FIRE ECOLOGY

Carbon loss from boreal forest wildfires offset by increased dominance of deciduous trees

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In boreal forests, climate warming is shifting the wildfire disturbance regime to more frequent fires that burn more deeply into organic soils, releasing sequestered carbon to the atmosphere. To understand the destabilization of carbon storage, it is necessary to consider these effects in the context of long-term ecological change. In Alaskan boreal forests, we found that shifts in dominant plant species catalyzed by severe fire compensated for greater combustion of soil carbon over decadal time scales. Severe burning of organic soils shifted tree dominance from slow-growing black spruce to fast-growing deciduous broadleaf trees, resulting in a net increase in carbon storage by a factor of 5 over the disturbance cycle. Reduced fire activity in future deciduous-dominated boreal forests could increase the tenure of this carbon on the landscape, thereby mitigating the feedback to climate warming.

The intensification of climate-sensitive disturbances, such as wildfire, can feed back to climate warming by altering net ecosystem carbon balance (NECB), the amount of carbon (C) sequestered or released to the atmosphere over time. Severe disturbance events can lead to loss of organic matter that survived previous events (*1*), triggering C losses that exceed the potential for reaccumulation during the following disturbance-free interval. Indirect effects of disturbance on C accumulation after fire may also drive NECB (*2*). Nitrogen (N) lost to the atmosphere during combustion could exacerbate N limitation to primary productivity, making it difficult for plant productivity to recoup combustion-driven C losses during post-disturbance recovery. Severe disturbances can alter the relationship between plant life history traits and habitat characteristics (*3*), giving rise to alternative successional pathways that affect the rates and patterns of C accumulation (*4*). Using empirical data to predict the impacts of disturbance on NECB is difficult because of the discrepancy between the time scales of direct and indirect effects on C accumulation. Some disturbances may result in direct effects such as instantaneous C losses, whereas changes to productivity and/or successional trajectory can lead to indirect effects that may lag one to several centuries after the disturbance (*2*).

The C balance of the boreal biome is of global importance because of the large size of C pools in forests and soils and their vulnerability to warming (*5*). Current climate-induced changes to boreal fire regimes (*6*) are expected to alter this biome's historic role as a net C sink relative to the atmosphere (*7*, *8*). Contemporary fires are burning more deeply into organic soils, releasing larger amounts of C (*9*) and depleting long-term C stores (*1*). Deeper burning that combusts a larger proportion of organic soil shifts ecosystems to a negative NECB (a net C source) if C losses are not replaced over the next disturbance-free interval. Understanding whether C accumulation during post-fire recovery compensates for C emissions during fire is essential for determining whether there is a positive feedback between climate warming and fire intensification.

Lightning-ignited wildfire has been a key structuring factor in boreal forests across Alaska and western Canada for most of the Holocene (*6*, *10*). These forests are dominated by conifer stands of black spruce (*Picea mariana*), where stand-replacing fires occur at ~100-year intervals (*11*). Black spruce release seed from semi-serotinous cones (*12*), and the successional trajectory of spruce self-replacement is entrained in the first decade after fire (*12*, *13*). In boreal Alaska, larger, more intense, and later season fires have caused deeper burning of the soil organic layer (SOL) (*9*), exposing suitable seedbeds for the establishment of deciduous tree seedlings such as aspen (*Populus tremuloides*) and birch (*Betula neoalaskana*) (*12*). Experimental manipulation of burn depth (*14*), remote sensing of deciduous forest fraction (*15*), and modeling forecasts (*16*) indicate that deeper, more severe burning will lead to increasing abundance of mixed and deciduous stands, particularly in moderate to well-drained soils (*17*). An emergent property of these alternative successional trajectories is a substantial

