest has primarily been considered a long-term global C sink, recent studies suggest that the rate of uptake may not be as high as once thought [22]. Various models additionally predict that the boreal biome is the region most likely to be altered by climate change over the next century, with warmer temperatures and longer growing seasons [23] shifting it from being a net C sink to a source [9]. This warming is also predicted to lead to boreal forest expansion northwards and upwards in elevation, whereas southern regions may shift to grassland or temperate zone forest types [24]. Changing tree lines would alter albedo because former winter snow-covered areas would then have decreased reflectivity, but warmer temperatures would also decrease the extent of snowfall and potentially lessen this impact [2]. Chen *et al.* [25] found that warmer forests had greater C sequestration, but others suggest that longer growing seasons and warmer temperatures are more likely to lead to greater decomposition rates [26]. An increased concentration of CO_2 and resulting fertilization could enhance boreal forest productivity [27], but this may not compensate for other negative influences of climate change on C sequestration processes, nor would the extent be equal across the globe [28].

Estimates of the spatial distribution of C stores within regions are not well-developed and can be highly variable [29]. Likewise, improved technological capacity has resulted in lowered estimates of C stocks for boreal forests in recent years [30]. Combined, this uncertainty has caused concern over the validity of some global C modelling projections [31]. Clearly, Russia contains the largest area of boreal forest of any country (Figures 1 and 2) and, by extrapolation, potentially the most extensive C stores, but some analyses suggest that the C stock is not proportional to forest area [29,30]. Nevertheless, the accuracy of these estimates is hindered by discrepancies not only in general methods, but also because of uncertainty in basic estimates of forest cover and which parts of the C pool should be included [31] (Online supplementary material Table S6).

Role of fire

Primary among the drivers of boreal forest dynamics and the associated C flux is fire [32]; its role in successional processes shapes the local and regional age structure and tree species composition of stands, thus influencing C sequestration patterns. Although high-intensity, stand-replacing fires are more frequent in the North American boreal zone than in the Siberian boreal zone [33], changing climate and weather patterns over the past 50 years have altered fire dynamics and the release rates of C throughout the circumpolar region [5]. More frequent fires have been associated with increasing frequency of temperature anomalies and more human-ignited fires [8,17], and a 74–118% increase in the area burnt annually across North America is predicted over the next 100 years [34]. As a result, increased annual rates of C release have been predicted [35] and indeed, forest fires in the boreal zone have released more C over time: fire emissions of total C in North America approximately doubled from around 30 Tg

C $year^{-1}$ in the 1960s to >60 Tg C $year^{-1}$ in the 1990s, and in Eurasia from 100–200 Tg C $year^{-1}$ in 1996–1997 to nearly 500 Tg C $year^{-1}$ in 2002 [36]. The impact that C released by fire has on overall greenhouse gas concentrations is an important component when trying to determine whether boreal forests are a net sink or net source of C.

Role of insect outbreaks

Insect infestations also appear to exert a cyclical (but strong) influence on boreal forest C dynamics. Canada's boreal zone has recently shifted from a C sink in the 1990s to a C source in 2001 as warmer temperatures reduced over-winter mortality of tree-killing insects, resulting in an increased frequency and severity of outbreaks and subsequent mass tree mortality [37]. Although some suggest that these outbreak dynamics are currently within the normal range for forest insects [5], an increased frequency and severity of insect disturbances is anticipated as warmer and potentially drier weather enables range expansions and intensification of outbreaks [37–39]. Some evidence indicates that a higher incidence and severity of insect outbreaks is already taking place, [e.g. 40] with the potential for sequential outbreaks by species such as the mountain pine beetle (*Dendroctonus ponderosae*) and spruce budworm (*Choristoneura fumiferana*) causing Canada's boreal forest to be a net source of C for several decades [37]. Although the implications for C dynamics have not been studied extensively [41], insect disturbance was responsible for a greater loss of stored C than was fire from Canadian forests in the late 20th century [42], and the estimated annual C release due to the current mountain pine beetle outbreak in western Canada is 50% more than rates attributable to fires during even the most severe fire years [40].

Role of timber harvest

The extent of boreal forest harvest varies widely by region (see above) but, even in areas with high harvest rates, the long-term impact of logging on C stores may be limited if there is regeneration to forested stands [43], particularly because much of the C removed is not released immediately but is stored in various commercial products or ends up in landfills. Following harvest, there can be an initial release of C depending on silvicultural practice, rotation length and harvest-related damage, but sequestration eventually returns to original rates as new stands grow [44]. Although there is disagreement [e.g. 45], soil C generally appears to remain approximately constant [46]. However, above-ground stores decrease in managed landscapes for ~10 years after harvest, after which the site becomes a net C sink as new stands grow [47]. Overall, the effects of natural disturbance such as fire on C sequestration are probably more important than the impact of management interventions such as extending harvest rotation, enhancing regeneration, or increasing stocking densities [37]. In fact, the opening up of forests for access to harvest sites in Russia may have led to a higher frequency of fire [17], indicating that landscape management can have broader implications for C storage. In other words, the fragmentation resulting from the harvest and management of timber can increase the frequency, intensity [17] and type (e.g. shifting dominance of surface fires to crownfires [48]) of fires. Natural disturbance is the pervasive force shifting C storage patterns in the boreal forest [32], and although management strategies may need to be modified to accommodate climate change [2,24], it is plausible that shifts in harvest management itself will have a limited effect [37].

