Increasing net ecosystem biomass production of Canada's boreal and temperate forests despite decline in dry climates

Robbie A. Hember[1,2] (iD), Werner A. Kurz[2] (iD), and Nicholas C. Coops[1] (iD)

[1]Faculty of Forestry, University of British Columbia, Vancouver, British Columbia, Canada, [2]Pacific Forestry Centre, Canadian Forest Service, Natural Resources Canada, Vancouver, British Columbia, Canada

Abstract Repeated measurements of tree biomass at field plots describe recovery from disturbances, sampling artifacts, and potential effects of environmental change on forest ecosystems. Challenges in differentiating between intrinsic and extrinsic sources of variation, both in theory and in practice, continue to confound claims of an anthropogenic carbon sink in forest biomass. Here we analyzed observations at 10,307 plots across southern ecozones of Canada to investigate temporal trends in stand-level biomass growth (G), biomass loss due to mortality (M), and net ecosystem biomass production (NEBP) of intact stands. Net extrinsic forcing (F_{ex}) was expressed by the collective dependence of biomass fluxes on climate anomalies, nitrogen deposition (N), and atmospheric carbon dioxide concentration (C). Inferences drawn directly from linear mixed-effects model coefficients only reflect the static behavior of the model specifically at field plot locations. We, therefore, defined a dynamic landscape-scale net extrinsic forcing (F_{ex}'), which additionally accounted for potential negative feedback responses to anthropogenic growth enhancement. Simulations were performed over 1501–2012 to estimate F_{ex}'. Overall, F_{ex}' was positive, suggesting that environmental changes drove a 90% increase in NEBP. The increase in NEBP was confined to wet regions, while the biomass sink in dry regions decreased, suggesting that large expanses of northern forests, historically located near the boundary between wet and dry climates, may be at high risk of decline under continued increases in evaporative demand. These results have important implications for the greenhouse gas balance of Canada's forest sector.

1. Introduction

While stand-replacing disturbances leave abrupt footprints on forest landscapes, gradual changes over time in the productivity of intact stands are less easily detected. In northern forests, productivity is limited by suboptimal supplies of heat, water, nutrients, and carbon dioxide concentration (C). It is, therefore, commonly assumed that a combination of recent warming, increasing nitrogen deposition (N), and increasing C is accelerating the growth rate of trees, leading to increased storage of anthropogenic carbon in long-lived woody biomass [*Broecker et al.*, 1979; *Cao and Woodward*, 1998; *Denman et al.*, 2007; *Ciais et al.*, 2013]. Direct evidence of anthropogenic growth enhancement in forest ecosystems is limited, however, by scarcity of observations and uncertainty in the attribution of time trends to specific factors.

Previous assessments of intact stands commonly indicated positive trends in forest productivity [*Ciais et al.*, 2008; *McMahon et al.*, 2010; *Pan et al.*, 2011; *Hember et al.*, 2012; *Erb et al.*, 2013; *Fang et al.*, 2014; *Kauppi et al.*, 2014; *Pretzsch et al.*, 2014; *Wu et al.*, 2014; *Binkley and Högberg*, 2016]. Conversely, a study covering several eastern U.S. regions indicated no significant trends in forest productivity [*Caspersen et al.*, 2000], while studies in western Canada consistently report negative trends in forest productivity [*Ma et al.*, 2012; *Chen and Luo*, 2015; *Zhang et al.*, 2015].

Studies that reported positive trends in productivity were overwhelmingly representative of forests in wet boreal and temperate climates. The detection of trends in two of the studies conducted in plantations suggests that growth enhancement may not necessarily be precluded by intense competition for resources when stands are managed [*Fang et al.*, 2014; *Pretzsch et al.*, 2014]. In studies that related productivity with environmental variables, temperature was consistently identified as an important driver, but not enough to explain the entire magnitude of observed growth enhancement [*Hember et al.*, 2012; *Kauppi et al.*, 2014]. Studies only speculated as to the potential roles of increasing carbon dioxide, nitrogen deposition, and changing forest management practices in driving long-term trends in productivity.

Negative trends in productivity in western Canada could be related to increasing mortality, decreasing growth, or a combination of both. Whereas increasing pollution is commonly identified as a potential explanation in instances of growth decline in eastern North America and Europe [*Schulze*, 1989; *Skelly and Innes*, 1994; *Aber et al.*, 1998; *Fenn et al.*, 1998; *Binkley and Högberg*, 2016], acid deposition is substantially lower across western Canada, where adverse effects are likely limited to smaller footprints of major industrial areas [*Olson et al.*, 1992; *Fenn et al.*, 2003]. Numerous studies in western North America indicate that productivity is limited by water availability [*Hogg et al.*, 2008; *Coops and Waring*, 2010; *Girardin et al.*, 2015; *Restaino et al.*, 2016]. All three observation-based studies of NEBP across regions of western Canada are more representative of dry climates, ranging from subhumid to semiarid classes in Thornthwaite's climate classification system [*North American Climate Integration and Diagnostics (NACID)*, 2015]. Strong increases in evaporative demand across western North America [*Williams et al.*, 2013; *Hember et al.*, 2016] are therefore a leading potential explanation for evidence of decreasing forest productivity. This is supported by studies that report positive time trends in the probability of individual tree mortality in west coast old-growth forests [*van Mantgem et al.*, 2009], old boreal forests [*Peng et al.*, 2011], and montane and boreal forests [*Zhang et al.*, 2015]. Conversely, a study of pine and spruce forests in west central Alberta found no evidence of trends in mortality [*Thorpe and Daniels*, 2012]. In a study encompassing a large number of North American tree species, *Hember et al.* [2016] reported positive time trends in the probability of tree mortality across large areas of western North America and attributed the trends to a combination of increasing evaporative demand and decreasing soil water content. Positive trends in mortality were strongest in the most arid regions of Canada, including southern British Columbia, the Boreal Plain, and the Taiga Plain, yet trend patterns were highly variable and heavily influenced by a small number of extreme regional drought events, consistent with studies that focused on specific regions of the western Canadian boreal forest [*Hogg et al.*, 2005; *Bond-Lamberty et al.*, 2014].

Taken together, the few available quantitative assessments of stand-level biomass fluxes suggest that responses to environmental change may range from enhancement in wet climates to decline in dry climates. However, this assertion is clearly not supported by all studies, with *Caspersen et al.* [2000] reporting an absence of trends for a large sample in wet climates, arguments by *Zhang et al.* [2015] that most of the variation in western Canadian forests can be explained by natural stand dynamics, and arguments by *Erb et al.* [2013] that most of the variation in central Europe can be explained by changes in forest management.

Repeated observations of stand biomass (B_S) at field plots placed in intact stands provides the benefit of isolating environmental effects on the growth and mortality of trees, yet it should be recognized that it only represents a component of the overall biomass dynamics of forest biomes (Figure 1). Expanding on earlier observation-based studies of forest biomass [*Binkley et al.*, 1997; *Clark et al.*, 2001; *Brown*, 2002; *Hember et al.*, 2012], we define net ecosystem biomass production (NEBP) as the change in tree biomass of forest stands during annual time steps in which there was no stand-replacing disturbance (i.e., "intact" stands):

$$NEBP = G - M \qquad (1)$$

where G is biomass growth (i.e., an increase in biomass of survivors plus the biomass of recruitment, or "ingrowth"), and M is the biomass loss due to mortality. The term NEBP is equivalent to change in biomass "ΔB" used in many previous studies. The word "ecosystem" in the term NEBP acts to distinguish it from net biome biomass production (NBBP) the same way the Fluxnet community uses "ecosystem" to distinguish net ecosystem production from net biome production [*Chapin et al.*, 2006], only here we are focusing entirely on the carbon balance of tree biomass rather than that of both biomass and dead organic matter. Together, NEBP and net biome biomass disturbance (NBBD, due to fire, harvesting, and insects) control net biome biomass production (NBBP):

$$NBBP = NEBP - NBBD \qquad (2)$$

For practical reasons, stand-level models of forest productivity, which specifically rely on statistical fits to field plot observations to predict NEBP, must adopt an operational distinction between tree mortality caused by stand-replacing disturbances and tree mortality caused by all other (nonstand-replacing) disturbances (Figure 1). This fits the strengths of modern forest inventory and satellite-based monitoring programs that can survey stand-replacing disturbances [*Hermosilla et al.*, 2015], which can then be prescribed as discrete events in model simulations [*Boisvenue et al.*, 2016]. However, it means that observations of M at field plots must be representative of the remaining (nonstand-replacing) disturbances. Although measurements of
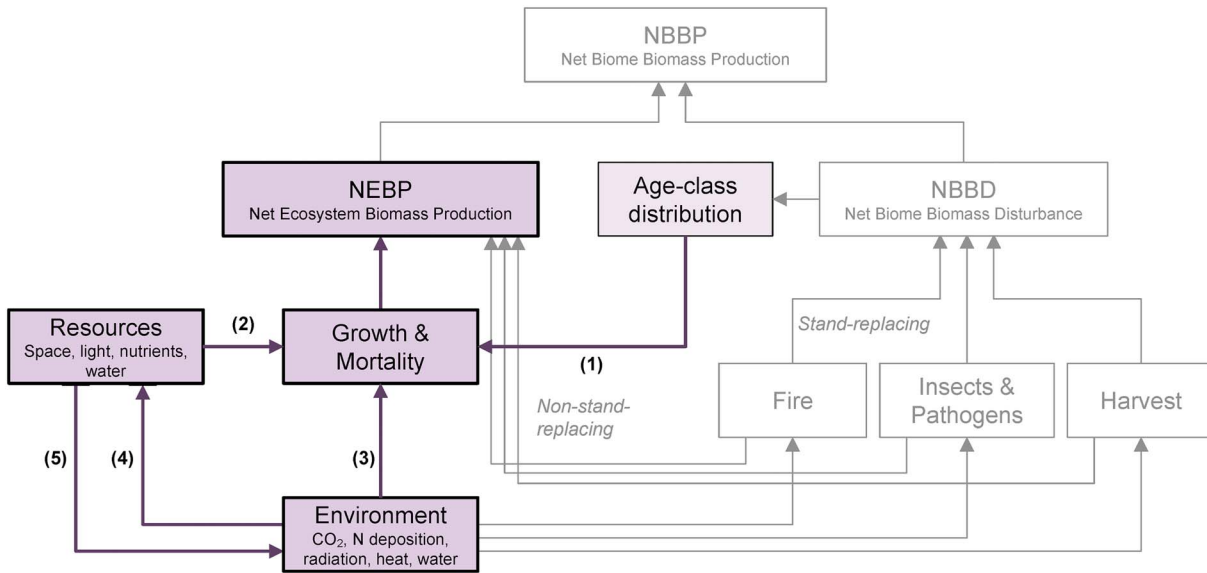
Figure 1. Defining the overall forest biomass system (all boxes), the subsystem of interest in this study (shaded boxes), and key processes that are represented in statistical models of stand-level biomass fluxes (numbered): (1) biomass fluxes vary with time since disturbance, which is expressed by dependence of biomass fluxes on stand age (A_S); (2) biomass fluxes are partially constrained by resources (e.g., space, light, nutrients, and water), which is expressed by dependence of biomass fluxes on stand-level biomass (B_S); (3) biomass fluxes depend on extrinsic factors, which is expressed by dependence of biomass fluxes on environmental variables; and (4 and 5) any sustained increase (or decrease) in NEBP caused by environmental change will increase (decrease) B_S, leading to a change in resources, introducing potential negative feedback responses to environmental change.

biomass loss due to mortality should be fully representative of competition and ontogeny, the extent to which they are representative of additional high mortality (e.g., from insect outbreaks) is not well understood.

Studies conducted on field plot samples face general uncertainty in the attribution of temporal variation to various causes. The contributions of natural regeneration following disturbance, changes in management activities, and anthropogenic growth enhancement are not well understood [*Caspersen et al.*, 2000; *Schimel et al.*, 2000; *Pacala et al.*, 2001; *Krankina et al.*, 2005; *Hember et al.*, 2012; *Williams et al.*, 2012; *Erb et al.*, 2013; *Vilén et al.*, 2015]. In some measurement networks, forest productivity is assumed to be in steady state and so there appears to be little emphasis on trying to partition actual temporal variation into components representing intrinsic factors (e.g., natural patterns of stand regeneration) and extrinsic factors (e.g., environmental change). Conversely, most samples drawn from North American forest monitoring programs are not in steady state, such that a component of temporal variation is expected to result from intrinsic factors, including change in stand age and stand biomass [*Gower et al.*, 1996; *Binkley et al.*, 1997; *Ryan et al.*, 1997; *Weiner and Thomas*, 2001; *Mencuccini et al.*, 2007].

In dendroecological studies, the problem has been approached by either standardizing the width of annual rings to remove the variance explained by geometry, aging, and ontogeny or by simultaneously accounting for the covariance between intrinsic and extrinsic factors in statistical models [*Martin-Benito et al.*, 2011; *Kint et al.*, 2012; *Yue and Kahle*, 2014]. In studies of stand-level biomass, intrinsic variation has most commonly been represented by including dependence of biomass fluxes on stand age [*Caspersen et al.*, 2000; *Hember et al.*, 2012; *Chen and Luo*, 2015; *Zhang et al.*, 2015]. *Hember et al.* [2012] additionally considered models with B_S, while *Zhang et al.* [2015] worked with relative growth rate, which inherently assumes that growth increases exponentially with mass.