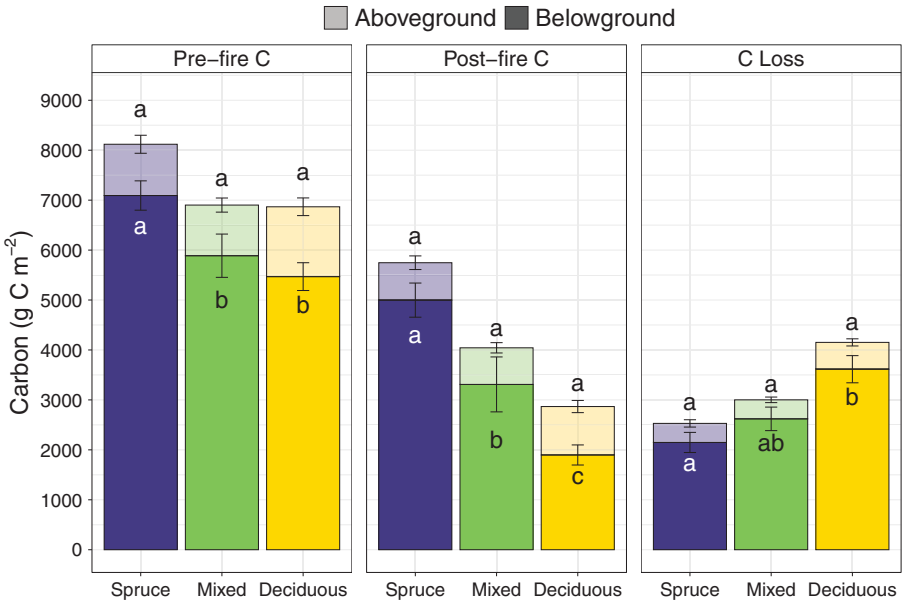

Fig. 1. Ecosystem carbon pools and wildfire losses across successional trajectories. Above- and belowground C across three successional trajectories of tree regeneration. In all stands (N = 75), black spruce dominated density and biomass prior to fire. Trajectories include stands that returned to spruce dominance (blue; n = 21), transitioned to dominance by deciduous broadleaf trees (yellow; n = 36), or transitioned to a mixture of black spruce and deciduous tree species (green; n = 18). See table S1 for structural classification of successional trajectories, table S3 for associated N pools and C:N ratios, and table S4 for text statistics. Letters represent significant differences (P < 0.05) between trajectories within the above- and belowground pools.

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difference in patterns of C accumulation. Spruce stands sequester large amounts of C in a thick SOL but accumulate relatively little biomass aboveground, whereas deciduous stands sequester more biomass aboveground and little in surficial soils (*18*, *19*). It is unknown whether stands that shift from spruce to deciduous trajectories can compensate for C lost in fire.

We examined the consequences of increasing fire severity for the C and N balance of black spruce stands in Interior Alaska, where this stand type covers >50% of the forested landscape (*20*). We asked whether the impacts of fire severity on successional trajectory, specifically shifts from spruce to deciduous tree dominance, were likely to exacerbate or mitigate the effects of large losses of soil C and N on NECB (*21*). We combined observations of individual fires with chronosequences of sites of different ages to estimate trajectories of forest recovery and C accumulation that could arise when black spruce forests burn (*22*).

In 2005, we established a long-term study of multiple burned areas from the 2004 fire year, when the total area burned in Alaska was more than seven times the long-term average (*20*). We studied 75 forest stands where black spruce was the dominant species prior to fire. Sites were located across a 250,000-km^2 region in Interior Alaska and were selected to cover the range of site conditions (e.g., topo-edaphic position) and fire severities (i.e., proportional combustion of canopy and SOL) (fig. S1). We used estimates of seedling species dominance to determine whether stands returned to black spruce or underwent compositional change to mixed or deciduous tree-dominated trajectories. By 2017, 28% of sites returned to black spruce dominating both relative density and relative biomass (fig. S2). The remaining 72% of sites transitioned to an alternative trajectory: mixed black spruce–deciduous (18 sites) or deciduous-dominated (36 sites). In almost all sites, black spruce density was equal to or greater than pre-fire density (fig. S3), which shows that variation in deciduous density drives initial trajectories. In 37% of stands, deciduous trees were present at low density (0.05 ± 0.02 trees m^{-2}, mean ± SEM) prior to fire, but neither their relative and absolute density nor their presence was related to the relative or absolute density of deciduous seedlings after fire (fig. S4), making it unlikely that post-fire deciduous dominance occurred through asexual suckering.

We determined whether post-fire successional trajectories differed in pre-fire and post-fire C and N pools and combustion losses. To project the consequences of these trajectories over longer time scales, we used a chronosequence approach to assemble data from 248 stands that varied in time after fire and tree species dominance (*20*). We examined C and N pools in biomass, necromass, and SOL across 100 years of post-fire succession in order to calculate rates of C and N accumulation over time, predict pool sizes at 100 years, and estimate NECB for each trajectory.

