



Global estimates of boreal forest carbon stocks and flux



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ABSTRACT

The boreal ecosystem is an important global reservoir of stored carbon and a haven for diverse biological communities. The natural disturbance dynamics there have historically been driven by fire and insects, with human-mediated disturbances increasing faster than in other biomes globally. Previous research on the total boreal carbon stock and predictions of its future flux reveal high uncertainty in regional patterns. We reviewed and standardised this extensive body of quantitative literature to provide the most up-to-date and comprehensive estimates of the global carbon balance in the boreal forest. We also compiled century-scale predictions of the carbon budget flux. Our review and standardisation confirmed high uncertainty in the available data, but there is evidence that the region's total carbon stock has been underestimated. We found a total carbon store of 367.3 to 1715.8 Pg (10^{15} g), the mid-point of which (1095 Pg) is between 1.3 and 3.8 times larger than any previous mean estimates. Most boreal carbon resides in its soils and peatlands, although estimates are highly uncertain. We found evidence that the region might become a net carbon source following a reduction in carbon uptake rate from at least the 1980s. Given that the boreal potentially constitutes the largest terrestrial carbon source in the world, in one of the most rapidly warming parts of the globe (Walsh, 2014), how we manage these stocks will be influential on future climate dynamics.

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1. Introduction

The boreal ecosystem constitutes about a third of the Earth's extant forests (FAO, 2006) and a substantial portion of the remaining large tracts of continuous forest (Bradshaw et al., 2009), as well as containing an estimated one third of the stored terrestrial carbon stocks (IPCC, 2007; Pan et al., 2011). Largely ignored in the context of international efforts to mitigate climate change through management of carbon storage and flux (Moen et al., 2014), the boreal zone has been considered by many to be a carbon sink (Jobbágy and Jackson, 2000; Ciais et al., 2010; Pan et al., 2011). This net carbon uptake is derived primarily from the expansion of the boreal forest following the deglaciation that occurred after the Last Glacial Maximum of 19–26.5 kyr ago (Adams et al., 1990; Foley et al., 1994) and the accumulation of carbon in deep peatlands (with peatland formation peaking around 7–8 kyr ago) (Gorham et al., 2007). However, and particularly important for the ongoing management of carbon stocks in the context of climate change, it appears that the strength of this sink has been weakening (Stephens et al., 2007; Bonan, 2008; Hayes et al., 2011), with estimates suggesting that some regions might well be hovering near zero flux intensity or will

soon become a net source (Bonan, 2008; Kurz et al., 2008b). The direction of flux and pace of conversion from sink to source appear to be driven at least in part by the relatively rapid temperature rise in the boreal region compared to other parts of the globe. Assessment of historical and current temperature regimes suggests greater rates of warming at high northerly latitudes over the 20th century, and particularly during the later decades of that century, than during the last 1000 years (Mann et al., 1999; Serreze et al., 2000; IPCC, 2001, 2007). Future scenarios also indicate a high probability that warming trends will continue and possibly increase during the coming century, further altering natural disturbance regimes through modified frequency and severity for both wildfire (Flannigan et al., 2005; Balshi et al., 2009; Tchepakova et al., 2009) and insect outbreaks (Bale et al., 2002; Dymond et al., 2010; Gustafson et al., 2010), as well as increasing rates of permafrost loss (Vitt et al., 2000; Schuur et al., 2008; Grosse et al., 2011).

Reliable estimates of total carbon storage and flux across this expansive region are required to craft government policies that effectively foster sustainable development and climate change mitigation. Likewise, assessing alternative forest management strategies as mitigation measures under changing environmental circumstances will be based, at least in part, on the same critical carbon accounting information. To address this data need, there has been enormous growth over the past three decades in the number of studies examining boreal carbon; a search for “boreal AND carbon” identified only two papers in the Web

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of Science® database during 1982–1983 versus 1066 papers published during 2012–2013.

