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Multi-Year Lags between Forest Browning and Soil Respiration at High Northern Latitudes

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Abstract

High-latitude northern ecosystems are experiencing rapid climate changes, and represent a large potential climate feedback because of their high soil carbon densities and shifting disturbance regimes. A significant carbon flow from these ecosystems is soil respiration (RS), the flow of carbon dioxide, generated by plant roots and soil fauna, from the soil surface to atmosphere, and any change in the high-latitude carbon cycle might thus be reflected in RS observed in the field. This study used two variants of a machine-learning algorithm and least squares regression to examine how remotely-sensed canopy greenness (NDVI), climate, and other variables are coupled to annual RS based on 105 observations from 64 circumpolar sites in a global database. The addition of NDVI roughly doubled model performance, with the best-performing models explaining ~62% of observed RS variability. We show that early-summer NDVI from previous years is generally the best single predictor of RS and is better than current-year temperature or moisture. This implies significant temporal lags between these variables, with multi-year carbon pools exerting large-scale effects. Areas of decreasing RS are spatially correlated with browning boreal forests and warmer temperatures, particularly in western North America. We suggest that total circumpolar RS may have slowed by ~5% over the last decade, depressed by forest stress and mortality, which in turn decrease RS. Arctic tundra may exhibit a significantly different response, but few data are available with which to test this. Combining large-scale remote observations and small-scale field measurements, as done here, has the potential to allow inferences about the temporal and spatial complexity of the large-scale response of northern ecosystems to changing climate.

Introduction

Climate changes in the coming century may affect permafrost thaw rates, greenhouse gas fluxes, wildfires, productivity, biota, and energy fluxes in northern ecosystems [1,2,3,4]. Such high-latitude ecosystems represent a large potential climate feedback [5,6] because of their high soil carbon densities [7] and rapid warming [8]. Any current or future carbon losses from these areas will mostly occur through combustion [9] or changes in the balance between net primary production and the heterotrophic component of RS, the soil surface CO₂ flux between the soil and atmosphere. At 80–100 Pg C yr⁻¹ [10,11], total RS is one of the largest fluxes in the terrestrial carbon cycle but its magnitude and dynamics remain poorly constrained.

We hypothesized that boreal tree stress or mortality [12,13] might be exerting a significant effect on the large-scale, high-latitude RS flux, as belowground carbon allocation drops in weakening or dying trees. Such forest stress and mortality has been observed in both boreal North America [14,15] and Eurasia [16,17], as well as more broadly worldwide [18]. These events are most frequently attributed to drought stress [19] or insect attack [20], and can be observed as trends in the remotely-sensed Normalized Differentiated Vegetation Index (NDVI), a measure of canopy greenness [21,22], as well as the Enhanced Vegetation Index (EVI) [23]. Such severe stress events are associated with canopy defoliation and depletion of carbon reserves, delayed recovery of surviving individuals, and tree death [24,25]. Because plant photosynthesis is the ultimate source of all ecosystem respiration, and forest soil respiration at large scales may be driven more by productivity than temperature [26], such events should also, in theory, be observable in RS data.

More generally, climate changes appear to be observable in the extant published record of RS fluxes [10], but how such large-scale changes interact to affect the major components of the high-latitude carbon cycle remains an open question [6]. To explore one aspect of this, we linked a global RS database [27], NDVI or canopy greenness [22,28] and gridded climate data using both machine-learning and classical statistical approaches. Our objectives were to analyze the relationship, if any, between forest ‘browning’ observed from satellites and large-scale patterns of annual RS, and to infer constraints that may be operating at high latitudes on this large carbon flux.
Methods

Soil Respiration, NDVI, and Ancillary Data

Observed soil surface CO₂ flux, or soil respiration (Rₛ, g C m⁻² yr⁻¹), was the primary response variable considered in this study. We used a recent version (20110224a, downloaded 24 February 2011 from http://code.google.com/p/srdb/) of a global soil respiration database [27]. The downloaded data were filtered to include only non-manipulated ecosystems (no agriculture or experimentally manipulated systems); positive Rₛ values, >50° N latitude; mean annual air temperature (1961–1990) of <2°C, following [10]; and measured using infrared gas analyzers or gas chromatography, relatively standardized techniques.

The primary independent data were Advanced Very High Resolution Radiometer-Normalized Difference Vegetation Index (AVHRR-NDVI, from http://giovanni.gsfc.nasa.gov/; MODIS Vegetation Continuous Field (Collection 4, Version 3, ORNL DAAC at http://webmap.ornl.gov/wcsdown/wcsdown."