Our survey of the 2004 wildfire network showed that sites classified as black spruce in 2017 burned at relatively low severity (13 ± 2 cm burn depth and 30 ± 5% combustion of SOL C). Sites classified as mixed or deciduous trajectory burned similarly in depth (13 ± 2 and 15 ± 2 cm, respectively) but lost a larger percent of the SOL C pool than spruce (50 ± 5% and 65 ± 4%, respectively; table S2). Sites that transitioned to a deciduous trajectory ranged in landscape position from dry, well-drained hillslopes with thin organic layers to moist valley bottoms with thick organic layers, but on average they had lower pre-fire SOL C pools than stands that returned to spruce (Fig. 1). This pattern is consistent with the idea that drier areas with thinner SOL are predisposed to burn more severely, making these landscape positions

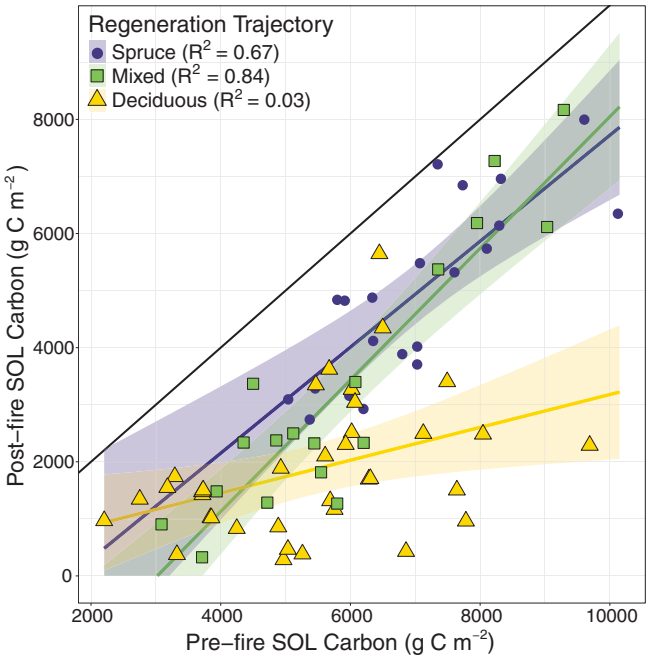

Fig. 2. Wildfire effects on soil organic layer carbon pools and successional trajectories. The relationship between pre- and post-fire SOL C pools was estimated across three successional trajectories of tree regeneration. See Fig. 1 for sample size and table S5 for model results; in the symbol key, R^2 represents marginal R^2 of models fitted for each trajectory separately (table S6). Lines represent model fitted slopes; colored shading denotes 95% confidence intervals.

Table 1. Net ecosystem carbon and nitrogen balance across successional trajectories. Mean (±SEM) or estimated ecosystem C and N pools and fluxes across three trajectories of forest regeneration after wildfire. Estimates with different superscript letters indicate significant post hoc differences at $P < 0.05$. See table S9 for explanation of ecosystem variables.

	Post-fire successional trajectory		
	Spruce	Mixed	Deciduous
Ecosystem variable	C or N pool (g m^{-2}) or flux (g m^{-2} year^{-1})		
Pre-fire C pool (t_0)	8,119 ± 309^a	6,901 ± 396^b	6,867 ± 297^b
Post-fire residual C pool (t_1)	5,748 ± 419^a	4,452 ± 522^b	3,282 ± 462^c
Net rate of C accumulation	21 ± 3^a	42 ± 14^a	90 ± 9^b
C pool 100 years after fire (t_{100})	7,800 ± 388^a	8,622 ± 1215^a	12,284 ± 766^b
Net C pool change ($t_{100} - t_1$)	2,052	4,170	9,002
% legacy C ($t_1/t_{100} \times 100$)	74	52	27
Net ecosystem C balance ($t_{100} - t_0$)	−319	1,721	5,417
Pre-fire N (t_0)	247 ± 12^a	202 ± 15^b	189 ± 10^b
Post-fire residual N (t_1)	158 ± 10^a	125 ± 15^a	71 ± 1^b
Net rate of N accumulation	0.5 ± 0.1^a	0.2 ± 0.5^a	1.6 ± 0.2^b
N pool 100 years after fire (t_{100})	207 ± 8^a	141 ± 42^a	226 ± 21^a
Net N pool change ($t_{100} - t_1$)	49	16	155
% legacy N	76	88	31
Net ecosystem N balance ($t_{100} - t_0$)	−40	−61	+37