Yet there is high uncertainty associated with these estimates (Shvidenko et al., 2010; Hayes et al., 2012). Substantial differences have been identified among 'bottom-up' forest inventory-based assessments of regional and global carbon stocks and flux due to the use of different biomass density estimates in combination with different, and sometimes even similar, forest area assessments (Fang et al., 2006; Houghton et al., 2007). This approach is also plagued by irregular updating of forest inventory data for some of the regions involved (Potapov et al., 2011). Similarly, 'top-down', atmosphere-based models have produced variable estimates attributed to gaps in spatial and temporal sampling effort, as well as measurement, modelling and scaling errors associated with the differing approaches used (Dargaville et al., 2006; Ciais et al., 2010). For example, permafrost deposits constitute a substantial storage pool for carbon in the boreal that is at risk from rising air temperatures (Grosse et al., 2011; O'Donnell et al., 2011). Yet quantifying both storage and flux from permafrost in the context of the boreal is confounded by datasets created to address issues across the northern cryosphere, rather than separating Arctic/tundra from strictly boreal deposits (McGuire et al., 2010; Grosse et al., 2011) (but see Tarnocai, 1998, 2000). Likewise soil carbon, which in the boreal accounts for at least three times the carbon that is stored in vegetation (Malhi et al., 1999), is often determined using model predictions rather than repeated soil measurement over sufficient time sequences at permanent sample plots (Häkkinen et al., 2011). Those assessments of soil carbon stores available are frequently made to only ≤ 1 m depth and consequently ignore any stores below (Jobbágy and Jackson, 2000; Seedre et al., 2011), although soils below 1 m are considered by many (e.g., Deluca and Boisvenue, 2012) not to contain substantial amounts of carbon (but see Tarnocai et al., 2009; Jorgenson et al., 2013; Kuhry et al., 2013; Hugelius et al., 2014). Equally problematic is the relatively young age of the soils underlying the boreal forest; they are highly variable in depth and are frequently shallow with limited development of mineral horizons due to recent glacial activity, particularly at the northern limit of the boreal zone (Sanborn et al., 2011). Consequent models built to extrapolate soil carbon stores from local-to regional- or biome-level scales are hampered by their capacity to incorporate this variability in the extent of soil types and depth, as well as the depth to which sampling for carbon density has been done.

Despite these uncertainties, a standardised inventory approach to examine and compare the available data can be effective in identifying broader trends, but also gaps and weaknesses in the information available. Our aims are therefore to provide comprehensive, global and up-to-date estimates of carbon storage and flux in the boreal zone.

2. Methods

We compiled a detailed list of scientific publications (mainly primary, peer-reviewed literature, but including books, and government and NGO reports) that reported carbon density (quantity per unit area), total carbon stores or carbon flux from within the boreal region. We searched Web of Science® using the terms 'boreal', 'carbon', 'flux' and 'storage' in different combinations to identify the primary literature, and cross-referenced papers in reference lists to identify missing source literature. We took values as presented when in either Pg (10^{15} g) or Mg (10^6 g) $C\ ha^{-1}$, or converted from reported values into these units. We recorded area extent as reported or estimated based on references provided in each paper. Most papers could be divided into one or more regional foci: circum-boreal, Russia, Canada, Scandinavia (i.e., Fennoscandia) and Alaska, and reported carbon values for one or more main components of the system—vegetation (both above- and below-ground, living and dead biomass), soils (typically the mineral horizons, but sometimes including organic horizons as well as forest-based peat) and peatlands.

2.1. Carbon stores

Carbon stores estimated for the boreal ecosystem among regions were generally restricted to particular components of the broad categories of 'vegetation', 'soils' and 'peatlands'. For example, many studies reported values for live biomass only, live and dead biomass, above- or below-ground biomass only, soils to a depth of 1 m only, soils to a depth of 3 m only, cryosols only, mineral soil horizons or mineral and organic soil horizons combined, peatlands to a depth of 1 m only, or average-depth peatlands only. In some instances, determining the exact components to which the estimates were attributed was difficult or impossible. As such, our reported ranges should be considered approximate only.

Furthermore, most papers approximated stores based on differing estimates of spatial extent for the various ecosystem components. We were therefore obliged to standardize all estimates to densities ($Mg\ C\ ha^{-1}$) first, and then estimate mean densities over comparable components (live biomass only, etc.). We then took standard area estimates for either circum-boreal or regional extents and multiplied these by the standardised density ranges to provide total carbon estimates. For vegetation and soils, we used the same spatial extents to estimate total stores, but peatland extent is considerably smaller, so we used the relevant extents for all peatland estimates (where appropriate, we averaged these across studies reporting different values within regions). In some cases, peatland extent was not specifically categorised into 'boreal' and 'tundra' biomes (i.e., the two were combined), so we have indicated where inflations due to the inclusion of strictly non-boreal peatlands likely occurred. As is common in such accounting-type summaries, our geographical sampling range was limited to that available in the literature. Consequently, our findings reflect a general scarcity of observations for high-latitude locations and a bias towards study of the more productive, southern portion of the boreal forest for both measures of carbon stocks and flux (Hayes et al., 2012); for example, unmanaged northern forests in boreal Canada were not included in assessments of carbon budgets for that region (Kurz et al., 2009).