A variety of ancillary data were included in the analysis. Time since disturbance (in years) was derived from the soil respiration database, above, with missing data assigned the median value (~50 years) as recommended by [31]. (Excluding the missing data resulted in a significantly smaller data set, but did not change the disturbance-related results below.) Global climate data (“Monthly Mean Air Temperature (Global 1900–2008)” and “Monthly Total Precipitation (Global 1900–2008)”) sets were downloaded from http://climate.geog.udel.edu/~climate/; these data were used because of their spatial resolution and currency. Mean (1961–1990) values and climate anomalies were then computed as the year-specific temperature or precipitation value minus the mean value for that 0.5° grid cell. Global leaf area index (5°, from ECOCLIMAP [32], grid area (0.5°, to derive a circumc ambrium flux from area-normalized predictions, from EOS-WEBSTER at http://eos-webster.cr.usf.edu/), nitrogen deposition (5°, from ORNL DAAC at http://webmap.ornl.gov/wcsdown/wcsdown.jsp?dg_id=830_2), a Thornwaite-based climate index [33], and the MODIS Vegetation Continuous Field (Collection 4, Version 3, from http://www.landcover.org/data/vcf/) were also used.

These data sets were matched spatially and temporally to the collected Rₛ studies using a nearest-neighbor algorithm. Temporally, each Rₛ observation was paired with climate and NDVI data from the year of that study as well as up to five years previously, i.e., a given Rₛ observation from year t was associated with temperature anomaly, precipitation anomaly, and NDVI (half-monthly, monthly, etc., as described above) data from year t, t-1, … t-5. This was done because multi-year carbon pools in northern ecosystems [34] may decouple observed carbon fluxes (e.g., tree growth) from ambient abiotic drivers [22,35].

Data Analysis

Two related machine-learning algorithms were used on the final, unified data set (105 observations and 289 variables, from 64 unique sites). The standard Random Forest algorithm [31], a nonparametric machine learning technique for classification and regression, is widely used for large-data analyses, and as a data-driven methodology makes no a priori theoretical assumptions about Rₛ drivers or behavior. The algorithm predicts by aggregating regression trees constructed using different random samples of the data, and choosing splits of the trees from subsets of the available predictors, which are randomly chosen at each node [31]. The use of random data and predictor subsets means that the full data set can be used and data need not be withheld for validation. The RF algorithm generally produces highly accurate and unbiased estimates and classification when potential predictors are drawn from the same scale or category, and it is particularly robust against overprediction for “m > n” (more potential predictor variables than observations) data sets.

Random Forest can produce unverifiable (exhibit biased variable selection), however, when potential predictor variables vary in measurement scale or categories [36]. For this reason we also used a conditional inference random forest (CI-RF) algorithm [37], the algorithm supports conditional inference trees [37] and aggregates using observation weights extracted from the trees [38]. Such conditional inference forests better handle variables of different types, and observations of different weights, than do trees generated using the original Breiman RF algorithm, although they do not entirely eliminate the preference for correlated predictors [37].