Body size is accepted as an important control on both growth and mortality of individual trees: Growth efficiency of perennial plants universally decreases with body size [*Paine et al.*, 2012], while the probability of tree mortality commonly increases with body size [*Lines et al.*, 2010; *Holzwarth et al.*, 2013; *Bennett et al.*, 2015; *Hember et al.*, 2016]. At the stand level, the relationship between productivity and stand biomass involves greater ecological complexity and has received less attention. From our own exploration of observations in temperate and boreal forests, we learned that recruitment decreases strongly with stand biomass and that biomass loss due to mortality increases with stand biomass. Based on the assumptions that intensity of

competition for resources increases with stand biomass and that there is a finite limit to the size of those few that survive competition, we might expect that stand biomass imposes a negative effect on biomass growth and a positive effect on biomass loss due to mortality. For example, the overall amount of shaded foliage should increase with stand biomass, under finite soil water holding capacity, water supply per unit biomass must decrease with the accumulation of stand biomass, and an increasing fraction of nutrients may be immobilized in long-lived tissues, causing soil nutrient supply per unit biomass to decrease with accumulation of stand biomass. In general terms, the greater stand biomass is the greater the likelihood that intrinsic factors (i.e., edaphic site conditions that are largely independent of environmental change) may become the most limiting factor as limitations due to heat, nutrients, and carbon are gradually alleviated over time [*Norby et al.*, 1999; *Körner*, 2006]. Hence, growth enhancement may act to accelerate the depletion of resources and accelerate the natural ontogeny of trees, such that biomass gained from growth of dominant individuals will be, at least partially, compensated for by decreased growth of nondominant individuals and biomass loss through mortality [*Bugmann and Bigler*, 2010; *Manusch et al.*, 2012; *Pretzsch et al.*, 2014].

Intrinsic and extrinsic sources of variation were discussed as independent conceptual entities above, yet interactions between them exist when there is statistical dependence between biomass fluxes and stand biomass (Figure 1). It leads to a dynamic "self-referencing" form of model [*Hannon and Ruth*, 2001], where any sustained perturbation in NEBP may be accompanied by negative feedback responses that collectively represent the ontogeny of tree growth and mortality and the intensity of stand competition. Such processes are important to consider in estimating biomass dynamics because they have the potential to decouple trends in NEBP from those of net primary production, yet they are not well understood in the context of imposing negative feedback responses to transient environmental change.

In this study, trends in forest productivity were estimated across southern Canada based on statistical analysis of field plot measurements and simplified scaling assumptions. The database of stand-level forest biomass remeasurements allowed us to test whether NEBP increased due to positive effects of increasing temperature, nitrogen deposition, and carbon dioxide concentration on the growth rate of trees, or alternatively whether growth enhancement was counteracted by negative feedback responses, or whether NEBP decreased due to increasing severity of water stress. To address these hypotheses, we first devised an approach that decomposed temporal variation in observed biomass fluxes into components driven by intrinsic and extrinsic factors based directly on the interpretation of coefficients from linear mixed-effects models. We then applied the dynamic models across forests of southern Canada to assess the influence of system feedback responses to historical environmental change. We then compared the methods and results against previous studies.

2. Data and Methods

The objectives of the study were met in four main steps: First, we compiled data from field plots, derived stand-level biomass fluxes, and combined estimates with corresponding environmental variables (sections 2.1 and 2.2). Second, statistical models were fit to the observations to estimate the sensitivity of biomass fluxes to various factors that were classified as either intrinsic or extrinsic in nature (section 2.3). Third, we described a conceptual framework for attributing temporal variation in biomass fluxes to individual driving factors, drawing on the convention of temporal forcings (section 2.4). Fourth, we applied the statistical models over the long-term historical period to address how dependence between biomass fluxes and stand biomass in these statistical models affected the transient responses to environmental change (section 2.5).

2.1. Field Plots

Field plot data were compiled from the Provinces of British Columbia, Alberta, Saskatchewan, Manitoba, Ontario, Québec, New Brunswick, Nova Scotia, and Newfoundland and Labrador (Figure S1 in the supporting information). We chose to focus on five ecozones with a high number of field plots, including the Pacific Maritime, Montane Cordillera, Boreal Plain, Boreal Shield, and Atlantic Maritime ecozones of southern Canada (Figure S2). The database included measurements of 1.00 million trees, covering a total area of 572 ha, distributed across 10,307 plots (Table 1). Measurement interval lengths were typically either 5 or 10 years. The time period of measurement was highly variable between source agencies and consist of rapid increases and decreases in sample size at the beginning and end of the record due to the periodic, tiled nature of the measurements (Figure S3). Despite the possibility of continuous plot additions over the time period, stand age still tended to increase over time (Figure S4).

Table 1. Field Plot Sampling and Descriptive Statistics by Ecozone: Stand Age (A_S), Stand-Level Biomass (B_S), Biomass Growth (G), Biomass Turnover Due To Mortality (M), Net Ecosystem Biomass Production (NEBP = $G - M$), Annual Number of Days With Frost (F), Warm-Season (May–September) Mean Incident Global Solar Radiation (R), Warm-Season Mean Air Temperature (T), Warm-Season Mean Equilibrium Rate of Evaporation (E), Warm-Season Mean Vapor Pressure Deficit (D), Warm-Season Mean Soil Water Content (W), Atmospheric Carbon Dioxide Concentration (C), and Annual Nitrogen Deposition (N)[a]

	Pacific Maritime	Montane Cordillera	Boreal Plains	Boreal Shield	Atlantic Maritime
Number of plots	1,596	2,067	1,387	4,087	1,170
Number of interval measurements	7,129	6,997	5,413	13,070	8,749
Number of trees	184,303	332,192	225,256	204,520	56,583
Area sampled (ha)	103.7	163.3	140.1	118.5	46.8
Plot attributes					
A_S (yr)	75.0	77.0	83.0	63.3	50.0
B_S (Mg C ha^{-1})	230.3	94.9	102.6	46.4	44.3
G (Mg C ha^{-1} yr^{-1})	5.6	2.6	1.7	1.8	1.5
M (Mg C ha^{-1} yr^{-1})	1.6	1.0	1.0	0.8	0.7
NEBP (Mg C ha^{-1} yr^{-1})	4.0	1.6	0.7	1.1	0.9
Climate normal					
F_n (d yr^{-1})	95.5	158.5	189.1	193.0	156.3
R_n (MJ m^{-2} d^{-1})	18.3	19.4	18.7	18.3	18.4
T_n (°C)	13.5	13.1	11.8	12.8	13.9
E_n (mm d^{-1})	2.9	3.0	3.0	2.9	2.9
D_n (hPa)	4.8	7.1	4.9	3.1	3.1
W_n (mm)	153.8	100.3	130.3	188.1	192.4
Climate anomalies					
F_a (d yr^{-1})	1.71	0.34	0.85	−1.37	−1.05
R_a (MJ m^{-2} d^{-1})	−0.05	−0.02	0.03	0.01	0.00
T_a (°C)	−0.12	0.00	−0.03	0.15	0.09
E_a (mm d^{-1})	−0.01	0.00	0.01	0.01	0.00
D_a (hPa)	−0.08	−0.01	0.01	0.02	0.05
W_a (mm)	−0.10	−1.23	−1.71	0.45	−0.26
Atmospheric composition					
N (kg ha^{-1} yr^{-1})	1.5	0.9	2.8	10.8	11.1
C (ppm)	343.9	343.7	342.3	355.3	350.2

[a]Climate normals indicate the 1971–2000 mean at each location. Climate anomalies indicate the deviation from the 1971–2000 normal.

Tree measurements included vital status, diameter at breast height, height, and age. Indicators of forest management were typically supplied at the level of individual plots or at the level of individual trees (i.e., damage agent codes). Vital status and diameter were measured for all trees, while heights and ages were typically only measured for a subsample of trees. Unmeasured heights were modeled in this study using nonlinear regression functions to predict the relationship between height and diameter fitted to the subsample of trees for each plot. The biomass of bark, branches, foliage, and stemwood were calculated based on relationships with tree diameter and height for each tree species [*Lambert et al.*, 2005; *Jenkins et al.*, 2007; *Ung et al.*, 2008]. In total, 76 species were explicitly recognized in the database. Equations for hardwood and softwood were applied for less-common species (constituting less than 2% of the data). Biomass in units of dry weight was converted to mass of carbon assuming a ratio of carbon to dry wood of 0.5 [*Lamlom and Savidge*, 2003]. Aboveground tree biomass was calculated from the summation of estimates for the above tissues. Belowground tree biomass was estimated based on functions of above-ground biomass and then partitioned into biomass of fine and coarse roots based on a function of total root biomass [*Li et al.*, 2003; *Kurz et al.*, 2009]. Rates of biomass turnover for bark branches, foliage, coarse roots, and fine roots were set constant based on separate parameterizations for coniferous tree and deciduous species [*Kurz et al.*, 2009; *Stinson et al.*, 2011].

Tree-level information was scaled to a standardized area of one hectare based on area expansion factors supplied for each tree. Stand-level tree density (N_S) was calculated as the summation of area expansion factors of all live trees at the first and second census. The annual change in stand-level tree density can be calculated based on

$$\Delta N = (N_{S1} - N_{S0})/\Delta t \tag{3}$$

where N_{S0} and N_{S1} are stand densities at censuses, t_0 and t_1, respectively, or it can be calculated from the difference between annual rates of tree recruitment and mortality:

$$\Delta N_S = R_N - M_N \tag{4}$$

where tree recruitment (R_N) is calculated by the summation of area expansion factors of new live trees in the plot record and tree mortality (M_N) is calculated by the summation of area expansion factors of trees that were classified as live at t_0 and dead at t_1.

Stand-level estimates of NEBP, defined as the change in live-tree biomass, included growth of survivors, G_s, which is the change in biomass of all trees that went from "live" at t_0 to live at t_1, and growth of recruits, G_r, which is the biomass of all trees that were absent at t_0 and live at t_1, and biomass turnover due to tree mortality, M, which is the biomass of all trees that went from live at t_0 to "dead" at t_1). The potential for growth of trees that died during a measurement interval was not considered because the dimension of dead trees at t_1 was commonly not measured. The summation of growth, $G = G_s + G_r$, corresponds with "gross" increment, while NEBP corresponds with "net" increment.

Some jurisdictions used nested sampling designs. For example, the lowest size class would only be measured over a subarea and those trees would therefore exhibit a high area expansion factor, while highest size classes would be measured over greater areas therefore exhibiting a lower area expansion factor. As trees grow, they commonly surpass a size threshold and migrate to a larger sampling area in the accounting, leading to decrease in the area expansion factor. The calculation of M_N is complicated by changes in the area expansion factor over time due to migrants. For example, if a tree that starts off as being small at t_0 and surpasses a size threshold by t_1, it migrates into a larger sampling area and its area expansion factor decreases. This will translate into a significant decrease in ΔN_S when it is calculated based on equation (3), but the vital status of the migrating tree remains unchanged (i.e., still classified as live) so it has no effect on M_N and does not translate into a decrease in ΔN_S when it is calculated based on equation (4).

The above artifact associated with nested sampling design does not affect the mass balance the same way that it does demographics, but it does confound the definitions of growth and mortality. In the hypothetical case of the migrating tree, the migrant remains live between t_0 and t_1 and the corresponding decrease in area expansion factor translates into a lower value of G_s. Hence, the mass balance is explicitly controlled by the growing stock according to equation (3), yet the population change is entirely translated through growth rather than mortality.

Several issues were identified that required decisions on whether to exclude specific types of observations. Several jurisdictions contained plot records with only one census. We assumed that this occurred because they were intended to be permanent sample plots but were then abandoned due to disturbance. Plots with fewer than two remeasurements were excluded to accommodate use of mixed-effects models. Plots with missing or obviously erroneous geographic coordinates were excluded. Measurement intervals with missing trees were excluded. Plots with indication of nutrient management were excluded. Observations that were synthesized from tallies (counts among discrete diameter classes) rather than explicit tree-level measurements were excluded. In Québec, the minimum diameter required to include a tree in the census changed from 9.0 cm at the beginning of the program (in 1970) to less than 9.0 cm after the mid 1990s. To ensure temporal consistency for stand-level analysis, it was necessary to exclude all trees with diameter < 9.0 cm.

The operational definition of an intact stand applied to any measurement interval with no recorded fire, no harvesting, and no thinning. Harvesting and thinning activity was excluded to isolate environmental effects on mortality in the models. Although we considered plots that burned at some point, we excluded measurement intervals in which burns occurred. We chose not to exclude insect activity for two reasons. First, documentation on insect attack during measurement intervals (according to individual tree damage agent codes) was not consistent among data sources. Second, distributions of mortality indicated the inclusion of some catastrophic events that likely partially reflect insect outbreaks. As an indicator of the distribution tails, the 99th percentile values of relative biomass turnover ($M/B_S \times 100$) were 3.7, 5.3, 4.6, 7.4, and 10.2% yr^{-1} in the Pacific Maritime, Montane Cordillera, Boreal Plain, Boreal Shield, and Atlantic Maritime ecozones, respectively. As these rates of mortality are not easily accounted for in stand-level simulation models (see Figure 1), it makes sense to include the fluxes in the estimation of NEBP. Ideally, they would be distinguished from growth and mortality, yet is not be achievable without more consistent documentation.