The interactive effect of increasing fire frequency and insect outbreaks arising from warmer temperatures, and a changing structure and composition of forests resulting from broad-scale harvest management, appears poised to lower boreal C stores and increase C emissions in the foreseeable future [35–37,49]. However, some models suggest that the higher albedo of deforested areas covered in snow [50] provides a cooling effect that more than offsets the warming associated with the release of CO_2 through deforestation [51,52]. Indeed, the heat retained by intact boreal forests contributes more to increased mean annual global temperature than any other biome [53]. It is our opinion that avoidance of deforestation and the maintenance of the boreal zone as a net C sink will provide more durable climate warming mitigation (and obviously better prospects for biodiversity maintenance) because the amplification effect (i.e. increasing temperatures melt more snow, decreasing surface albedo and raising temperatures further) [54] will eventually erase short-lived cooling effects.

Recommendations to manage biodiversity and carbon retention simultaneously

Considering that boreal regions are at latitudes where climate warming will be globally most profound [4], it is our opinion that current practices of boreal forest management (Box 1) are inadequate to deal with the pace and magnitude of expected changes [55]. The essential role of boreal forests in C sequestration itself is strong justification to create large forest reserves [44]. Such large forest reserves are possible in Canadian and Russian boreal forests, and we argue that these countries in particular have a moral and global responsibility to create such reserves. However, while old-growth forests are important for C sequestration [44], reserves should be sufficiently large to accommodate a natural disturbance regime which, in turn, will maintain a wide range of seral stages to maximize the area available for habitat-specialist species [56]. This can be achieved by incorporating stand structure and complexity into reserve-design algorithms [57]. Large reserves in the boreal forest are also needed as 'living laboratories' to understand the effects of natural disturbances, and as a 'natural capital bank' against the unforeseen [58]. To maximize C sequestration, increasing the scale of reforestation in heavily disturbed Fennoscandia and restricting the massive deforestation and fragmentation in Russia arising from timber harvest, mining, hydropower dam construction, and the development of oil and gas should be a top priority for forest managers [6]. One possible way to offset the lost economic opportunities from curtailing industrial exploitation is to extend 'reducing carbon emissions from deforestation and forest degradation' (REDD) credits [59] to these regions.

Box 1. Principles of current boreal forest management for biodiversity conservation

Boreal forest management is driven by local context. Live tree retention is widely practised to achieve various outcomes (reseeding potential, wildlife use) [62], yet this technique may not be adequate to conserve many taxa. Insects, cryptogams and fungi are essential for the decomposition of woody debris and nutrient cycling, but saproxylic species richness correlates positively with the amount of dead wood retained [63–65] and species have already disappeared from Fennoscandia due to the paucity of dead wood in managed forests [66]. Dead and decaying trees may also be important for maintaining birds through the provision of nesting habitat [67]. Likewise, trees are retained as corridors to facilitate animal movement among fragments, but it is unclear if these are effective for population persistence at broader scales [68,69].

In Fennoscandia, small patches containing threatened species are preserved in managed forests [70,71], but it is uncertain if these maintain vital ecosystem functions such as seed dispersal [69] critical for forest regeneration [72]. Similar management approaches more broadly applied include the retention of riparian buffer strips in logged forests to protect wetlands and biodiversity, but there is a greater need to be able to vary the width of these strips depending on wetland position, watershed connectivity, hydrology and biodiversity requirements [73,74]. Likewise, because some rural communities in the boreal region rely on non-timber resources such as bushmeat, mushrooms, berries and firewood, institutions and logging companies have begun to devise plans to manage forests for diversity beyond the timber products they provide [58].

The dominance of natural fire in shaping boreal forests [58] has been used to justify the practice of clear-felling [68], and the application of fire itself is used as a management tool [75]. However, this strategy can be problematic because natural fire regimes can be difficult to emulate [69] principally because the high spatio-temporal variability makes single-prescriptions unrealistic [68]. Additionally, the uncommon practice of repeated burning might be needed for the germination of seed banks [67,68]. Other types of disturbances such as insect outbreaks, pathogens, windstorms, droughts and floods [68] and their complex synergies with fire are generally intractable to emulate as management tools. The mushrooming certification schemes available for sustainable boreal forestry [58,76] driven by demands from enlightened consumers and environmental activists might only be partially effective [77] to maintain biodiversity values, but more research is needed to test their efficacy.

Given the dominance of natural disturbances in driving boreal ecosystem dynamics [17], greater emphasis on managing expected modification of these disturbances resulting from climate change can be more effective than concentrating exclusively on managing harvest regimes, from both a C sequestration and biodiversity conservation perspective. The sheer extent of the boreal forests within Russia and Canada, combined with the large ranges of many shared taxa [4], are most likely responsible for the relative low frequency of endangerment observed (Online supplementary material Tables S3–S5). Thus, continued fragmentation from natural and human-driven processes is perhaps the greatest future concern for species conservation there. While fragmentation remains a clear threat [63], forest management must not only consider fragmentation, it must also attempt to avoid creating large stands of even-aged trees [60], maximize connectivity of existing fragments, and consider the implications of the storage and release of C at regional and continental scales. Clearly, there must also be better management in Russia to reduce the frequency of human-caused fires.

It is our opinion that the status quo of current rates of forest fragmentation, stale management practices ill-equipped to adapt to the effects of climate warming on natural fire patterns, and a vestigial appreciation of experimental adaptive management will quickly compromise this relatively intact, but latently threatened [61], biodiversity haven. Unlike many of the world's highly degraded ecosystems, we have the opportunity to preserve boreal forests and the species they harbour while maintaining an effective C sink. Ideally, civil society, economists, social scientists, biologists, policymakers and politicians must work more closely to manage the boreal forest effectively.

Acknowledgements

NSS was supported by a Sarah and Daniel Hardy Visiting Fellowship at Harvard University while this manuscript was prepared. We thank F. Achard (Institute for Environmental Sustainability, Joint Research Centre of the European Commission) and C. Pollock (IUCN Species Programme) for assistance in accessing data.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.tree.2009.03.019.

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