We allowed these algorithms to access varying amounts of NDVI (from the original 15-day data, to monthly, seasonal, and annual means, to none at all) and previous-year information ‘lookback,’ from 0 to 5 years in the past). Importantly, each level
tested included all previous coarser ones; for example, models using monthly NDVI data were also given seasonal and annual data, to see if the new level of detail resulted in significant model improvement. Because late-winter snow interferes with the satellite sensor, resulting in many missing values for this time period, we excluded December-April NDVI after extensive testing: none of these data was significant (i.e., ranked in the top 25 most important variables; cf. Table 1) in any tested R\textsuperscript{2} model, and their exclusion resulted in no decrease in model explanatory power. The RF and CI-RF routines were run with default settings (in particular,
Table 2. Summary of the best-performing ordinary least squares (OLS) model.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Year</th>
<th>Estimate</th>
<th>SE</th>
<th>t</th>
<th>P</th>
<th>Signif.</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td></td>
<td>−16760</td>
<td>9687</td>
<td>−1.73</td>
<td>0.087</td>
<td></td>
</tr>
<tr>
<td>NDVI (early summer)</td>
<td>1</td>
<td>13.96</td>
<td>5.02</td>
<td>2.78</td>
<td>0.007</td>
<td>**</td>
</tr>
<tr>
<td>NDVI (late summer)</td>
<td>4</td>
<td>7.77</td>
<td>5.15</td>
<td>1.51</td>
<td>0.135</td>
<td></td>
</tr>
<tr>
<td>NDVI (early summer)</td>
<td>0</td>
<td>6.85</td>
<td>4.81</td>
<td>1.43</td>
<td>0.158</td>
<td></td>
</tr>
<tr>
<td>Air temperature</td>
<td>4</td>
<td>1.03</td>
<td>1.66</td>
<td>6.21</td>
<td>&lt;0.001</td>
<td>***</td>
</tr>
<tr>
<td>NDVI (late summer)</td>
<td>1</td>
<td>−1.53</td>
<td>4.96</td>
<td>−0.308</td>
<td>0.303</td>
<td>**</td>
</tr>
<tr>
<td>Precipitation</td>
<td>0</td>
<td>0.70</td>
<td>0.34</td>
<td>2.05</td>
<td>0.043</td>
<td>*</td>
</tr>
<tr>
<td>Year</td>
<td></td>
<td>8.51</td>
<td>4.84</td>
<td>1.76</td>
<td>0.082</td>
<td></td>
</tr>
<tr>
<td>Air temperature</td>
<td>0</td>
<td>−55.19</td>
<td>22.81</td>
<td>−2.42</td>
<td>0.017</td>
<td>*</td>
</tr>
<tr>
<td>Mean annual precip.</td>
<td></td>
<td>−0.58</td>
<td>0.20</td>
<td>−2.90</td>
<td>0.005</td>
<td>**</td>
</tr>
<tr>
<td>NDVI (annual)</td>
<td>1</td>
<td>−14.43</td>
<td>6.31</td>
<td>−2.29</td>
<td>0.025</td>
<td>*</td>
</tr>
<tr>
<td>NDVI (fall)</td>
<td>0</td>
<td>9.21</td>
<td>3.35</td>
<td>2.75</td>
<td>0.007</td>
<td>**</td>
</tr>
</tbody>
</table>

Potential parameters of the best OLS model (RMSE = 156.9 g C m⁻² yr⁻¹) on 94 d.f., adjusted R² = 0.61. P < 0.001 were selected by the CI-RF algorithm before OLS was performed (see Methods and Table 1). Columns include variable included in OLS regression, year of data stream (0 = current year, 1 = previous year, etc.); OLS estimate and standard error (SE); t-value; P-value; and significance (**: <0.1; ***: <0.05; ****: <0.01; *****: <0.001).

doi:10.1371/journal.pone.0050441.t002

Results

The two machine-learning models accounted for 50–62% of the observed variability for 105 annual Rs observations at high latitudes. When allowed to use more-detailed NDVI data, and look back further into the past (i.e., consider previous-year conditions to explain current Rs), the models’ performance improved (Figure 1). The best-performing model (a CI-RF type, root mean square error RMSE = 139.9 g C m⁻² yr⁻¹) used monthly NDVI and up to five previous years’ NDVI/climate data; this was also identified as the best model by the classical RF algorithm. OLS models built using the most important variables from the machine-learning analyses showed a dramatic improvement, with explained variability almost doubling from 33% (no NDVI, only current-year data) to 61% (seasonal NDVI, up to four years ‘lookback’ allowed). The best-performing OLS model is summarized in Table 2. For all algorithms, the use of half-monthly NDVI did not improve model performance relative to mean monthly NDVI.

Previous-year NDVI—in particular, early-summer greenness—was generally the most important Rs predictor. Nine of the top ten CI-RF variables, and five of the top ten RF ones, were NDVI in early summer (May, June, July) in years before the Rs measurement, especially the previous year (Table 1). The best-performing models also followed this pattern, with previous-year June NDVI the best predictor and previous-year temperature the best non-NDVI predictor. A number of potential explanatory variables were almost never highly ranked, including nitrogen deposition, time since disturbance, leaf area index, and percent tree cover. As in a previous study [10], mean annual air temperature was negatively associated with Rs—i.e., warmer years were consistently associated with lower respiration at high latitudes. In summary, NDVI proved a far better tree-out-of-bag error rate.