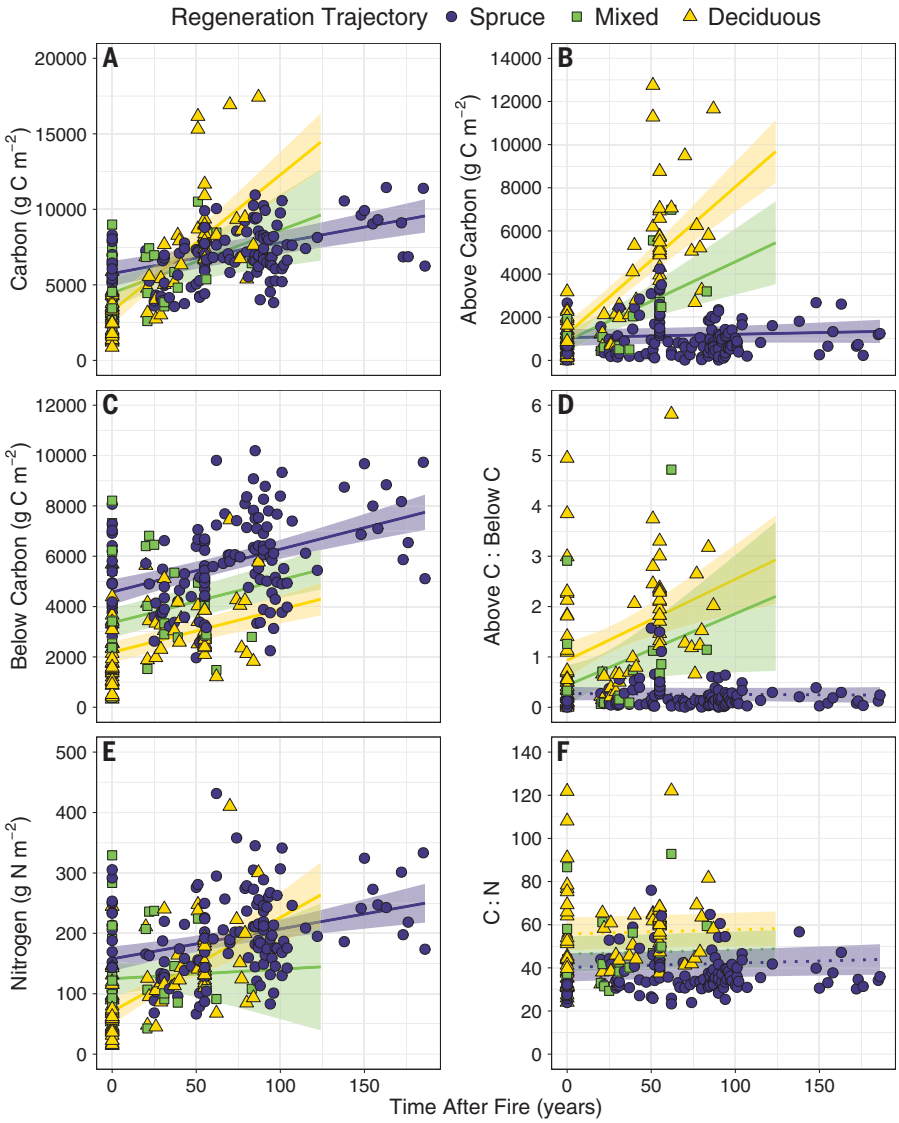

Fig. 3. Ecosystem recovery across trajectories of forest regeneration after wildfire. (**A** to **F**) Black spruce (n = 139), mixed (n = 32), and deciduous (n = 77) stands that constitute a chronosequence approach to estimating long-term dynamics of ecosystem C pools (A), aboveground C pools (B), belowground C pools (C), ratio of aboveground to belowground C pools (D), ecosystem N pools (E), and ecosystem C:N ratio (F) over time after fire. See table S7 for results. Solid lines indicate significant slopes; dashed lines indicate slopes not different from zero (table S8). Colored shading denotes 95% confidence intervals. Four high deciduous trajectory data points [(A) and (B)] are discussed in (*20*).

more vulnerable to fire-driven change in species dominance (*13*, *23*).