2.2. Environmental Data

Effects of climate on forest productivity were represented based on annual number of days with freezing, F (d yr^{-1}), warm-season (May–September) mean incident global solar radiation, R (MJ m^{-2} d^{-1}), warm-season mean air temperature, T (°C), warm-season mean equilibrium rate of evaporation, E (mm d^{-1}), warm-season mean vapor pressure deficit of the air, D (hPa), and warm-season mean soil water content, W (mm). Variables corresponding to each plot and time period of measurement were extracted from the nearest grid cell of a 1 km raster database of monthly climate [*NACID*, 2015]. Time trends in the climate variables are shown in Figure S5.

Effects of changing atmospheric composition were also considered by including annual total nitrogen deposition, N (kg N ha^{-1} yr^{-1}), and annual mean atmospheric carbon dioxide concentration, C (ppm). A combination of ground observations, satellite observations, and model predictions were compiled to estimate total nitrogen deposition [*North American Nitrogen Deposition-Version 2 (NANDEP2)*, 2016]. Briefly, wet nitrogen deposition was interpolated from point measurements conducted between 1990 and 2013 by Environment Canada NAtChem Data website and the National Atmospheric Deposition Program in the U.S. Dry nitrogen deposition was approximated from estimates of ground-level nitrogen dioxide concentration from the Ozone Monitoring Instrument [*Jia et al.*, 2016]. Estimates of total nitrogen deposition in 1860 were taken from a global gridded model [*Galloway et al.*, 2004; *Dentener*, 2006]. To interpolate annual values of total nitrogen deposition between 1860 and 1990, we assumed that nitrogen deposition scaled with the increase in global anthropogenic carbon dioxide emissions [see *NANDEP2*, 2016, Figure 2d]. Annual mean carbon dioxide concentration was derived from the RCP Concentration Calculations and Data Final Version for the Coupled Model Intercomparison Project phase 5 experiments [*Meinshausen et al.*, 2011]. Mean conditions of each sample are listed in Table 1.

2.3. Statistical Models

Linear mixed-effects models were developed to estimate the magnitude of temporal trends in stand-level forest productivity and attribute low-frequency temporal variability to specific factors. Models were fit to observations within each of five ecozones, including the Pacific Maritime, Montane Cordillera, Boreal Plain, Boreal Shield, and Atlantic Maritime ecozones (Figure S2). As these models include mixed effects, only a subsample of plots with greater than or equal to two measurements were considered. For response variable y (i.e., G, M, or NEBP) at $j = 1 \ldots m$ plots, predictions were given by:

$$y_j = \left(\lambda_1 + \gamma_{1,j}\right) + \lambda_2 B_S + \lambda_3 A_S + \lambda_4 A_S^2 + \lambda_5 F_n + \lambda_6 R_n + \lambda_7 T_n + \lambda_8 E_n + \lambda_9 D_n$$
$$+ \lambda_{10} W_n + \lambda_{11} F_a + \lambda_{12} T_a + \lambda_{13} E_a + \lambda_{14} D_a + \lambda_{15} W_a + \lambda_{16} N + \lambda_{17} C \tag{5}$$

there λ_1 is a fixed intercept, $\gamma_{1,j}$ is a random effect on the intercept at the level of each plot, $\lambda_2 \ldots \lambda_{17}$ are fixed effects of stand biomass, B_S, stand age, A_S and a quadratic term, A_S^2, a series of explanatory variables that express long-term mean climate (F, R, T, E, D, and W denoted by the subscript "n" for normal), followed by a series of predictor variables that express temporal deviations from the long-term normal (denoted by the subscript "a" for anomaly), followed by annual total atmospheric nitrogen deposition (N) and atmospheric carbon dioxide concentration (C).

The design of equation (5) solely reflects our expectation of the biophysical factors that control productivity. The present study was confined to describing the behavior of equation (5), documenting the consequent level of multicollinearity, and discussing the potential implications for interpretation. Spatial autocorrelation was not considered based on evaluation of semivariograms for NEBP of each ecozone, which failed to identify a clear sill and no strong changes in variance over distances within the ecozones (Figure S6).

2.4. Temporal Forcings

Overall temporal variation in forest productivity was attributed to individual driving factors using the convention of forcings. Here we define forcing as the expected temporal response in a dependent variable to a specific stimulus in isolation from all other simultaneous stimuli. In the context of forest biomass dynamics observed at field plots, let

$$F_y = \sum_{x=1}^{n} F_{yx} \tag{10}$$

where F_y is the net temporal forcing of response variable, y (i.e., G, M, or NEBP), and F_{yx} is the change in response variable, y, over a specified time period imposed by change in $x = 1 \ldots n$ predictor variables over that time period. Predictor variables each impose a unique forcing defined by the product of the marginal sensitivity of the dependent variable to that predictor variable, $\lambda_{y,x}$, and the temporal change in each independent variable, $\beta_{x,t}$, over a specified time period

$$F_{yx} = \lambda_{y,x} \times \beta_{x,t} \tag{11}$$

A distinction is made between whether a predictor variable represents variation of intrinsic or extrinsic origin:

$$F_{y,\text{in}} = \sum_{x=1}^{P} F_{yx,\text{in}} \tag{12}$$

and

$$F_{y,\text{ex}} = \sum_{x=1}^{q} F_{yx,\text{ex}} \tag{13}$$

where $F_{y,\text{in}}$ is the net intrinsic forcing and collectively represents the net effect of $x = 1 \ldots p$ intrinsic forcings, and $F_{y,\text{ex}}$ is the net extrinsic forcing and collectively represents the net effect of $x = 1 \ldots q$ extrinsic forcings. Intrinsic factors collectively define net intrinsic forcing, while extrinsic factors collectively define net extrinsic forcing. Stand-level biomass and stand age are perceived as intrinsic factors because they impose a forcing on forest productivity irrespective of environmental conditions. As the models include a random plot effect, trends in productivity of the sample can, in principle, be attributed to "random" processes. We chose to treat the temporal forcing due to random plot effects as an intrinsic factor. We suspect that it is most likely explained by change in the sample-average level of site fertility (i.e., local nutrient levels and soil water holding capacity) that can change through time as a result of addition and removal of plots to and from the sample (herein described as sample instability). Classifying the temporal forcing caused by the random plot effect as an intrinsic factor constitutes the most conservative assumption with respect to conclusions drawn from the models to test the hypothesis that environmental change has affected productivity over time.

Just as sample instability can potentially change the average level of site fertility, it can also change the normal climate of the sample. That is, as plots are added and removed from the sample, temporal trends in forest productivity can arise either from change in spatial climate of the sample or from environmental change. By incorporating both dimensions in climate separately (normals vs. anomalies), we assume that variation imposed by plot additions and removals can be attributed to the climate normals, which in the current context of study are interpreted as intrinsic factors, while temporal climatic changes can be accounted for by the anomalies and classified as extrinsic forcings. Lastly, the effects of nitrogen deposition and carbon dioxide were treated as extrinsic factors.

The above expression of F_{yx} is relatively similar to the type of information presented in previous studies [*Hember et al.*, 2012; *Ma et al.*, 2012; *Chen and Luo*, 2015; *Zhang et al.*, 2015]. However, there are two caveats to consider. First, the above values of F_{yx} are specifically representative of the field plot sample, which must be distinguished from that of landscapes due to the possibility that time trends in the predictor variables at the plot locations differ from those of landscapes, $\beta_{x,t,\text{plot}} \neq \beta_{x,t,\text{landscape}}$. For extrinsic factors, this may seem trivial, particularly where field plots are evenly distributed across a region of interest. However, for field plots drawn from forest inventory programs that are not in steady state, it is not safe to assume that change in stand age and stand biomass of the plot sample are equivalent to that of the region. Second, estimation of temporal forcing must consider the possibility of significant interaction between intrinsic and extrinsic temporal forcings, as defined in the models by the representation of potential dependence of both growth and mortality on B_S. Hence, the value of F_{yx} inferred directly from estimates of $\lambda_{y,x}$ and $\beta_{y,t}$ is an expression of the static behavior of what is actually a dynamic model. We hypothesized that $\lambda_{G,Bs}$ and $\lambda_{M,Bs}$ are negative and positive, respectively; any sustained positive perturbation in growth will drive increases in B_S (for an equivalent stand age or time since disturbance), and this will feed back on NEBP through negative dependence of growth on B_S. Equivalent feedbacks, but in the opposite direction, would be expected upon sustained decrease of NEBP. Although the relationships are strictly empirical, we hypothesized that $\lambda_{G,Bs}$ is negative due to a combination of increasing overall demand for light, nutrients, and water and decreasing whole-plant, leaf-specific hydraulic conductance.

To understand the implications of these concepts, we made the distinction between static plot-scale temporal forcing that are based directly on estimates of $\beta_{y,t}$ specifically observed at the field plots and $\lambda_{y,x}$ from the models (i.e., F_y, $F_{y,in}$, and $F_{y,ex}$) and dynamic landscape-scale temporal forcing ($F_{y,ex}'$), where temporal forcing is calculated from applications of the models to predict transient responses of NEBP and B_S to historical environmental change over landscapes that are controlled by a realistic (landscape-scale) variation in intrinsic factors defined by a predefined disturbance regime. So whereas $\lambda_{y,x}$ remains the same, $\beta_{y,t}$ differs between estimates of static plot-scale forcing and dynamic landscape-scale forcing.

2.5. Model Application

Estimates of static plot-scale forcings (i.e., F_G, F_M, and F_{NEBP}) were reported from estimates of $\beta_{x,t}$ and $\lambda_{y,x}$ directly from trend analysis of the independent variables and fixed effects from equation (5), respectively. The forcing due to random effects was calculated by running the models at the field plot locations with all fixed effects held constant through time, so that temporal variability in predictions solely reflected variation in the intercept parameter as it varied with the addition and removal of plots from the sample.

Dynamic landscape-scale forcing (i.e., $F_{NEBP,ex}'$) was estimated by running the models at every fifth grid cell of the same 1 km raster databases of nitrogen deposition and climate that were used in model fitting. Area-integrated biomass fluxes for each grid cell were calculated by multiplying the predicted flux density by the percent tree cover of that grid cell. Estimates of percent tree cover at 1 km resolution were resampled from higher resolution grids derived from the landsat-based Earth Observation for Sustainable Development of Forests [*Wulder and Nelson*, 2003].

Although gradual changes in age class distribution over time may have influenced NEBP in southern Canadian forests, it was not the focus of this study and it was assumed, based on the design of the study, that any actual increase or decrease in mean stand age that might have occurred over the study period would have little influence on the results of the present study. Nevertheless, we developed a simple approximation of NBBD based on basic assumptions and available information about stand-replacing disturbances from previous studies. Harvesting rates for Canada's managed forest were compiled by *Kurz and Apps* [1999] up to 1987 and by *Stinson et al.* [2011] between 1990 and 2008. Harvest events were distributed randomly across grid cells within the managed forest boundary with $A_S > 80$ years, while harvesting outside the managed forest was assumed to be absent. Annual area burned by fires was rasterized from the Canadian National Fire Database [*Amiro et al.*, 2001; *Canadian Forest Service*, 2015]. All fires and harvests were assumed to replace the stand. To account for large areas affected by Mountain Pine Beetle, aerial surveys from the Forest Insect and Disease Survey database and annual aerial surveys conducted by the Government of British Columbia were compiled and rasterized. We assumed that the four severity classes resolved by the surveys represented biomass losses of 5, 15, 30, and 50% and reduced stand age by equivalent proportions. Aerial surveys for other dominant insects were not available. Outside the area affected by Mountain Pine Beetle, we applied artificial stand-replacing insect outbreak events defined by a constant annual probability of outbreak, distributed randomly across grid cells that were unaffected by harvest, fire, or Mountain Pine Beetle. Implementing the above compilation of stand-replacing disturbances led to a stable age class distribution over time and a mean stand age of 90 years old over 1951 2012.

Simulations were performed from 513 years before present to spin up biomass. Annual climate prior to the start of climate records (1901) were drawn randomly from the climate record for 1901–1930. Prior to 1850, carbon dioxide concentration was set as 280 ppm. Prior to 1860, nitrogen deposition was set at the rate for 1860 [*Galloway et al.*, 2004; *Dentener*, 2006]. Stand biomass stabilized by 1850 in all ecozones.

2.6. Presentation of Results

To document static plot-scale temporal forcings from each ecozone model, we start with a high-level summary of the temporal forcing imposed by all climate variables together, by carbon dioxide concentration, by nitrogen deposition, and finally by all extrinsic temporal forcings, $F_{y,ex}$. We then document the temporal forcings due to various combinations of the climate variables. The forcings for climate variables collectively describing heat limitations (F_F and F_T) and radiation limitations (F_R and F_E) were grouped based on consideration that moderate multicollinearity existed within those groupings. We then describe the more detailed individual temporal forcings for both intrinsic and extrinsic factors in each ecozone.