2.2. Carbon flux

As for carbon density and total stocks, we estimated mean carbon dynamics across the boreal zone by standardising estimates of carbon flux, typically expressed as either a total exchange per unit time (e.g., $Pg\ C\ year^{-1}$) or exchange per unit area per unit time (e.g., $Mg\ C\ ha^{-1}\ year^{-1}$). Our principal aim was to estimate the range of net flux density, i.e., whether a study measured net carbon uptake ('sink') or release ('source'). We standardised all estimates to flux density ($Mg\ C\ ha^{-1}\ year^{-1}$) based on area of extent provided in each study, or applied area estimates from other relevant studies. In all analyses of carbon flux density we based our assessment on both the entire dataset compiled as well as using just those data from studies where area of extent was provided.

Given recent observations that, at least in certain parts of the boreal forest, the region has become a net carbon source (see more below), we attempted to divide estimates into decadal spans to examine if any temporal trends were apparent. Most carbon flux estimates date back only to the 1980s, so we estimated decadal trends in the 1980s, 1990s and 2000s, with one study projecting dynamics to 2050 (Metsaranta et al., 2010) and one study projecting to 2100 (Yarie and Billings, 2002). Many modelling studies in particular estimated carbon dynamics over longer periods (e.g., over the entire last century, late post-glacial, etc.), or examined particular forest stand types (e.g., a particular species composition, only young and growing; only recently disturbed) often across limited spatial scales. We excluded these studies from mean flux density estimates. Estimates spanning two decades (e.g., 1985–1995) were included in the means of both decades (e.g., '1980s' and '1990s'), so there is some inevitable overlap among decades (i.e., trends should be viewed partially as 'running' means).

Given the high variability within decade and the inevitable overlap in estimates, we could not test temporal trends statistically.

3. Results

3.1. Carbon densities and total stores

The results of our compiled carbon estimates are summarised in Figs. 1 and 2, Tables 1–3, and supplementary Tables S1–S6. Carbon density ranges were broadly consistent across regions, demonstrating the dominance of peatland carbon in total estimates (Fig. 1) relative to soil and vegetation in all regional cases (ranging from approximately 47% to 83% of total density). The two estimates of peatland carbon densities from Alaska (1174.2 and 1545.5 Mg ha⁻¹; Table 3) (Birdsey, 1992; Apps et al., 1993) exceed most of those from Russia, Canada and Scandinavia (Fig. 1) and so should be considered with caution. In all cases, the vegetation densities were the lowest, representing 3% to 17% of total carbon densities (Fig. 1). Circum-boreal density estimates for vegetation and peatlands were broadly comparable to regional estimates, but soil estimates were larger (first bar, Fig. 1).

Using the spatial extents for circum-boreal vegetation and soils (1.370 × 10⁹ ha) (IPCC, 2007) and peatlands (3.367 × 10⁸ for 'northern peatlands' and 1.200 × 10⁸ ha for 'boreal peatlands'; Table 2), we estimated a total circum-boreal carbon store of 367.3 to 1715.8 Pg (Table 2; Fig. 2). The mid-point of this range (1095 Pg) is larger than previous 'total' C estimates of 800 Pg reported by Apps et al. (1993), 550 Pg (Gt) reported by the IPCC (2007), and 272 ± 23 Pg C reported in the global assessment by Pan et al. (2011) (the latter is admittedly an underestimate because it includes peatlands down to 1 m depth only). This 1095 Pg is also considerably larger than the range 567.8 to 721.0 Pg determined from summing the regional values (Table 3).

Even though regional sums do not include smaller areas of boreal forest in northern Mongolia, north-eastern China and Iceland (Bradshaw et al., 2009), the disparity between the circum-boreal estimate and the regional sums is most likely due to underestimates of both peatland and soil carbon stores in the regional assessments, given that most estimates typically extend to only 1 m depth (or are of uncertain depth) (Tables S1–S6). There is also likely an upward bias in the total circum-boreal peatland estimates given that some assessments do not readily separate strictly 'boreal' peatlands from all northern peatlands (i.e., they include an unknown component of strictly tundra peatland stores). Nonetheless, the comparable carbon density and total estimates between the circum-boreal and regional assessments (Figs. 1 and 2) suggest that the potential bias is minor. Therefore, we conclude that the anomaly arises most likely from a large underestimate of soil carbon in regional assessments, such that our calculated