We also examined the effect of including the most important variables, as identified by the RF and CI-RF algorithms, into ordinary least squares (OLS) models, as OLS is a fundamental tool for analyzing sources of variance in many studies. For each of the 30 NDVI/lookback models we built ordinary least squares (OLS) models, as OLS is a fundamental tool for analyzing sources of variance in many studies. For each of the 30 models (5 levels of NDVI information times 6 levels of temporal lookback); we found that altering these parameters did not change the results in any meaningful way. The algorithms ranked all variables by importance. For CI-RF, we included the most important variables identified by the RF and CI-RF algorithms, into OLS regression, year of data stream (0 = current year, 1 = previous year, etc.), OLS estimate and standard error (SE); t-value; P-value; and significance (**: <0.1; ***: <0.05; ****: <0.01; *****: <0.001).

doi:10.1371/journal.pone.0050441.t002

The model did not predict extremely low (<100 g C m⁻² yr⁻¹) Rs values observed at some Arctic sites, probably due both to the paucity of observed Rs data at these extreme latitudes, and the presence of late-lying snow that interferes with the satellite sensor. High observed Rs values also tended to be underpredicted (Figure 4). The mean predicted Rs integrated over the entire study area was 8.6 Pg C yr⁻¹, ~9% of the global flux [10], and declined (0.04 Pg yr⁻²). Mann-Kendall τ = −0.511, P = 0.049 over the last ten years of the study period. Large areas of declining Rs in western North America (yellow patches in Figure 2) drove the circumpolar slowdown in the model output.

Discussion

The dominance of lag effects—in previous-year NDVI and air temperature—in this analysis is consistent with both theory and observations. Short-turnaround, labile C comprises a significant component of ecosystem C fluxes [41], while field experiments

number of variables randomly selected at each node = 5, number of trees = 500) for all 30 models (5 levels of NDVI information times 6 levels of temporal lookback); we found that altering these parameters did not change the results in any meaningful way. The algorithms ranked all variables by importance. For CI-RF, we computed a pseudo-R² following the original randomForest package, as lSS_jtot/Sserr, because the party package does not currently compute a true out-of-bag error rate.

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Circumpolar Modeling

The best-performing (based on pseudo-R²) model was used to predict Rs fluxes across the circumpolar region. A circumpolar 0.5° grid was used, with grid cells matched to all required climate, NDVI, and ancillary data. Predicted fluxes for years 1989–2008—roughly the period of methodologically standardized and published Rs measurements [10]—were calculated using the cell area data and summed to produce a global high-latitude flux for boreal and Arctic (>50° N, mean annual air temperature <2° C) cells. A nonparametric Mann-Kendall test was used to test for temporal trends in the model output, and D’Agostino’s K² goodness-of-fit [40] to test for skew or departures from normality. All analyses were performed using R 2.15.1 [38].
have shown a lack of correlation between boreal tree ring width increment and net ecosystem exchange [35], while ring width and NDVI are only inconsistently correlated in high-latitude forests [42,43]. This suggests that multi-year C pools play a significant role in buffering ecosystem carbon fluxes from changing abiotic drivers. Lags between $R_S$ and its drivers (soil temperature and gross primary production) of up to 88 days were shown by Vargas et al. [44], but we are unaware of previous studies documenting multi-year lag effects. We note that RF and CI-RF models using no current-year data at all—simply previous-year NDVI, air temperature, and precipitation—explains $\sim$60% (RMSE = 140.9 g C m$^{-2}$ yr$^{-1}$) of observed $R_S$ variability, i.e., adding current-year data yields very little improvement in model performance.

What mechanisms would link increases in temperature with declines in $R_S$, as observed here? Largely following the logic of Peng et al. [14], we hypothesize that drought and water stress engender hydraulic failure and inability to maintain carbon balance (i.e., starvation) [25]. The dominant sources of $R_S$ are root (autotrophic) and microbial (heterotrophic) respiration, and both are affected—albeit at different temporal lags—by changes in the photosynthate supply [45]. The resulting declines in belowground tree respiration and root exudates then depress the $R_S$ flux as measured at the soil surface.

Such a mechanism would be consistent with other studies performed at a variety of scales. Drought has deleterious effects on CO$_2$ uptake [46], and has been shown to reduce $R_S$ in field studies [47]. Tree mortality in western boreal North America has increased [14], and field studies have observed aspen and white spruce stress and dieback in North America has been linked to moisture indices [12]. Silva et al. [15] reported that temperate and boreal trees in Ontario, Canada, exhibited widespread growth decline consistent with warming-induced stress, in spite of increases in water use efficiency over the last half-century. At larger scales, FLUXNET analyses have inferred significant drought effects on ecosystem carbon cycling [48,49], and productivity (for which NDVI, in this study, is a proxy) has been shown to be more important than temperature in determining landscape-level $R_S$ [26]. Finally, remote sensing analyses suggest that changes in annual temperature and precipitation across North America are negatively affecting forest resilience as measured...
using the MODIS Enhanced Vegetation Index [23]. The use of previous-year NDVI in this study is thus a significant strength, as it provides an integrated signal of forest canopy stress tightly linked with the photosynthates stored for the following year’s growth and respiration.