To summarize the dynamic landscape-scale simulations, we show the ecozone-average interannual variability, 10 year moving averages, and long-term time trends in predicted NEBP for the modern era (1901–2013) for each of the five ecozones across southern Canada (Figure S2). To summarize the dynamic landscape-scale forcings, we show the ecozone-average 10 year moving averages in the various extrinsic temporal forcings on NEBP for the period 1850–2013. For simplicity, we group the extrinsic forcings into those describing heat limitation ($F_{NEBP,F}$ and $F_{NEBP,T}$), water limitation ($F_{NEBP,R}$, $F_{NEBP,E}$, $F_{NEBP,D}$, and $F_{NEBP,W}$), atmospheric composition ($F_{NEBP,N}$ and $F_{NEBP,C}$), feedback ($F_{NEBP,Bs}$), and finally the dynamic landscape-scale net extrinsic temporal forcing (F_{NEBP}').

Forcings were initially calculated in the absolute units of the dependent variable. To facilitate comparison with other studies, they were converted from absolute units to relative units by dividing the initial estimate of F_{yx} by the mean observation of y and multiplying by 100 to report it as the percent change in the dependent variable per year.

3. Results

3.1. Model Fits

Out of a possible 85 fixed effects parameters per response variable, only 8 and 12 were nonsignificant and not retained in the models for growth and mortality, respectively (Tables S1 and S2). As expected, the models exhibited signs of multicollinearity, with mean variance inflation factors ranging from 8 to 25 among ecozones (Table S4). Variance inflation factors for stand age were high due to the inclusion of both a linear and quadratic term. Considering only the extrinsic variables, mean variance inflation factors were consistently < 10. Extremely high standard errors for the fixed effects parameters, which would imply extreme multicollinearity, were also not encountered. Herein, we avoid potential implications of moderate mulicollinearity among environmental variables by limiting summaries and discussion to the collective forcings related to heat (i.e., T_a plus F_a) and the collective forcings related to radiation (i.e., R_a plus E_a).

3.2. Static Plot-Scale Extrinsic Forcing

The overall summary of static plot-scale extrinsic temporal forcings showed a high degree of variability among ecozones (Figure 2). The net forcing of all climate variables on growth was strongly positive in the Boreal Shield ecozone, insignificant in the Atlantic Maritime ecozones, and weakly negative in the Pacific Maritime, Montane Cordillera, and Boreal Plain ecozones (Figure 2a). Climate forcing on mortality was positive in the Pacific Maritime and Montane Cordillera ecozones, insignificant in the Boreal Plain and Atlantic Maritime ecozones, and negative in the Boreal Shield ecozone (Figure 2b). These patterns for growth and mortality translated into strong positive climate forcing on NEBP in the Boreal Shield ecozone, moderate negative climate forcing on NEBP in all other ecozones (Figure 2c).

Nitrogen deposition imposed weak positive forcing on growth in the Montane Cordillera ecozone and weak negative forcing on growth in the Boreal Plain ecozone (Figure 2a). Nitrogen deposition forcing on mortality was moderately negative (i.e., mortality decreased) in all ecozones except the Boreal Shield and Atlantic Maritime ecozones (Figure 2b). These contrasting effects led to weak positive overall forcing on NEBP in the Pacific Maritime and Montane Cordillera ecozones (Figure 2c).

Carbon dioxide concentration consistently imposed positive forcing on growth, yet it also imposed positive forcing on mortality in all but the Atlantic Maritime ecozone. The resulting carbon dioxide forcing on NEBP ranged from minor and moderate negative values in the driest ecozones and positive values in the wet ecozones (Figure 2c).

Estimates of net extrinsic temporal forcing on growth were consistently positive with the exception of the insignificant value for the Boreal Plain ecozone. Net extrinsic temporal forcing on mortality was only significant in the Montane Cordillera and Boreal Plain ecozones. Lastly, net extrinsic forcing on NEBP was strongly positive in the Boreal Shield and Atlantic Maritime ecozones, weakly positive in the Pacific Maritime ecozone, and negative in the Montane Cordillera and Boreal Plain ecozones (Figure 2c).

Extrinsic forcing imposed by individual climate variables showed little consistency across ecozones (Figure 3). As a generalization, heat (i.e., the combined effect of decreasing annual days with freezing and increasing warm-season air temperature anomalies, Figure S5) imposed positive overall forcing on growth and NEBP
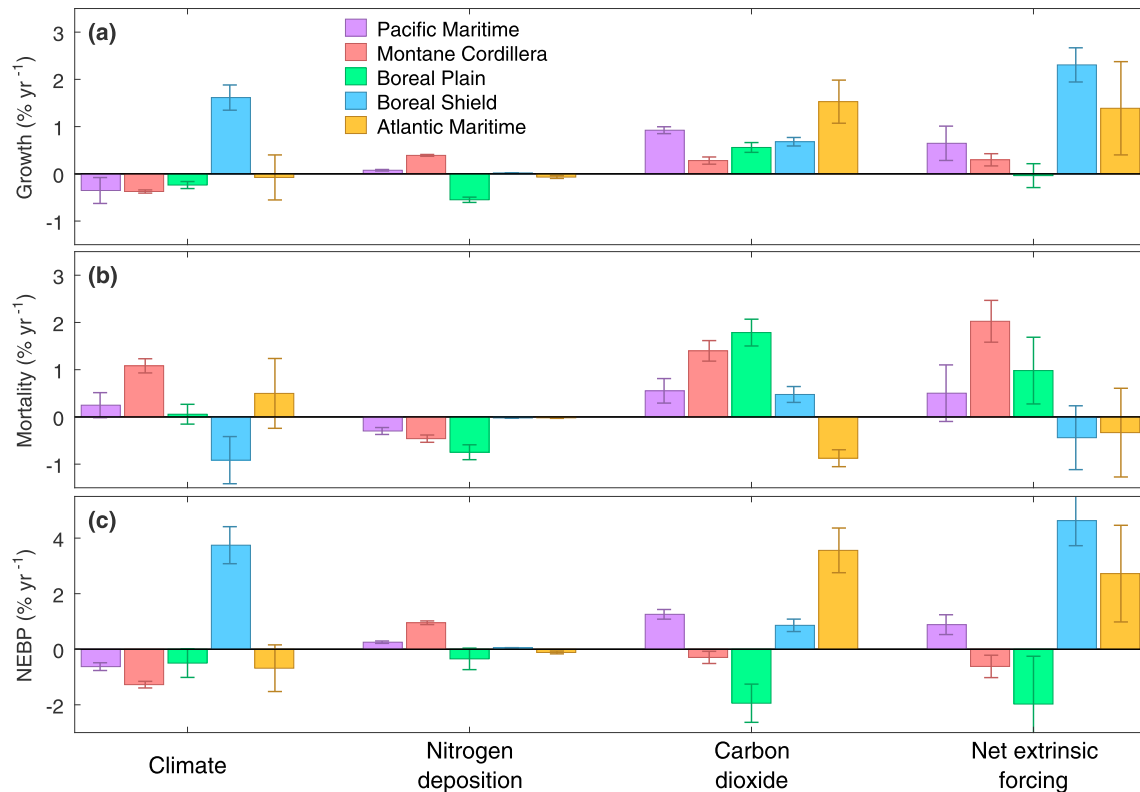
Figure 2. Summary of static plot-scale extrinsic temporal forcings on stand-level biomass growth, mortality, and net ecosystem biomass production (NEBP). Climate includes the net forcing from individual forcings imposed by anomalies in incident global solar radiation, days with freezing, air temperature, equilibrium evaporation, vapor pressure deficit, and soil water content. Net extrinsic forcing includes forcings imposed by climate anomalies, nitrogen deposition, and carbon dioxide concentration. Note that forcings for NEBP do not necessarily match the difference in forcings for growth and mortality because the results for NEBP reflect independent model fits to NEBP, rather than calculating NEBP from subtracting fitted estimates for mortality from those of growth.

in the boreal and Atlantic Maritime ecozones (Figure 3c). Climate variables that were strongly associated with radiation (i.e., incident global solar radiation and the equilibrium rate of evaporation) imposed negative forcing on NEBP in the Pacific Maritime, Montane Cordillera, and Boreal Plain ecozones and positive forcing on NEBP in the Boreal Shield ecozone. Forcing from vapor pressure deficit was consistently negative for both growth and NEBP (Figures 3a and 3c), despite variable effects on mortality (Figure 3b). Forcing attributed to soil water content was consistently weak compared to other variables.

The high-level summaries of extrinsic forcings outlined in Figures 2 and 3 reflect subsets and groupings drawn from the complete sets of (extrinsic and intrinsic) static plot-scale forcings for each ecozone. Figure 4 provides more detailed summaries of the change in dependent variables, the sensitivity of biomass fluxes to driving variables, and the individual forcings for each ecozone.

In the Pacific Maritime ecozone, growth of the sample increased, as indicated by the net forcing (dark bar in Figure 4a). This is the net balance between negative net intrinsic forcing and positive net extrinsic forcing (red bars in Figure 4a). Negative net intrinsic forcing was largely driven by negative forcing from stand biomass and normal air temperature; the sampled stands accrued large amounts of biomass ($\beta_{Bs, t} = 190.1 \, \mathrm{Mg \, C \, ha^{-1}}$) over the time period and the marginal sensitivity to stand biomass was moderately strong and negative ($\lambda_{G,Bs} = -0.61$). The detection of significant intrinsic forcing from climate normals (e.g., T_n) suggests that the temporal variation in productivity of the sample was weakly influenced by change in normal climate associated with plot additions and removals through time. Extrinsic forcings on growth did not always conform with expectation: We expected that decreasing number of days with frost, increasing temperature, and increasing incident solar radiation would impose positive forcing, and that increasing equilibrium evaporation would impose negative forcing, yet model results show the opposite. This inability to reproduce expected responses may reflect high uncertainty in anomalies of radiation and tight correlation,
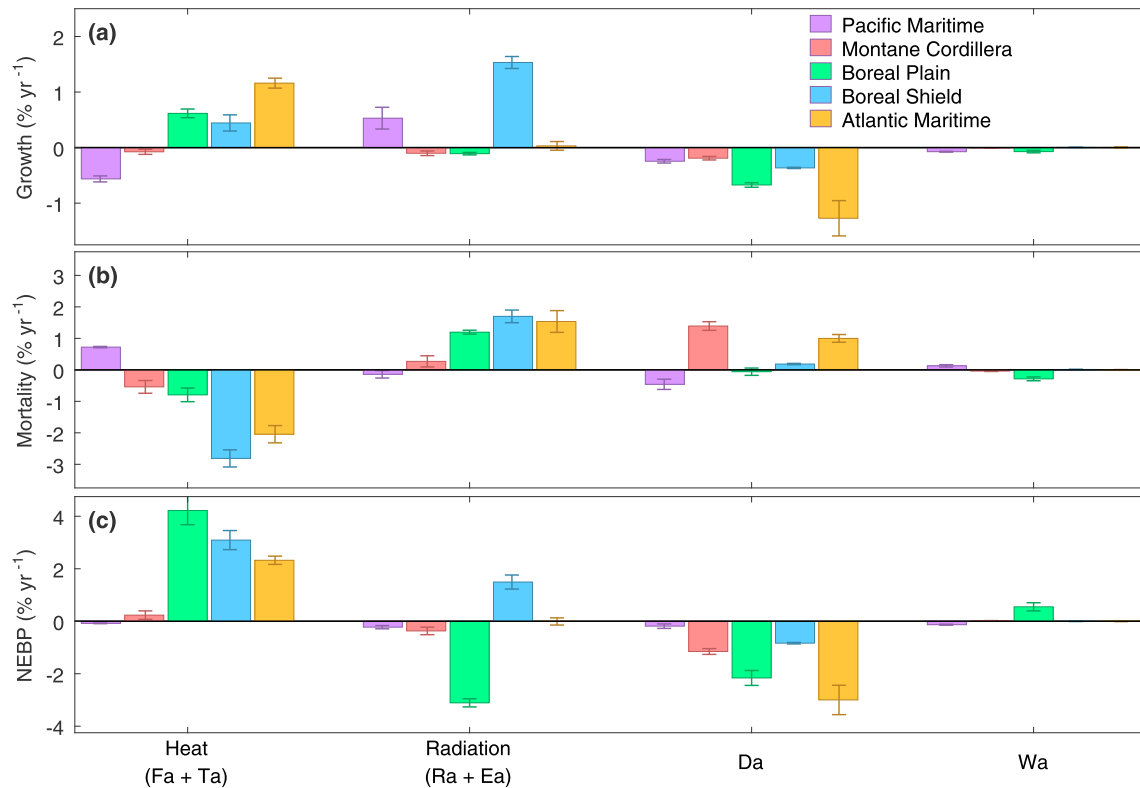
Figure 3. Summary of static plot-scale climate forcings on stand-level biomass growth, mortality, and net ecosystem biomass production. Net forcing imposed by heat (deviations from long-term mean days with freezing and air temperature, $F_a + T_a$), net forcing imposed by radiation (solar radiation and equilibrium evaporation, $R_a + E_a$), forcing imposed by vapor pressure deficit (D_a), and forcing imposed by soil water content (W_a).

and thus deleterious effects of multicollinearity, among those variables. Other forcings conformed to our expectation: Vapor pressure deficit increased and imposed negative forcing, soil water content decreased and imposed negative forcing, and nitrogen deposition and carbon dioxide both increased and imposed positive forcing. Net intrinsic forcing on mortality was strong and positive owing to large increases in stand biomass that counteracted negative forcings from the random plot effects and stand age. Net extrinsic forcing of mortality was not significantly different from zero. Temperature increased and imposed strong positive forcing on mortality. Increases in equilibrium evaporation, radiation, vapor pressure deficit, and nitrogen deposition imposed negative forcing on mortality. Interestingly, stand age increased and imposed moderate positive forcing on NEBP. Extrinsic forcings from the model of NEBP were more consistent with expectation, with positive forcing imposed by temperature, nitrogen deposition and carbon dioxide, and negative forcing imposed by equilibrium evaporation, vapor pressure deficit, and soil water content.