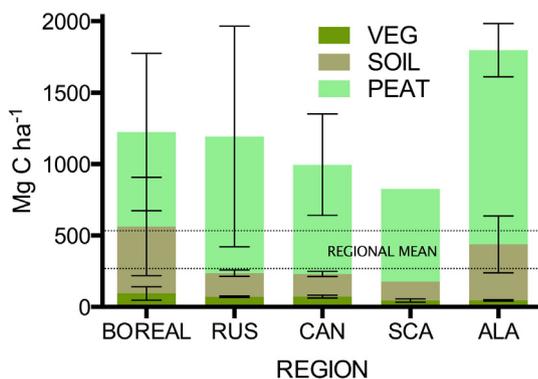


Fig. 1. Mean (±1 SD) carbon densities (Mg C ha⁻¹) estimated for various components of forest ecosystems (broadly, vegetation, soils and peat) across the entire boreal zone and for each major boreal region (Russia, Canada, Scandinavia and Alaska). Most density estimates calculated from total carbon pool (Pg C) per component divided by area of coverage (ha). 1 Mg C = 10³ kg C.

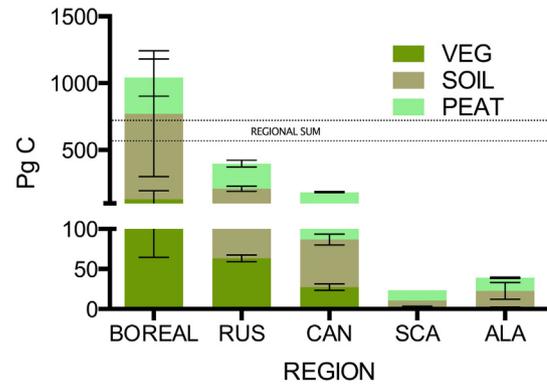


Fig. 2. Total (±1 SD) carbon stocks (Pg C) estimated for various components of forest ecosystems (broadly, vegetation, soils and peat) across the entire boreal zone and for each major boreal region (Russia, Canada, Scandinavia and Alaska). 1 Pg C = 10⁹ Mg C = 10¹² kg C.

range of 367.3 to 1715.8 Pg is probably more realistic than previous circum-boreal estimates.

While acknowledging that the Pan et al. (2011) biome estimates of total carbon pools are likely to be downwardly biased, especially with respect to soil and peatland contributions, our new estimated range is still higher than other major biomes (Fig. 3). Even allowing for the possible soil/peatland biases, our mid-point estimate is still higher than all tropical biomes combined (Americas, Africa and Asia). For example, even a hypothetical doubling of the Pan et al. (2011) estimates puts the total tropical store at 943 Pg. In the absence of more realistic global estimates per biome, we can only conclude that the boreal forest region's carbon stores have been under-estimated.

3.2. Carbon flux

Across the entire boreal region, the mean flux density over all estimates was 0.130 Mg C ha⁻¹ year⁻¹ (Table 4) indicating a net sink, but this value belies high variability (SD = 0.493 Mg C ha⁻¹ year⁻¹). Removing those estimates from studies for which area values were not provided, mean flux density was 0.263 Mg C ha⁻¹ year⁻¹ (SD = 0.339). Overall, Scandinavia had the highest regional estimated net flux (0.690 ± 0.331 Mg C ha⁻¹ year⁻¹; Table 4), although the lowest number of estimates ($n = 5$; Tables 4 and S9). Canada had the lowest mean flux density whether including (0.056 ± 0.574 Mg C ha⁻¹ year⁻¹) or excluding (0.176 ± 0.223 Mg C ha⁻¹ year⁻¹) studies with no area estimates (Tables 4 and S8).

Categorising flux estimates by decade revealed an interesting trend—although highly variable, there was an indication of a decline in flux from the 1980s to 2000s (Fig. 4), with mean negative flux predicted at least for Canada by the 2050s (Metsaranta et al., 2010) and Alaska by 2100 (Yarie and Billings, 2002). When excluding no-area estimates, the downward trend persisted (Fig. 4), albeit mean flux densities were greater than when including all estimates.

4. Discussion

We have compiled the most up-to-date and complete, standardised inventory of total circum-boreal carbon storage and flux. Although estimates are highly variable across temporal and spatial scales of investigation, our principal conclusion is that previous estimates of total carbon storage in the boreal zone have likely been too conservative. Our standardised inventory produced a total carbon store of 367.3 to 1715.8 Pg (mid-point = 1041.5 Pg), which is approximately 3.8 times the mean value reported by Pan et al. (2011), 1.9 times the estimate from the IPCC (2007) and 1.3 times the largest previous estimate from Apps et al. (1993) (Table 3). This result questions the conclusions by

Table 1

Circum-boreal estimates of carbon density (Mg C ha^{-1}) estimated for various components of forest ecosystems (broadly, vegetation, soils and peat). Most density estimates calculated from total carbon pool (Pg C) per component divided by area of coverage (ha). In most cases, errors (SD) for individual estimates were not provided. $1 \text{ Pg C} = 10^9 \text{ Mg C} = 10^{12} \text{ kg C}$.