Sites that transitioned in dominance had higher C and N losses from fire and carried significantly less C forward into the next successional cycle than did stands that returned to black spruce (Fig. 1 and table S3). Net "carry forward" of C and N pools for the deciduous trajectory was ~30% of pre-fire pools, primarily in the form of coarse woody debris and SOL (Table 1). Spruce self-replacement sites carried forward ~75%, primarily in SOL (Table 1). Across spruce and mixed sites, pre- and post-fire SOL C pools were highly correlated (Fig. 2), showing that pre-fire variation in the SOL was retained post-fire. Across deciduous sites, by contrast, pre- and post-fire C pools were only weakly related (Fig. 2), hence relatively little pre-fire variation was retained. Pre-fire deciduous tree presence had no effect on C pools or their relationships (fig. S5). Post-fire initial ecosystem C pools for 2004 network trajectories were similar to starting pool size estimates of the independent chronosequence dataset (fig. S6), giving us confidence in linking the two datasets.

Over a 100-year period of post-fire succession, the deciduous trajectory accumulated ecosystem C pools faster than the black spruce trajectory by a factor of 4, reaching 12,284 ± 766 g C m^{-2}, 1.6 times as much C as spruce stands (Fig. 3A and Table 1). Most of the rapid element accumulation on the deciduous trajectory was in aboveground tree biomass (Fig. 3B), not belowground SOL C (Fig. 3C). Immediately after fire, trajectories had similar ratios of aboveground/belowground C pools. Deciduous, but not spruce, trajectories increased aboveground C pools over succession, such that after 100 years, the aboveground/belowground C ratio was higher in deciduous than in spruce trajectories by an order of magnitude (Fig. 3D and Table 1). The deciduous trajectory also accumulated N pools faster than the spruce trajectory by a factor of 3, resulting in no difference in N pools after 100 years (Fig. 3E and Table 1).

In these Alaskan black spruce forests, high-severity burning and a transition from spruce self-replacement to a deciduous-dominated trajectory led to a ~5000 g C m^{-2} increase in NECB over the 100-year fire cycle (Table 1). Rapid C accumulation and high C:N ratios

of deciduous stands more than compensated for lower pre-fire C and N pools and higher C and N emissions relative to the spruce replacement trajectory.

Observed increases in NECB and aboveground/belowground C ratios associated with a shift from black spruce to deciduous dominance are consistent with plant-soil-microbial feedbacks that emerge from these contrasting plant functional types (*24*). Black spruce dominance is characterized by long nutrient residence time in plants and slow C and nutrient turnover in soils, resulting in accumulation of thick organic soils with large C pools. Deciduous stands, by contrast, are characterized by high plant nutrient use efficiency (*19*). Deciduous litter decomposes rapidly and regenerates nutrients that reinforce high tree growth rates, rapid turnover of organic soil layers, and low soil C storage (*18*, *19*). This litter can also suppress the accumulation of recalcitrant moss, further shifting the balance of accumulating C from belowground to aboveground pools (*25*).

Similar transitions in aboveground/belowground C ratios have been observed with climate warming and increasing fire severity in other northern ecoregions where rapidly growing species replace slow-growing species, which suggests that this mechanism may have more general application to NECB in these transitional systems. In Canada, increased fire has led to transitions from black spruce to deciduous species (*26*) or equally rapidly growing pine (*27*). In Northeastern Eurasia, the monodominant species Cajander larch (*Larix cajanderi*) responds to increased fire severity by increasing density and increasing aboveground/belowground C ratios (*28*), thus mimicking trait changes associated with a shift to faster-growing tree species. In Arctic tundra, deciduous shrub expansion associated with climate warming alone increases aboveground/belowground C ratios (*29*).

More rapid N accumulation in deciduous trajectories than in mixed or spruce trajectories suggests higher N inputs or lower N losses as drivers of C accumulation. Lower N losses seem unlikely because soils in deciduous stands have higher rates of N mineralization and nitrification (*19*) and more enriched plant ^{15}N signatures indicating more N loss (*30*). If high N inputs are the cause of rapid N accumulation, the source is unlikely to be deposition because inputs to these forests are low (<0.1 kg N ha^{-1} $year^{-1}$) (*31*) and similar across trajectories. Moss- or alder-associated N_2 fixation is also an unlikely cause; deciduous litterfall suppresses moss growth (*25*), and there was no evidence of increased alder density in deciduous stands relative to spruce stands (*18*). A plausible driver of rapid N accumulation in deciduous stands is N acquisition from deep soils because deciduous trees have deeper roots than black spruce (*32*). Differences in rooting depth could be particularly important when thaw depth increases after fire (*33*) and exposes N frozen in permafrost (*34*).