In the Montane Cordillera ecozone, net forcing of growth was not significant and net forcing of mortality was strong and positive (Figure 4b). Increase in stand biomass over the fitting period (22.6 Mg C ha^{-1}) was lower in the Montane Cordillera sample than the Pacific Maritime ecozone sample and so it imposed weaker forcings, but in the same direction as the Pacific Maritime ecozone. Random effects also imposed significant forcing. Net extrinsic forcing of growth and mortality were both positive. Greater forcing from mortality led to negative net extrinsic forcing of NEBP. Extrinsic forcing of growth was most strongly controlled by negative forcings from vapor pressure deficit and positive forcings from nitrogen deposition and carbon dioxide. Warming and nitrogen deposition imposed negative forcing on mortality, while solar radiation, vapor pressure deficit, and carbon dioxide all imposed strong positive forcings on mortality.

In the Boreal Plain ecozone, both net forcings and net intrinsic forcings were not significant (Figure 4c). Again, random effects were found to impose significant forcing. Increasing stand biomass of the plot sample was intermediate between Pacific Maritime and Montane Cordillera ecozones and imposed significant forcings, causing decreases in growth and increases in mortality. Net extrinsic forcing on growth was not
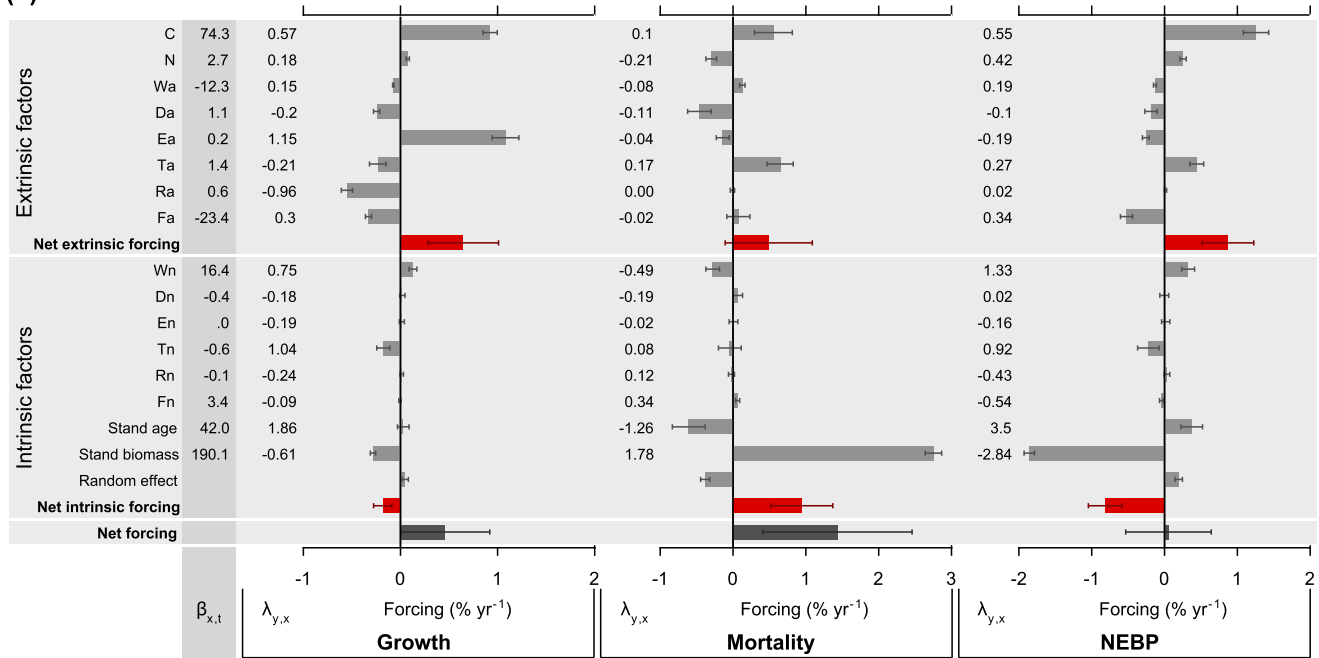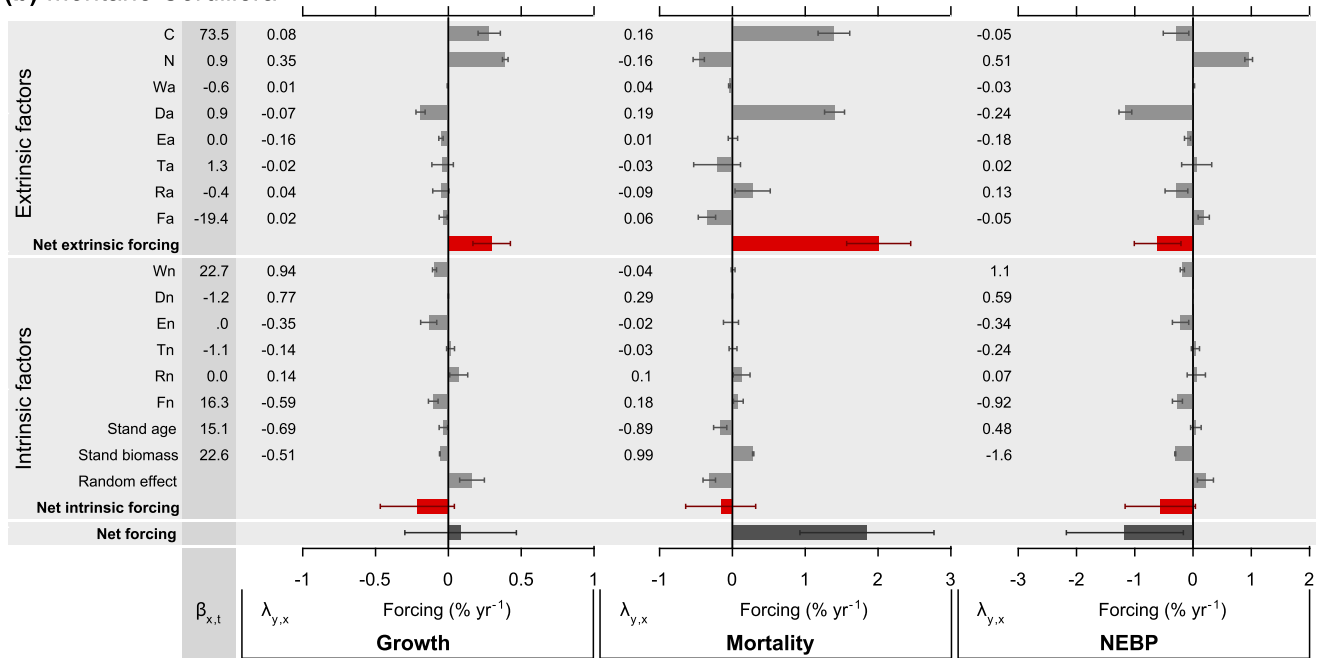
Figure 4. Temporal forcing of the plot sample in the (a) Pacific Maritime and (b) Montane Cordillera ecozones. Bars indicate the temporal forcing on forest productivity derived from fitting linear mixed-effects models to field plots. Temporal forcing describes the effect of each predictor variable on the temporal trend in the response variable (biomass growth due to a combination of survivor growth and recruitment, biomass turnover due to mortality, and net ecosystem biomass production, NEBP). Net forcing is the net change imposed by all forcings. Net intrinsic forcing is the net change imposed by all intrinsic forcings. Net extrinsic forcing is the net change imposed by all extrinsic forcings. Intrinsic forcings included change imposed by random effects (i.e., a random intercept at each plot), stand biomass (Mg C ha^{-1}), stand age (year), and long-term (1971–2000) mean climate variables, including days with freezing (F_n, d yr^{-1}), solar radiation (R_n, MJ m^{-2} yr^{-1}), air temperature (T_n, °C), equilibrium evaporation (En, mm d^{-1}), vapor pressure deficit (D_n, hPa), and soil water content (W_n, mm). Extrinsic forcings included change imposed by deviations from long-term mean climate, including days with freezing (F_a, d yr^{-1}), solar radiation (R_a), air temperature (T_a), equilibrium evaporation (E_a), vapor pressure deficit (D_a), nitrogen deposition (N, kg N ha^{-1} yr^{-1}), and atmospheric carbon dioxide concentration (C, ppm). Time trends in each predictor variable ($\beta_{x,t}$) are listed adjacent to labels. The sensitivity of the response variables to each predictor variable ($\lambda_{y,x}$) are listed to the left of the bar (forcings) for each response variable. Because all variables were standardized (z-scored) $\lambda_{y,x}$ can be interpreted as the expected increase, expressed in standard deviations of the response variable, per one standard deviation increase in the predictor variable. Temporal forcing of the plot sample in the (c) Boreal Plain and (d) Boreal Shield ecozones.

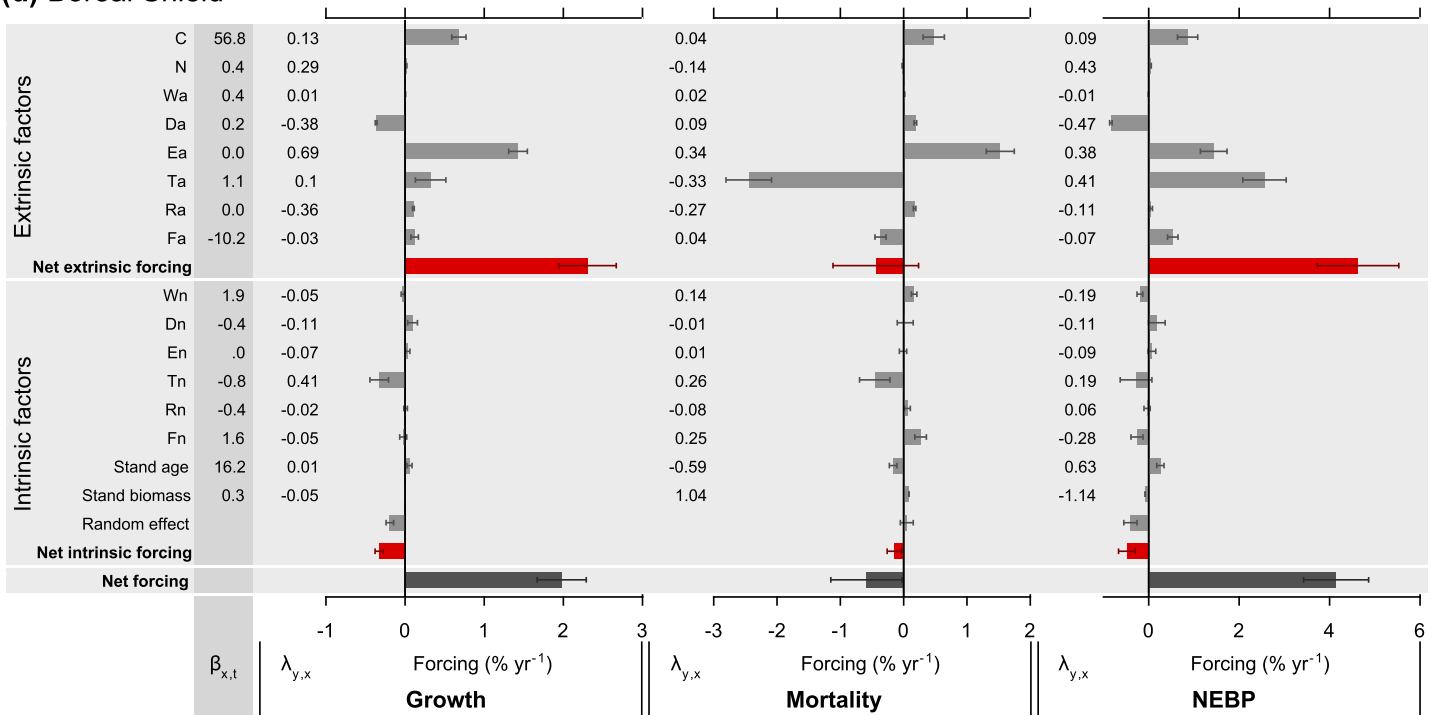**(c)** Boreal Plain
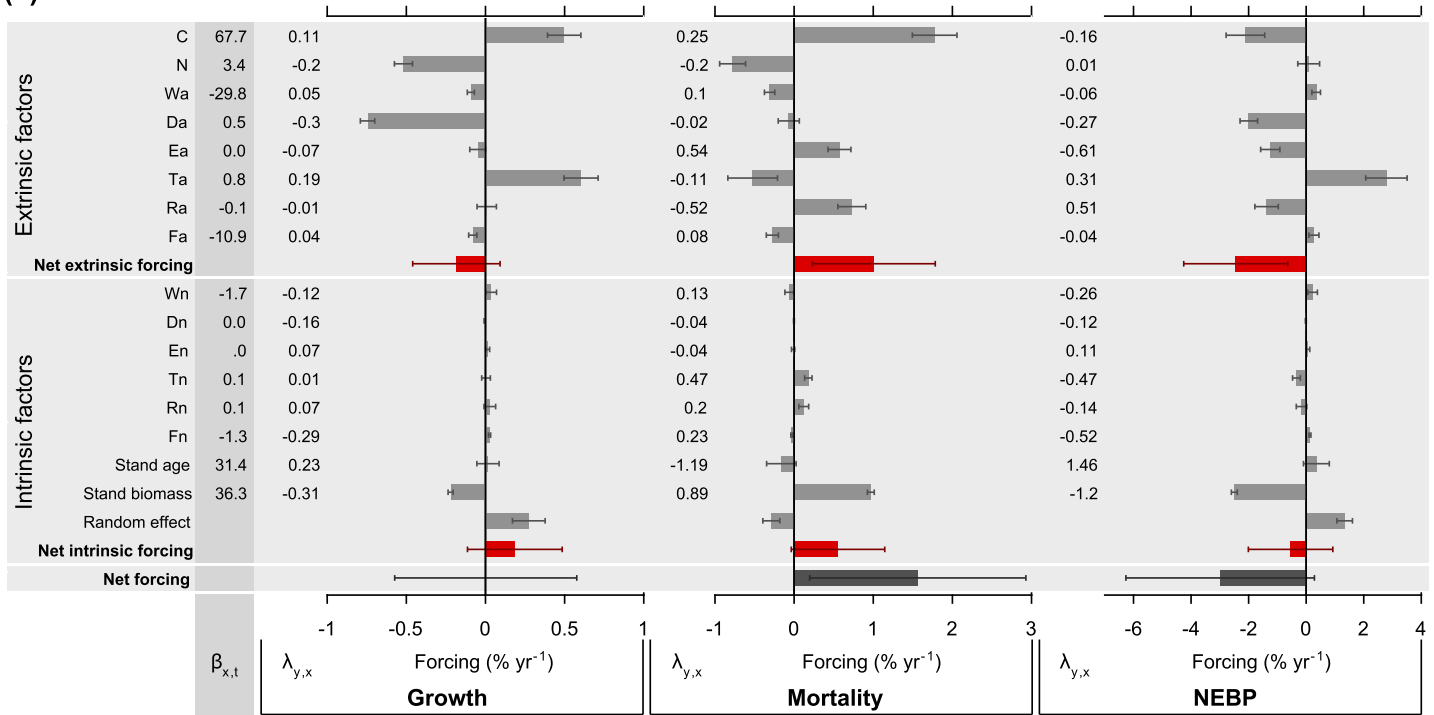
(d) Boreal Shield