Description	Component	Density (Mg ha^{-1})	Density (SD)	Area (ha)	Total (Pg)	Total (SD)	Reference
VEGETATION							
Northern peatlands	above-ground biomass (live plants)	101.0	107	3.367×10^8	34.0	36.0	(Zoltai and Martikainen, 1996; Anderson-Teixeira and DeLucia, 2011)
Northern peatlands	dead wood	3.0	3	3.367×10^8	1.0	1.0	(Zoltai and Martikainen, 1996; Anderson-Teixeira and DeLucia, 2011)
Boreal forest	above-ground biomass (live plants)	128.0	64	1.200×10^9	153.6	76.8	(Whittaker, 1975; Anderson-Teixeira and DeLucia, 2011)
Boreal forest	dead wood	6.0		1.200×10^9	7.2		(Whittaker, 1975; Anderson-Teixeira and DeLucia, 2011)
Boreal forest (MODIS)	live above- and below-ground tree biomass and understory vegetation	44.1		5.236×10^8	23.1		(Houghton et al., 2007)
Boreal forest (GLC2000)	live above- and below-ground tree biomass and understory vegetation	40.3		8.266×10^8	33.3		(Houghton et al., 2007)
Boreal forest	above- and below-ground biomass (growing stock volume)	40.0	15.4	1.019×10^9	40.7	15.7	(Turner et al., 2014)
Vegetation	vegetation	64.2		1.370×10^9	88.0		(IPCC, 2007)
Northern peatlands	below-ground biomass (roots)	18.0	8	3.367×10^8	6.1	2.7	(Zoltai and Martikainen, 1996; Anderson-Teixeira and DeLucia, 2011)
Forest	below-ground biomass (roots)	28.0	18	1.200×10^9	33.6	21.6	(Whittaker, 1975; Anderson-Teixeira and DeLucia, 2011)
SOILS							
Boreal forest	mineral soils to 3 m	125.0		1.200×10^9	150.0		(Whittaker, 1975; Jobbágy and Jackson, 2000)
Boreal zones	mineral soils to 1 m	152.9		1.868×10^9	285.6		(Post et al., 1985)
Permafrost distribution	all soil carbon – all depths*	890.3		1.868×10^9	1672.0		(Tarnocai et al., 2009)
permafrost distribution	all soil carbon – all depths**	734.3		1.780×10^9	1307.0		(Hugelius et al., 2014)
Boreal	soil carbon pool – to 1 m	338.8		1.390×10^9	471.0		(IPCC, 2007)
PEAT							
Northern peatlands	litter and below-ground peat	946.0	508	3.367×10^8	318.5	171.0	(Zoltai and Martikainen, 1996; Anderson-Teixeira and DeLucia, 2011)
Northern peatlands	soil organic matter – to 1 m	369.0		3.367×10^8	124.2		(Zoltai and Martikainen, 1996; Anderson-Teixeira and DeLucia, 2011)
Boreal forest	litter and below ground peat	59.0		1.200×10^9	70.8		(Whittaker, 1975; Anderson-Teixeira and DeLucia, 2011)
Boreal forest	soil organic matter - to 1 m	160.0	121	1.200×10^9	192.0	145.2	(Whittaker, 1975; Anderson-Teixeira and DeLucia, 2011)
Boreal and subarctic	peat – to average depth 2.3 m	1360.2		3.345×10^8	455.0		(Kivinen and Pakarinen, 1981; Tarnocai, 1984; Gorham, 1991)
Peatland permafrost	peat in permafrost – depth unspecified	1179.1		3.367×10^8	397.0		(Zoltai and Martikainen, 1996)
Northern peatlands	total peat depth, but not underlying soil organic carbon in mineral soils (frozen and unfrozen peatlands)	1367.5	92.5	4.000×10^8	547.0	37.0	(Maltby and Immirzi, 1993; Yu et al., 2010)
Northern peatlands	peatlands (based on Finnish data)			–	273.0		(Turunen et al., 2002)
Boreal and subarctic	peatlands based on bulk density and age			–	249.0		(Armentano and Menges, 1986)

* 0 to 30 cm: 191 Pg; 0 to 100 cm: 496 Pg; 0 to 300 cm: 1024 Pg; deltaic deposits and Siberian Yedoma sediments > 300 cm: 648 Pg.