Shifts in C storage from organic soil layers in spruce stands to aboveground biomass in deciduous stands could negate increased NECB if deciduous biomass C has a shorter lifetime on the landscape (*35*). Burned spruce stands in our study were, on average, 94 ± 3.8 years old at the time of fire, which fits within estimates of fire return interval for western black spruce forests (70 to 130 years) (*36*). Little is known about the long-term fate of deciduous stands in Alaska, and our study did not include old stands or a second fire cycle for this stand type. Deciduous stands have low flammability, slow fire spread, and low-severity burning (*37*), which may enable trees to avoid or withstand fire and reduce fire spread on the landscape (*38*). There is limited empirical evidence of relay succession in this region (*39*), but where it does occur, deciduous tree mortality and canopy emergence by understory black spruce could drive C accumulation later in succession, revitalizing the plant-soil feedbacks that lead to the formation of a thick SOL (*39*).

When deciduous-dominated stands do burn, they are likely to regenerate via suckers as well as seed (*40*). These regeneration traits mean that once alternative deciduous trajectories are in place, they could be resistant to change. Studies of contemporary increases in wildfire disturbance indicate that deciduous trees will dominate the forests of Interior Alaska in this century (*16*, *41*, *42*). Longer fire-free intervals, lower fire severity, reduced fire spread on the landscape, and asexual regeneration in deciduous stands support the idea that once initiated, these forests will persist and maintain C pools longer on the landscape—a negative or stabilizing feedback to climate warming.

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ACKNOWLEDGMENTS

We thank T. Chapin and T. Hollingsworth for help with initiating the 2004 wildfire site network, T. Schuur and L. Boby for help with combustion methods and soil sampling and processing, and C. Mojica and G. Crummer for help with laboratory analyses. Finally, we thank our dear friend and colleague, J. Reiskind, for inspiring confidence, perseverance, and comradery in us and many other women scientists. **Funding:** Supported by US Department of Defense Strategic Environmental Research and Development Program (grants RC-2754 and RC-2109) and NASA Arctic Boreal Vulnerability Experiment (NNX15AT71A, NNX17AE44G and 80NSSC19M0112) (M.C.M.), by the US Joint Fire Sciences Program (05-1-2-06) (J.F.J.), and by the Bonanza Creek Long-term Ecological Research Program, which is supported by the US NSF (DEB-1636476) and the USDA Forest Service (RJVA-PNW-01-JV-11261952-231) (M.C.M. and J.F.J.). **Author contributions:** M.C.M. conceived the study. J.F.J. and M.C.M. designed the 2004 wildfire network study and M.C.M. and H.D.A. designed the chronosequence study. M.C.M., J.F.J., H.D.A., A.M.M., X.J.W., and M.J. carried out fieldwork, and S.N.M., A.M.M., and H.D.A. carried out lab work. X.J.W. designed the statistical analyses and figures. M.C.M. wrote the paper and all authors commented on the manuscript. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All data from this study are archived in the NSF-funded Bonanza Creek Long-Term Ecological Research Data Catalog (www.lter.uaf.edu/data), which is part of EDI Data Portal (https://portal.edirepository.org/nis/home.jsp) (*43*, *44*). Soils, tree cores, and plant materials are archived in the lab of M.C.M.

SUPPLEMENTARY MATERIALS

science.sciencemag.org/content/372/6539/280/suppl/DC1
Materials and Methods
Tables S1 to S11
Figs. S1 to S6
References (*45*–*73*)

27 October 2020; accepted 8 March 2021
10.1126/science.abf3903

Science

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Science **372** (6539), 280-283.
DOI: 10.1126/science.abf3903

Carbon cycling after boreal forest fire

Wildfire activity has been increasing in the boreal forests of the Northern Hemisphere, releasing carbon into the atmosphere from biomass and soil, with potential feedback to climate warming. In a long-term study, Mack *et al.* analyzed wildfire impacts on the carbon balance of boreal forest in Alaska, with particular focus on forest-regeneration patterns. After fire, the species composition in most of the study sites changed from black spruce to a mixture of conifers and deciduous broadleaf tree species. The stands that had shifted to deciduous dominance stored fivefold more soil carbon than stands that returned to black spruce dominance. Therefore, the functional traits of deciduous trees compensated for the combustion loss of soil carbon, pointing to a potential mitigation of the feedback effect of boreal forest fire to climate warming.

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