Figure 4. (continued)

significant. Increases in vapor pressure deficit and nitrogen deposition imposed strong negative forcing on growth, while increasing air temperature anomaly and carbon dioxide imposed strong positive forcing. Net extrinsic forcing on mortality was positive, driven by a combination of positive forcings imposed by radiation, equilibrium evaporation, and carbon dioxide.
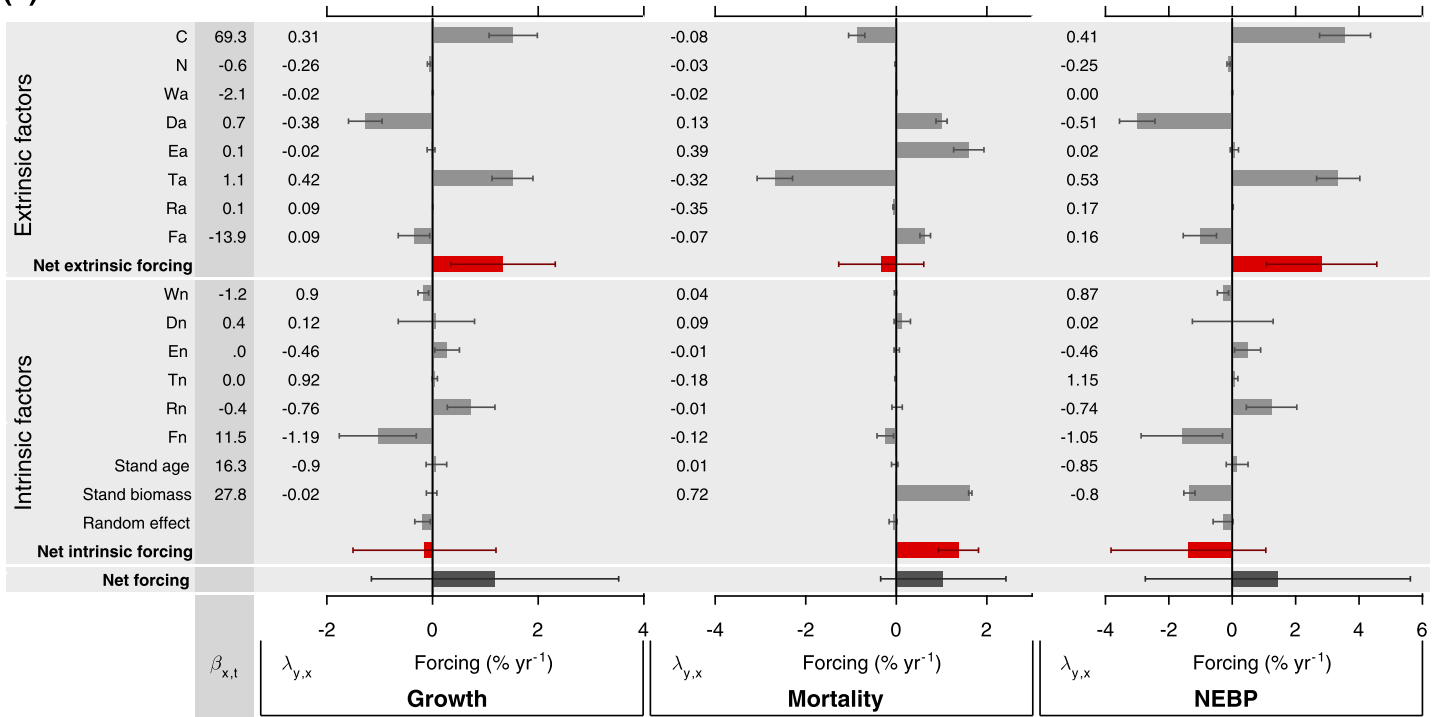
(e) Atlantic Maritime

Figure 4. (continued)

In the Boreal Shield ecozone, stand biomass did not change substantially over time because, unlike previous ecozones, harvesting was more prevalent in the Boreal Shield ecozone sample (Figure 4d). (Although harvesting does not directly affect the calculations of growth, mortality, or NEBP, it does indirectly affect productivity of the sample by influencing stand biomass and stand age.) As a result, the net intrinsic forcing on growth, mortality, and NEBP was relatively minor in the Boreal Shield ecozone. Net extrinsic forcing on growth was strongly positive and was attributed to strong positive forcings from air temperature, equilibrium evaporation, and carbon dioxide. Net extrinsic forcing on mortality was negative, but not significant. Increasing temperature anomaly imposed strong negative forcing on mortality, while equilibrium evaporation anomaly and increasing carbon dioxide both imposed positive forcing. Net extrinsic forcing of NEBP was strongly positive, driven largely by increasing air temperature, equilibrium evaporation, and carbon dioxide, which counteracted weaker negative forcing from increasing vapor pressure deficit.

In the Atlantic Maritime ecozone, stand biomass and stand age increased moderately (Figure 4e). The moderate increase in stand biomass was large enough to impose strong positive forcing on mortality, which led to strong negative forcing on NEBP. Extrinsic forcing on growth was overwhelmingly attributed to strong positive forcing from temperature and carbon dioxide, which collectively exceeded strong negative forcing from vapor pressure deficit. Similar to the Boreal Shield, increasing temperature imposed strong negative forcing on mortality. Similar to the Pacific Maritime ecozone, decreasing annual number of days with frost imposed negative (positive) forcing on growth (mortality) in the Atlantic Maritime ecozone. Extrinsic forcings on NEBP very closely matched those of growth.

3.3. Summary of Sensitivity to Intrinsic Factors

While the above section reported the forcing from individual intrinsic factors, here we also briefly summarize the sensitivity of biomass fluxes to stand biomass, stand age, and the random effects. Combining the estimates of sensitivity of growth to stand biomass from each ecozone formed a nonsignificant negative relationship between sensitivity and mean stand biomass of the ecozones (Figure S7a). Values for the Atlantic Maritime and Boreal Shield ecozones, where harvesting more strongly affects the sample, were close to zero. The sensitivity of growth to stand biomass in the Boreal Plain ecozone was intermediate, and values for
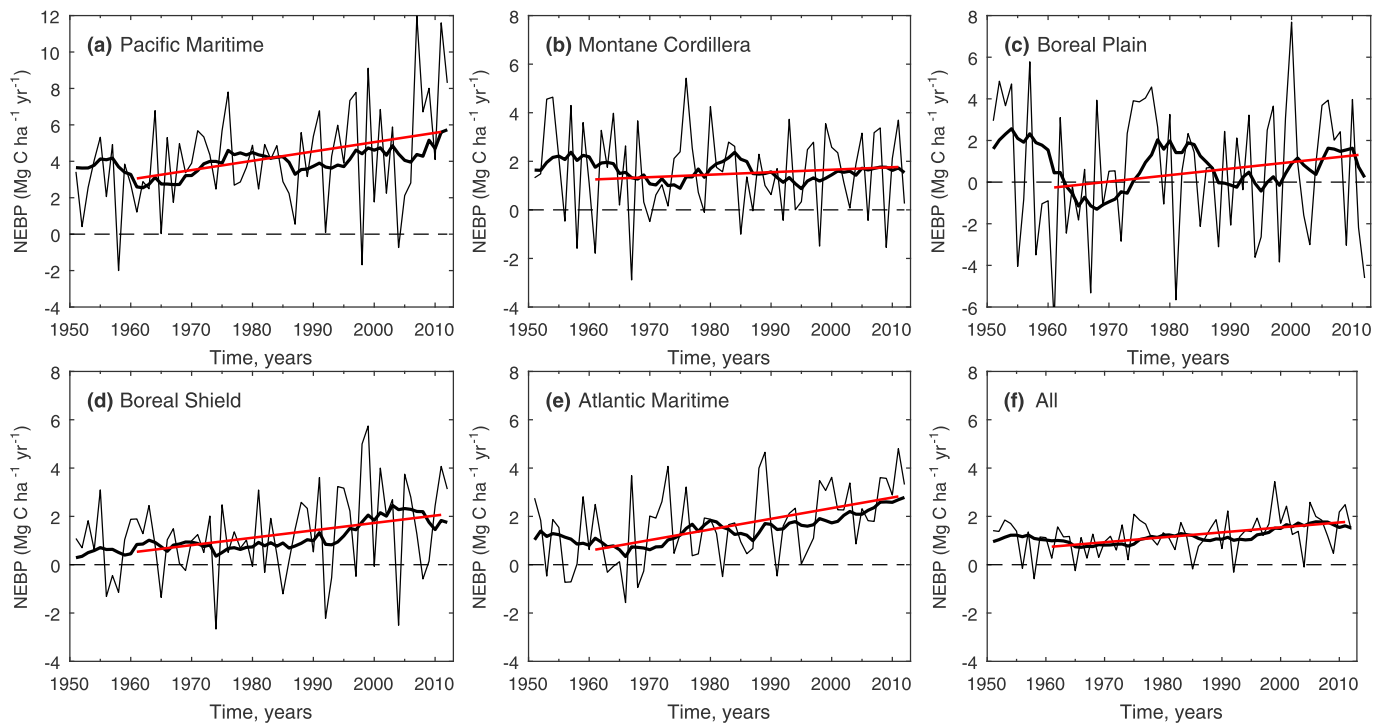
Figure 5. Time series of predicted annual net ecosystem biomass production (NEBP) from dynamic landscape-scale simulations of biomass growth and loss due to mortality across Canada's southern forests during the period of field plot measurements. Thick curves indicate 10 year moving averages. Red curves indicate least squares fits to time over 1961 2011 (to be consistent with the static plot-scale analysis period). There were no substantial changes in age class distribution under the imposed disturbance regimes so temporal variation reflects effects of environmental change and negative feedback responses to change in stand biomass.

Montane Cordillera and Pacific Maritime ecozones were relatively similar despite large differences in stand biomass. Sensitivity of mortality to stand biomass increased with mean biomass of the ecozones (Figure S7b). In the case of mortality, the relationship was significant. Sensitivity was relatively similar in all ecozones except for a higher value for Pacific Maritime. The sensitivity of NEBP to stand biomass formed a stronger negative relationship, again largely driven by Pacific Maritime as an outlier (Figure S7c). It is interesting to note that outside of the Atlantic Maritime ecozone, the sensitivity of NEBP to stand age was positive (Figure 4). Lastly, the random effects (applied to the intercept for each plot) commonly imposed significant temporal forcing, such as positive forcings on NEBP in the Pacific Maritime, Montane Cordillera, and Boreal Plain ecozones (Figures 4a–4c) and negative forcing on NEBP in the Boreal Shield and Atlantic Maritime ecozones (Figures 4d and 4e).