** 0 to 30 cm: 217 Pg; 0 to 100 cm: 472 Pg; 0 to 300 cm: 1035 Pg; deltaic deposits and Siberian yedoma sediments > 300 cm: 272 Pg.

Pan et al. (2011) that the tropics harbour the most carbon globally compared to boreal and temperate forests.

Most (approximately 95% on average) of the boreal zone's terrestrial carbon resides below ground in its peatlands and soils (Table 3), which contrasts starkly with tropical systems where most (>50%) carbon resides in its living biomass (Pan et al., 2011). Unfortunately, it also appears that the major discrepancies between our and previously reported values stem from underestimates of both soil and peatland stocks, with soil estimates in particular requiring refinement across broad spatial scales. The obvious difficulty in assessing sub-surface carbon across scales meaningful for boreal assessments has historically hindered progress (indeed, Pan et al. qualified the uncertainty of the boreal carbon estimates in particular as being partially due to the lack of data below 1 m in peatlands) (Pan et al., 2011); however, our accumulation of dozens of standardised, finer-scale estimates provides novel insight into the entire region's potential stock. The rarity of standardised, widespread sampling to depths > 1 m probably means that even our revised estimates of soil carbon are still too conservative,

reinforcing our central claim that the total carbon pool of the boreal zone has been underestimated.

As has been suggested previously (Shvidenko et al., 1996; Myrneni et al., 2001; Stephens et al., 2007; Bonan, 2008; Kurz et al., 2008b; Hayes et al., 2011), the boreal region's impressive stock of terrestrial carbon is possibly being reduced due to a combination of different anthropogenic pressures. Although highly variable given the temporal span and mismatched spatial scales, standardised flux estimates made since the 1980s support the hypothesis that the boreal zone is transitioning from a net carbon sink to a source. It is clear that certain regions such as western Canada are already emitting more carbon than they take up due to the widespread, but still localised, disturbances linked to a warming climate (Kurz et al., 2008a, 2008b). By contrast, other regions such as Fennoscandia are clearly net sinks (Table 4), likely because of the relatively young age structure arising from long-term, intensively managed harvesting (Moen et al., 2014).

Even in the absence of some of the most rapid rates of warming in the world (Walsh, 2014), the boreal forest has been slowly equilibrating

Table 2

Summary (means and SD) of circum-boreal estimates of carbon density (Mg C ha^{-1}) and total carbon (Pg) estimated for various components of forest ecosystems (broadly, vegetation, soils and peat). Ranges are estimated by various combinations of components indicated by upper-case letters in brackets. $1 \text{ Pg C} = 10^9 \text{ Mg C} = 10^{12} \text{ kg C}$. See Table 1 for generating values and references.

Component	Mean density (Mg ha^{-1})	SD density (Mg ha^{-1})	Mean total (Pg)	SD total (Pg)
VEGETATION (area = 1.370×10^9 ha)				
Above-ground biomass (A)	114.5	19.1	156.9	26.2
Below-ground biomass (B)	23.0	7.1	31.5	9.7
Above- and below-ground biomass (C)	47.2	11.5	64.6	15.8
Dead wood (D)	4.5	2.1	6.2	2.9
Lower (C)	47.2	11.5	64.6	15.8
Upper (A + B + D)	142.0	20.5	194.5	28.0
SOILS (area = 1.370×10^9 ha)				
Soils to 1 m (E)	245.9	131.5	336.8	180.1
Soils to 3 m (F)	125.0	-	171.3	-
All permafrost soils (G)*	812.2	-	1112.8	-
Lower (F)	125.0	-	171.3	-
Upper (G)	812.2	-	1112.8	-
PEAT**				
Average-depth northern peatlands (H)	1213.2	198.3	408.5	66.8
Average-depth boreal peatlands (I)	109.5	71.4	131.4	85.7
Lower (I)	109.5	71.4	131.4	85.7
Upper (H)	1213.2	198.3	408.5	66.8
Total		Upper	367.3	$-\infty$
		Lower	1715.8	$-\infty$

* Includes tundra.