There are other possible mechanisms to explain a putative Rs slowdown: climate changes might enable more pathogen and pest outbreaks in drought-weakened trees [25] or increase freeze-thaw events [12], for example, resulting in tree death, lower NDVI and lower Rs. Increased nitrogen deposition could also be depressing forest Rs, as has been shown to occur in temperate forests [50], although most North American boreal and Arctic sites are considered nitrogen-limited. We found no association between Rs and nitrogen deposition and thus a water-related mechanism, as laid out above, seems more consistent with the available data.

It is not surprising that time since disturbance exerted no effect on Rs in this analysis. This is not to say that disturbance exerts no effect: plant productivity exerts a dominant role on Rs [26], and fire in particular plays an important role in many high-latitude forests [51], altering Rs by killing plants, increasing litter inputs, changing soil moisture conditions, and increasing the active layer depth [52]. Disturbances can also cause soil C losses (via Rs) so large that sites become multi-year carbon sources [26]. The time-since-disturbance variable may simply not have added any extra information, however, given the strong NDVI effect found in this analysis and the fact that NDVI and time since disturbance tend to be well-correlated for several decades following disturbance [53]. In addition, while post-disturbance Rs changes may be visible in meta-analyses [54] and syntheses [26], many studies have observed inconsistent or invariant ecosystem respiration [55] and Rs [56] in the decades after disturbance. Finally, relatively few Rs studies have been performed in post-disturbance forest and tundra [27].

This analysis has a number of limitations. First, although we used two more years of data (observations published 2009–2010) than a previous Rs meta-analysis [10], these results are based on

Figure 3. Predicted high-latitude soil respiration (Rs), by year, with main driver variables. Panels show, from top, Rs predicted flux; mean annual temperature (MAT); mean annual precipitation (MAP); and previous-June canopy greenness (NDVI, unitless). Rs points show integrated result of the best-performing Random Forest model; to highlight trend, a loess smoother is shown by the dark line. Smoother errors (gray regions) were computed as the least-squares error on locally weighted scatterplot smoothing. doi:10.1371/journal.pone.0050441.g003
only 105 annual flux measurements spread across a large (~24×10^6 km^2) circumpolar region. The possibility of a type I (false positive) error remains [10] significant: future data may resolve the curiosity of high-latitude \( R_S \) changes not being positively correlated with air temperature increases. Second, the \( R_S \) data used here are dominated by well-drained, boreal, upland sites, reflecting an imbalance in the published literature [27]. But the respiration of peatland and permafrost ecosystems—which store an outsized fraction of global soil organic carbon—may change in different ways than a simple temperature- and NDVI-based model would predict, driven by species shifts, permafrost thaw, and increasing peat oxygenation. Tundra ecosystems will also likely respond differently to warming than will boreal forests, as processes such as warming-induced thermokarst and woody plant encroachment may increase plant productivity [6,57,58]. Finally, \( R_S \) cannot by itself be used to infer carbon balance, as ecosystem carbon balance is driven by the balance between net primary production and heterotrophic respiration from snags, woody debris, and soil. Few such comprehensive data are available at high latitudes, however.

Conclusions
This study has shown that remotely-sensed NDVI and climate data explain a large fraction of the variability of \( R_S \), the dominant component of ecosystem respiration, at high latitudes. Combining large-scale observations (NDVI) and a compilation of small-scale observations (\( R_S \)) allowed us to show that lag effects imply multi-year carbon pools exerting significant large-scale effects, to the point that no current-year data are needed (at this scale) to predict total \( R_S \) in a given year. Finally, we suggest that high-latitude \( R_S \) has declined significantly over the last ten years, as warmer summers stress some northern ecosystems, in particular the boreal forests that constitute most of the data used here [46]; we caution that tundra ecosystems may respond very differently. Although we cannot prove causality between the observed NDVI and \( R_S \) data, such an effect would be consistent with other recent studies (e.g., [59]). Because the boreal and Arctic carbon cycles may exert strong global climate feedbacks [6], the question of whether this decline is truly a symptom of water stress and forest mortality deserves further exploration.

Author Contributions
Conceived and designed the experiments: BBL AGB AMT. Performed the experiments: BBL AGB. Analyzed the data: BBL AGB AMT. Contributed reagents/materials/analysis tools: BBL AGB AMT. Wrote the paper: BBL AGB AMT.
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