3.4. Dynamic Landscape-Scale Forcing

Model predictions averaged by ecozone indicated high interannual variability over 1951–2012 (Figure 5). The standard deviation of annual NEBP was 2.8, 2.5, 3.9, 2.8, and 1.1 Mg C ha^{-1} yr^{-1} for the Pacific Maritime, Montane Cordillera, Boreal Plain, Boreal Shield, and Atlantic Maritime ecozones. For all of Canada's southern ecozones, NEBP was typically positive but was slightly negative during 6 years (Figure 5f). With coefficients of variation exceeding 100% in three of the largest ecozones, it is clear that focus on specific measurement periods will have significant influence over estimated time trends.

Focusing on the 1961–2011 period (to be consistent with the analysis of static plot-scale forcings), transient simulations of the landscape indicated positive trends in NEBP in all ecozones (red curves in Figure 5). Whereas selecting the 1961–2011 analysis period yielded positive NEBP trends in the Montane Cordillera and Boreal Plain ecozones, consideration of the 1951–2012 period would yield negative trends, more consistent with 10 year moving averages time series (Figure 5b and 5c).

Unlike the estimate of static plot-scale net extrinsic forcing on NEBP, the dynamic landscape-scale net extrinsic forcing on NEPB, $F_{NEBP,ex}'$, simultaneously integrates the environmental stimuli and feedback responses to
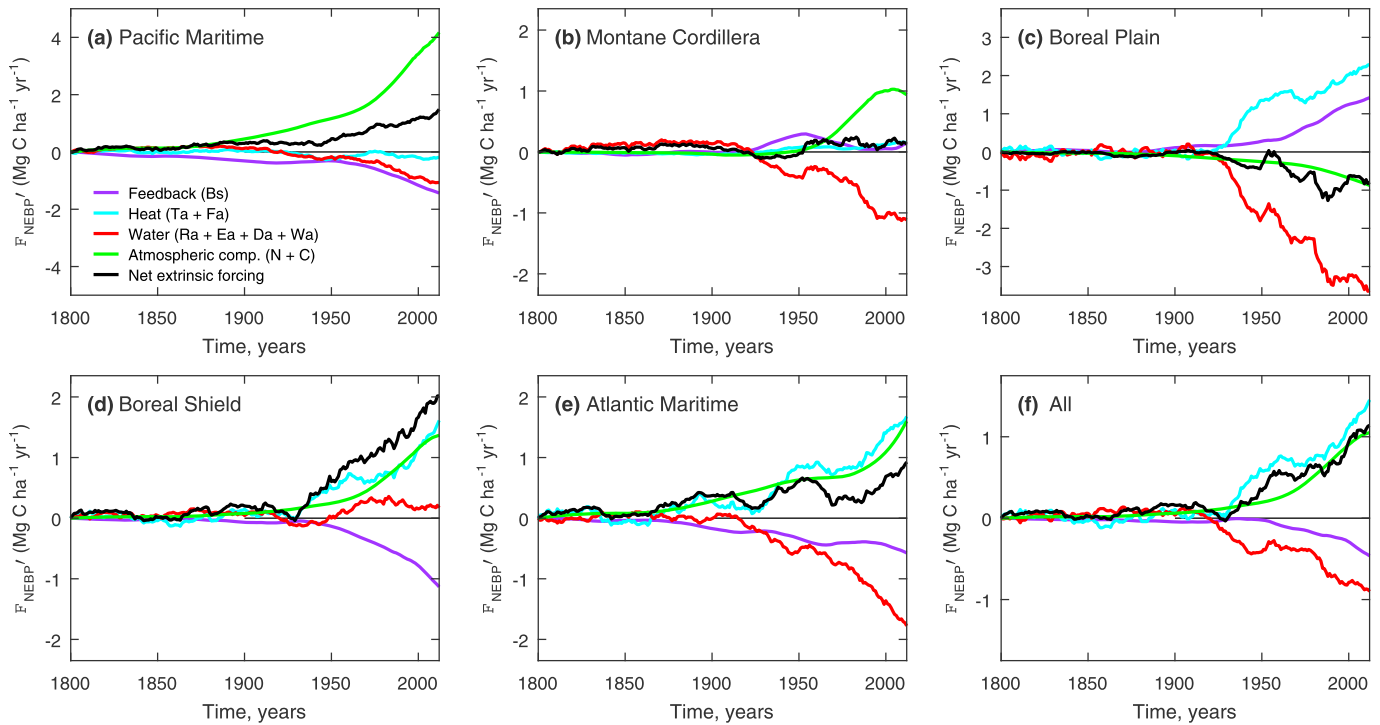
Figure 6. Time series of 30 year moving average dynamic landscape-scale extrinsic temporal forcing on net ecosystem biomass production (NEBP) derived from application of statistical models of biomass growth and biomass loss due to mortality. Values indicate the difference between how factors affected NEBP in any given year relative to how they affected predictions of NEBP in 1800. Extrinsic temporal forcings were grouped according to feedback (the change in stand biomass over time), change in heat (i.e., the net effect of changes in annual days with frost and warm-season air temperature), change in radiation and water balance (i.e., the net effect of change in incident global solar radiation, equilibrium rate of evaporation, vapor pressure deficit, and soil water content), and atmospheric composition (i.e., the net effect of change in nitrogen deposition and atmospheric carbon dioxide concentration).

changing biomass, as defined by the fitted dependence between biomass fluxes and stand biomass. Over 1801–2012, $F_{\mathrm{NEBP,ex}}'$ was positive in all regions with the exception of the Boreal Plain ecozone (Figure 6). Warming led to strong enhancement of NEBP in the boreal ecozones and the Atlantic Maritime ecozone, and negligible enhancement in the Pacific Maritime and Montane Cordillera ecozones. Strong negative forcing from the collective effect of changes in water balance-related variables was evident in all ecozones except the Boreal Shield. Changes in atmospheric composition led to strong positive forcing on NEBP in all regions except the Boreal Plain ecozone. The prediction of increasing stand biomass in ecozones with long-term positive net extrinsic forcing translated into significant negative forcing on growth and positive forcing on mortality, which drove decreases in NEBP ranging from 0.6 to 1.7 Mg C ha^{-1} yr^{-1} (Figure 6). Conversely, predicted decline in stand biomass in the Boreal Plain ecozone (Figure 6c) caused by negative long-term net extrinsic forcing demonstrated negative feedback in the opposite direction, acting to counteract strong positive impacts of drought and carbon dioxide on mortality. Interestingly, the Montane Cordillera ecozone showed a transition between positive and negative forcing due to stand biomass around 1950.

4. Discussion

Studies of the time trend in observations of NEBP are rare, and attribution of variation to natural stand recovery, sampling artifacts, management, the legacy of past disturbances, and anthropogenic environmental change remains a topic in development and debate [*Caspersen et al.*, 2000; *Joos et al.*, 2002; *Krankina et al.*, 2005; *Foster et al.*, 2010; *McMahon et al.*, 2010; *Price et al.*, 2015; *Vilén et al.*, 2015; *Zhang et al.*, 2015]. In this study, we outlined a methodology for attributing temporal variation in observed biomass fluxes directly from the results of linear mixed-effects models based on the convention of temporal forcings. We additionally considered a second methodology based on dynamic simulations of the transient response to environmental change in order to better understand potential feedback responses involving the ontogeny of trees and stand competition.

We followed four principles: First, temporal forcing of the response variable for the plot sample was defined by the summation of individual forcings from predictor variables, which were calculated from the product of the sensitivity of the response variable to predictor variables, $\lambda_{y,x}$, and time trend in the predictor variables at the field plot locations, $\beta_{xt,\text{plot}}$. Second, a distinction was made between forcing of the plot sample and that of the landscape because $\beta_{xt,\text{plot}}$ is not necessarily equivalent to time trend of predictor variables across the landscape, $\beta_{xt,\text{landscape}}$. Third, we assumed that predictor variables can be grouped into net intrinsic forcing and net extrinsic forcing according to whether they represent natural patterns of stand recovery (i.e., competition, ontogeny, and succession), or environmental change, respectively. The incomplete structure of the data means that temporal forcing can arise from sampling artifacts (i.e., plot additions and removals), which were counted as intrinsic forcing. Fourth, we assumed that any sustained change in NEBP due to environmental change will lead to a change in stand biomass, influencing the intensity of competition for resources, which may act to attenuate the initial perturbation. By considering dependence of biomass fluxes on stand biomass, such feedbacks will be manifested in dynamic applications of the model where time trends in stand biomass occur.

4.1. Positive Overall Impact of Environmental Change

It was hypothesized that increasing air temperature, nitrogen deposition, and carbon dioxide concentration would cause partial alleviation of constraints imposed on tree growth by suboptimal levels of heat, nutrients, and substrate. This hypothesis was supported by analysis of static plot-scale net extrinsic forcing. Significant increases in biomass growth were indicated in all ecozones except the Boreal Plain, where there was no significant change (Figure 2a). However, enhancement of biomass growth only translated into significant enhancement of NEBP in the Pacific Maritime, Boreal Shield, and Atlantic Maritime ecozones (Figure 2c). Hence, increasing mortality was more than strong enough to counteract weak growth enhancement in the Montane Cordillera.

The hypothesis was also supported by analysis of dynamic landscape-scale net extrinsic forcing on NEBP. These estimates demonstrated with additional clarity that even though increases in stand biomass (in response to growth enhancement) imposed significant negative feedback responses to environmental change, they did not completely counteract the impacts of environmental change (Figure 6).

We conclude the overall impact of environmental change on NEBP from the dynamic simulations. Positive trends in NEBP in the Montane Cordillera and Boreal Plain ecozones over 1961–2011 could be misleading in the long-term context (Figures 5 and 6), so we report trends based on the simulations for the 1951–2012 period (a period that considers the quality of the climate data and the representativeness of the field plot records). Based on the mean least squares time trend in simulations of NEBP from grid cells across the five ecozones, we estimate an overall trend in NEBP of $0.78\,\text{g C m}^{-2}\,\text{yr}^{-1}$ ($1.5\%\,\text{yr}^{-1}$) (Table 2). This means that, between 1951 and 2012, NEBP increased by $48\,\text{g C m}^{-2}\,\text{yr}^{-1}$, or 90% above what it was in 1951. The high magnitude of the estimate partially reflects the dominant contribution from trends in the Boreal Shield.

It must be recognized that this constitutes a subcomponent of the processes controlling NEBP (Figure 1), as the effect of potential changes in age class distribution on NEBP was not explored. Although the reported positive trends in NEBP must have a substantial impact on the cycling of forest carbon, we caution that the overall impact on the greenhouse gas balance of Canada's forest sector will depend additionally on environmental impacts on disturbances and dead organic matter dynamics. Some of the same factors that enhance tree growth may also accelerate decomposition rates, with the net effect of the combined changes still highly uncertain [*Kurz et al.*, 2013].

The magnitude of trend estimates remains highly uncertain and should be interpreted with caution. High interannual variability at the regional scale (Figure 5), for example, means that trend estimates can be highly influenced by the choice of short time periods. Although extensive effort was taken to include all available data, inventory programs were not collected continuously through space and time. For example, placement of field plots across the Boreal Shield is highly uneven. Although considerable attention was given to the intrinsic factors that are readily available, it remains difficult to assess the impact of human activity [*Krankina et al.*, 2005; *Erb et al.*, 2013], although we note that only a very small fraction of the study area has any history of human activity beyond cutting. Lastly, future studies could benefit from gaining a better understanding the extent to which field plot records are representative of catastrophic mortality.