** Northern peatlands area = 3.367×10^8 ha; boreal peatlands area = 1.200×10^9 ha.

∞ No combined SD provided given absence of SD for major component (soils).

throughout the Holocene warming period following the Last Glacial Maximum. Forests rapidly expanded northward as the great ice sheets retreated, followed by the accumulation of deep peatlands peaking some 7000 to 8000 years ago (Gorham et al., 2007). The relaxation of forest expansion rate and the successional climax of the greater forest extent mean that in a stable climate, boreal forests would eventually reach a carbon equilibrium or become sources (Apps et al., 1993). Indeed, He et al. (2014) and Yu (2012) estimated that the rates of CH_4 and net primary productivity-based carbon emissions were substantially higher during the Holocene Thermal Maximum (11,000–9000 years ago) than today (Zhuang et al., 2007). Even future forest extensions into the tundra will likely be offset by grassland encroachments in the south, resulting in a net loss of high-carbon forests (Apps et al., 1993). Increasing the severity and frequency of the disturbance regime from warming- and human-altered natural processes means that a carbon-source future is plausible (Yarie and Billings, 2002; Metsaranta et al., 2010; Spahni et al., 2013).

Table 3

Summary means and sums of regional carbon density (Mg C ha^{-1}) and total carbon (Pg) estimated for various components of forest ecosystems (broadly, vegetation, soils and peat) for each major region of the boreal zone. Summary information derived from Tables S2, S4 and S6. $1 \text{ Pg C} = 10^9 \text{ Mg C} = 10^{12} \text{ kg C}$. UP = upper confidence limit; LO = lower confidence limit.

Region	Vegetation				Soils				Peat				Mean		Sum		Sum
	Density (Mg ha^{-1})		Total (Pg)		Density (Mg ha^{-1})		Total (Pg)		Density (Mg ha^{-1})		Total (Pg)		Density (Mg ha^{-1})	Total (Pg)	Total (Pg)	Total (Pg)	
	LO	UP	LO	UP	LO	UP	LO	UP	LO	UP	LO	UP	LO	UP	LO	UP	2007*
Russia	66.8	76.5	59.0	67.6	144.0	187.7	127.3	165.9	184.0	1726.9	162.7	212.5	131.6	663.7	349.0	446.0	209.3
Canada	62.1	83.9	23.4	31.5	139.9	175.8	52.6	66.1	410.4	1121.0	92.2	102.6	204.1	460.2	168.2	200.2	50.4
Scandinavia	32.8	56.8	2.0	3.4	132.3	132.3	8.0	8.0	650.0	650.0	13.0	13.0	271.7	279.7	22.9	24.4	11.8
Alaska	42.3	50.2	2.2	2.6	192.3	592.5	10.0	30.8	1174.2	1545.5	15.5	17.0	469.6	729.4	27.7	50.4	-
Total			86.5	105.2			197.9	270.8			283.4	345.1			567.8	721.0	
Mean	51.0	66.9			152.1	272.1			604.7	1260.8							

* All biomass components, including soil to 1 m for peatlands from Pan et al. (2011).

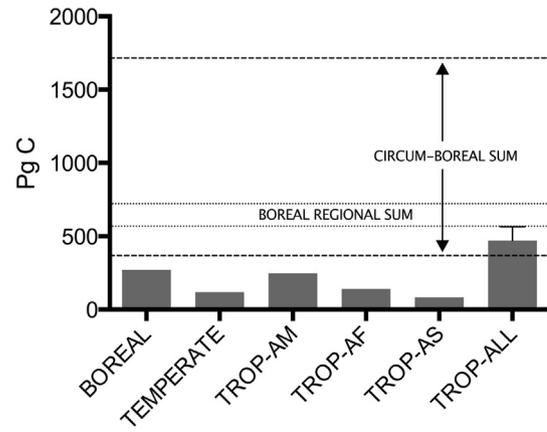


Fig. 3. Total carbon stocks (Pg C) for major global forest biomes. Grey bars indicate estimates from Pan et al. (2011). Regional sum = the sum of total carbon stores from each major boreal region (Russia, Canada, Scandinavia and Alaska) (Table 3). Circum-boreal sum = total carbon stocks estimated across the entire boreal zone (Table 2). $1 \text{ Pg C} = 10^9 \text{ Mg C} = 10^{12} \text{ kg C}$.

Attempts to mitigate the effects of greenhouse gas emissions and resulting climate change must be based on a long-term perspective, managing the boreal as an integral component of the biosphere with value beyond the substitutive carbon stores it possesses. Rather than managing for carbon, the boreal and other forest ecosystems should ideally be managed for resilience (Bradshaw et al., 2013; Moen et al., 2014); along with a coordinated and global effort to reduce emissions and possibly geo-engineer carbon-uptake solutions. This will require both national and international agreements to limit net deforestation from logging (Bradshaw et al., 2009), plan better long-term harvest rotations (Warkentin and Bradshaw, 2012), manage fire and insect outbreaks more effectively, and limit penetration of roads and other infrastructure into remote regions (Laurance et al., 2014). Not only will this limit the worst of the predicted carbon losses, such approaches will maximise biodiversity retention across the expanse of the boreal zone (Bradshaw et al., 2009). Future studies of boreal carbon should also attempt to provide finer-scale regional assessments to avoid extrapolating over large areas, and thus lower the uncertainty of total stock measurements and flux.

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Table 4

(a) Circum-boreal estimates of carbon flux density ($\text{Mg C ha}^{-1} \text{yr}^{-1}$) estimated from total flux (Pg C yr^{-1}) and area of forest. Positive values indicate net carbon sink, and negative values indicate a net carbon source. (b) Regional summaries (mean and SD) for each region (including circum-boreal above)—see Tables S7–S9 for values (n = number of studies) and sources. $1 \text{ Pg C} = 10^9 \text{ Mg C} = 10^{12} \text{ kg C}$.

Description	Note	Period	Flux density ($\text{Mg ha}^{-1} \text{yr}^{-1}$)	Area (ha)	Flux (Pg yr^{-1})	Reference
(a) Circum-boreal						
Boreal and subarctic	accumulation based on radiocarbon dating for long-term estimates	recent post-glacial	0.227	3.345×10^8	0.076	(Kivinen and Pakarinen, 1981; Tarnocai, 1984; Gorham, 1991)
Forest biomes	ecosystems, peatlands and harvested products	1980s	0.566	1.249×10^9	0.707	(Apps et al., 1993)
Northern forests	modelled based on timber volume and carbon density	1980s	0.277	$*2.477 \times 10^9$	0.686	(Sedjo, 1992)
Northern forests	above- & below-ground live and dead tree biomass	early 1990s	0.484	1.343×10^9	0.650	(Goodale et al., 2002)
Northern forests	includes all temperate and boreal woody biomass	1990s	0.355	2.477×10^9	0.880	(Liski et al., 2003)
Boreal nations	forest biomass and normalised difference vegetation index	1995–1999	0.730	9.310×10^9	0.680	(Dong et al., 2003)
North of 45 lat	process-based model (with CO_2 fertilisation)	1996–2002	0.106	3.826×10^9	0.406	(Balshi et al., 2007)
North of 45 lat	process-based model (without CO_2 fertilisation)	1996–2002	−0.001	3.826×10^9	−0.005	(Balshi et al., 2007)
North peatlands	site-based measurements; meta-analysis	2000–2010	0.323	3.700×10^9	1.195	(Yu, 2012)
(b) Regional summary						
		Mean		SD		n
Pan-boreal		0.341		0.227		9
Russia		0.076		0.369		39
Canada		0.056		0.574		44
Scandinavia		0.690		0.331		5
Alaska		0.337		0.710		7
Overall mean		0.130		0.493		104

* No area estimate provided—used area given in Liski et al. (2003).

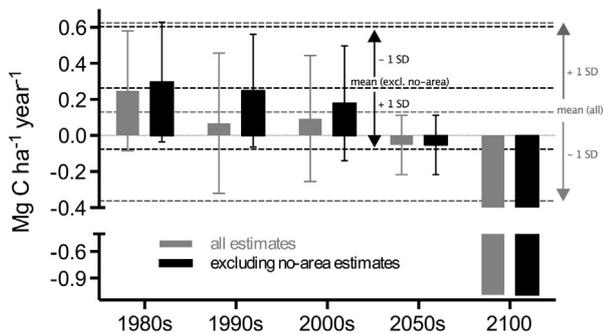


Fig. 4. Mean (± 1 SD) carbon flux densities ($\text{Mg C ha}^{-1} \text{year}^{-1}$) summarised by decade (Tables 4 and S7–S9). Positive values indicate a net carbon sink, and negative values indicate a net source. Means include some decadal overlap given that some estimates spanned decades (see Methods). Future projections are to the 2050s for the Canadian boreal region (Metsaranta et al., 2010). Projections to 2100 apply to the Alaskan boreal forest (Yarie and Billings, 2002). Global mean taken from Table 4. Grey bars indicate means calculated from all estimates, and black bars indicate means calculated only from values including individual area estimates (see Methods).

commented on an early draft. We dedicate this paper to the memory of Navjot Singh Sodhi.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.gloplacha.2015.02.004>.

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