Table 2. Comparison of Trends in Stand-Level Net Ecosystem Biomass Production (NEBP) Reported by Observation-Based Studies[a]

Region	Period	Actual Trend $(g\,C\,m^{-2}\,yr^{-1}\,yr^{-1})$	Relative Trend $(\%\,yr^{-1})$	Source
		Boreal Forests		
Western Canada[b]	1963–2008	−5.1	−2.6	*Ma et al.* [2012]
Western Canada (DEC)[c]	1958–2011	-3.5		*Chen and Luo* [2015]
Western Canada (ESC)[c]	1958–2011	−2.1		*Chen and Luo* [2015]
Western Canada (MIX)[c]	1958–2011	−3.2		*Chen and Luo* [2015]
Western Canada (LSC)[c]	1958–2011	−6.9		*Chen and Luo* [2015]
Boreal Plain, Canada	1961–2011	−1.1	−2.0	This study ($F_{NEBP,ex}$)
Boreal Plain, Canada	1951–2012	−0.8	−0.8	This study ($F_{NEBP,ex}'$)
Eastern Canada[b]	1971–2006	0.9	32.7	*Ma et al.* [2012]
Boreal Shield, Canada	1961–2011	4.6	4.6	This study ($F_{NEBP,ex}$)
Boreal Shield, Canada	1951–2012	2.0	5.8	This study ($F_{NEBP,ex}'$)
Finland[d]	1962–2008	1.4	2.3	*Kauppi et al.* [2014]
Sweden[e]	1925–1990	0.8	0.9	*Elfving et al.* [1996]
Sweden	1970–2010		1.2	*Binkley and Högberg* [2016]
		Temperate Forests		
Pacific Maritime, Canada[f]	1959–1998		0.4 to 0.6	*Hember et al.* [2012]
Pacific Maritime, Canada	1961–2011	3.4	0.9	This study ($F_{NEBP,ex}$)
Pacific Maritime, Canada	1951–2012	5.1	2.1	This study ($F_{NEBP,ex}'$)
Plantations, Japan	1980–2005		0.3 to 0.9	*Fang et al.* [2014]
Plantations, Germany[g]	1960–2000		0.3, 0.8	*Pretzsch et al.* [2014]
Montane Cordillera, Canada	1961–2011	−1.0	−0.6	This study ($F_{NEBP,ex}$)
Montane Cordillera, Canada	1951–2012	−0.7	−0.4	This study ($F_{NEBP,ex}'$)
Atlantic Maritime, Canada	1961–2011	2.7	2.7	This study ($F_{NEBP,ex}$)
Atlantic Maritime, Canada	1951–2012	3.1	6.7	This study ($F_{NEBP,ex}'$)
		Canada		
All five ecozones	1951–2012	0.8	1.5	This study ($F_{NEBP,ex}'$)

[a]Relative trend for results from this study was calculated as $(NEBP_{t1} - NEBP_{t0})/NEBP_{t0} \times 100/\Delta t$. Estimates of $F_{NEBP,ex}$ do not account for feedback responses to changing stand biomass and reflect conditions at the field plot locations, while estimates of $F_{NEBP,ex}'$ account for feedback responses to stand biomass, as controlled by approximations of landscape variation in disturbances.
[b]Reproduced by digitizing time series in Figure 2, panel B, relative trend calculated as $(NEBP_{t1} - NEBP_{t0})/NEBP_{t0} \times 100/\Delta t$.
[c]DEC: deciduous broadleaf stands; ESC: early-successional coniferous stands; MIX: mixed stands; LSC: late-successional coniferous stands.
[d]Converted assuming forest area is 20.25 Mha, dry mass production is $0.5 \times$ volume increment, and carbon content is $0.5 \times$ dry mass.
[e]Converted assuming dry mass production is $0.5 \times$ volume increment and carbon content is $0.5 \times$ dry mass.
[f]Just coastal Douglas-fir and western hemlock.
[g]Spruce and beech.

4.2. Regional Differences in Trends

Results for all ecozones indicated significant changes in NEBP. Whereas the overall change in NEBP over 1951–2012 was estimated to be 90%, change varied considerably among ecozones: 413% (Atlantic Maritime), 357% (Boreal Shield), 128% (Pacific Maritime), −25% (Montane Cordillera), and −47% (Boreal Plain). These results suggested an association between trends and regional hydrology. The Pacific Maritime, Boreal Shield, and Atlantic Maritime ecozones all showed positive trends in NEBP and are all dominated by humid or hyperhumid lands. The Montane Cordillera ecozone spans a wide range of hydrological conditions (only 70% hyperhumid and humid climates) and showed no long-term trend in NEBP. The Boreal Plain is dominated by subhumid-dry and semiarid lands and exhibited decline in NEBP. Calculating the mean trend in NEBP over 1951–2012 for grid cells for each of Thornthwaite's hydrological classes suggested that strong growth enhancement occurs in hyperhumid and humid classes and transitions from enhancement to decline between subhumid-wet and subhumid-dry classes (Figure 7). Hence, although we report an increase in NEBP of southern ecozones of Canada, it is important to consider strong regional differences, which include decline in NEBP over vast expanses of western Canada. The results are qualitatively similar to conclusions for boreal forests spanning broad range of hydrological conditions in Alaska [*Beck et al.*, 2011]. These results may suggest that large expanses of northern forests, historically located at the boundary
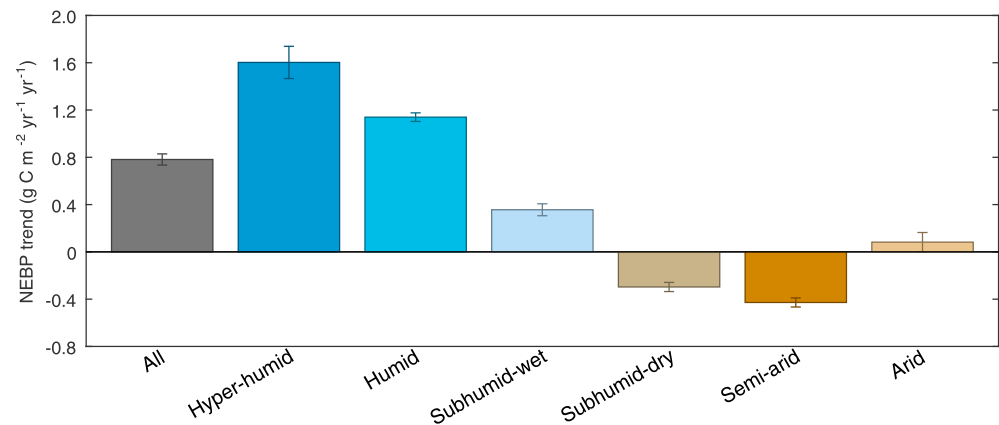
Figure 7. Summary of 1951–2012 trends in net ecosystem biomass production (NEBP) based on dynamic simulations across southern ecozones of Canada organized by Thornthwaite's hydrological classes. Error bars indicate the 95% confidence intervals.

between wet and dry climates, may be at high risk of abruptly transitioning from being a strong biomass sink to a strong source under continuation of current increasing trends in evaporative demand. Further insight could be gained by testing whether this general pattern holds true when warm temperate and tropical forest biomes are considered.

4.3. Sensitivity to Climate Change and Atmospheric Composition

We argue that the decision to distinguish climate normals and anomalies as intrinsic and extrinsic sources of variation provided a more conservative means of testing the impacts of environmental change, as it helps to ensure sample instability was not confused for environmental change. Yet it also complicates the interpretation of climate forcings because they strictly reflect the response to deviations from the mean, rather than actual variation. We also caution that the individual climate forcings were affected by moderate multicollinearity. Lastly, we must recognize that observations of biomass fluxes over 5 or 10 year remeasurement intervals fail to resolve interannual variability and, therefore, may not effectively represent the impact of years with extreme climate. These three features may partially explain some surprising findings.

For example, we did not expect large fractions of the increasing trend in mortality to be attributed to carbon dioxide (Figure 2b). However, if carbon dioxide leads to growth enhancement, then it likely accelerates density-dependent mortality [*Pretzsch et al.*, 2014] and density-independent mortality [*Lines et al.*, 2010; *Holzwarth et al.*, 2013; *Bennett et al.*, 2015; *McDowell and Allen*, 2015; *Hember et al.*, 2016]. Alternatively, a large number of adverse physiological effects of carbon dioxide have also been identified by previous studies. Lastly, we must consider the possibility that it reflects long-term antecedent responses to worsening droughts that are falsely attributed to carbon dioxide.

Other results on environmental sensitivity were less surprising. Warming trends had a positive effect on growth across the boreal ecozones and negative effect on mortality across four ecozones. This supports the generalization that boreal forests operate, on average, at suboptimal temperature [*Way and Oren*, 2010; *Kauppi et al.*, 2014]. Increasing vapor pressure deficit consistently had negative effects on NEBP. This is consistent with strong regulation of gas exchange by feed-forward responses of stomata to vapor pressure deficit [*Schulze*, 1986; *Franks et al.*, 1997; *Oren et al.*, 1999; *McAdam and Brodribb*, 2015] and close relationships between humidity and growth at scales ranging from individual to region [*Hogg et al.*, 2008; *Köcher et al.*, 2012; *Jiang et al.*, 2014]. Results also suggested that radiation may be limiting in eastern regions and excessive in the Montane Cordillera and Boreal Plain ecozones. In the latter, we speculate that negative indirect effects of radiation on evaporative demand exceed any direct benefit of higher radiation for photosynthesis. The negligible role of decreasing soil water content perhaps reflects the absence of nonlinearity considered in the statistical models, as soil water content is only expected to have negative effects as it approaches zero in most cases.

Increasing carbon dioxide concentration consistently had a positive effect on growth across all ecozones, consistent with the mean response of trees to carbon dioxide enrichment under experimental conditions

[*Idso and Idso*, 1994; *Wullschleger et al.*, 1995; *Saxe et al.*, 1998; *Norby et al.*, 1999; *Kirschbaum and Lambie*, 2015]. Nitrogen deposition had weak positive and insignificant impacts on NEBP, which is qualitatively consistent with many other studies that suggest weak positive impacts [*Nadelhoffer et al.*, 1999; *Thomas et al.*, 2010; *de Vries et al.*, 2014; *Gundale et al.*, 2014]. Responses were strongest in the Montane Cordillera ecozone, where nitrogen deposition is low and nitrogen fertilization experiments show mixed results [*Mika et al.*, 1992; *Kishchuk et al.*, 2002; *Brockley*, 2010]. In that ecozone, the decrease in nitrogen deposition associated with the introduction of regulations to reduce industrial emissions was strong enough to attenuate the forcing attributed to atmospheric composition after 1990 (Figure 6b). An absence of overall effects in the boreal ecozones is consistent with recent experiments [*Gundale et al.*, 2011; *D'Orangeville et al.*, 2013].

4.4. Significant System Feedbacks

The assumed effects of competition and ontogeny of trees on stand-level forest productivity were represented in these models according to the effect of stand biomass on growth and mortality. The universal positive dependence of biomass loss due to mortality on stand biomass is intuitive; studies overwhelmingly express mortality in relative terms as a percent loss of biomass. Negative effects of stand biomass on growth (found in the three most productive ecozones) are a bit more puzzling and not as commonly discussed in the literature. We speculate that negative dependence between growth and stand biomass occurs because rates of tree recruitment decrease strongly as stand biomass increases and secondly because of the universal decrease in growth efficiency in perennial plants associated with the decreasing ratio between live and dead tissues [*Paine et al.*, 2012] and various other physiological limitations [*Ryan et al.*, 1997].

Though substantial in magnitude, the negative feedbacks did not negate positive responses to environmental change. As of 2012, growth enhancement of tree biomass across Canada's wet southern ecozones, therefore, shows no sign of saturation. Further insight could be gained by applying similar models in temperate Europe, where it is suspected that biomass fluxes have begun to saturate [*Nabuurs et al.*, 2013]. The strength of the relationships varied between the temperate and boreal ecozones (Figure S7). The fact that sensitivities of growth and mortality to stand biomass, themselves correlate with stand biomass, suggest that the relationship may change under extreme environmental change scenarios. The assumption of stationarity in the relationship within ecozones, therefore, may lead to bias in the feedbacks when applied to future scenarios of extreme environmental change. As the relationships were strongly influenced by outlier sensitivity in the Pacific Maritime ecozone, it stands to reason that the stationarity assumption may be least valid in regions near the 0°C isotherm in cold-season temperatures.

4.5. Comparison With Other Studies

Relative trends for the 1961–2011 period were mostly consistent with previous studies performed in Canada [*Hember et al.*, 2012; *Ma et al.*, 2012; *Chen and Luo*, 2015; *Zhang et al.*, 2015]. An important exception was the greater positive trend in NEBP reported in this study for the Boreal Shield compared with that reported for eastern Canada of *Ma et al.* [2012]. This discrepancy could reflect either differences in sampling or differences in the design of models. Our study considers an order of magnitude more interval measurements and additionally attributes a large component of temporal variation to change in stand biomass.

Large growth enhancement over wet regions of Canada is consistent with global vegetation models [*Peng et al.*, 2009; *Friend et al.*, 2013] and trends in Landsat composite greenness [*Ju and Masek*, 2016]. Evidence of growth enhancement in boreal and temperate forests located in wet climates is also consistent with evidence of growth enhancement from other regions [*Fang et al.*, 2014; *Kauppi et al.*, 2014; *Pretzsch et al.*, 2014] and from analysis of forest stock change in northern regions outside of Canada [*Pan et al.*, 2011].

Our results are similar to evidence of a divergence in trend direction between wet and dry regions of the boreal forest [*Beck et al.*, 2011] and reinforce the conclusions from *Ma et al.* [2012] and *Chen and Luo* [2015] that stand-level NEBP decreased over the last 60 years in dry (i.e., subhumid and semiarid) regions of western Canada. In the Montane Cordillera ecozone, this was driven by weakening of growth enhancement due to higher water stress and strong increases in mortality. In the Boreal Plain ecozone, decline in NEPB was driven by preclusion of growth enhancement and strong increases in mortality. It is becoming apparent that tree growth and mortality were strongly affected by extreme drought events in many regions of western Canada [*Hogg et al.*, 2008; *Hember et al.*, 2016].

In a similar analysis of field plots in western Canada, *Zhang et al.* [2015] concluded that the historical trends in forest productivity were primarily driven by competition, whereas extrinsic factors were of secondary importance. The authors suggested that studies have been conducted with "surprisingly little attention being paid to the possible effects of endogenous processes" but neglected to recognize studies within and adjacent to their study area that strongly emphasized the need to decompose overall variation of forest productivity into intrinsic and extrinsic components [*Hember et al.*, 2012; *Wu et al.*, 2014]. They proceeded to test for time trends by fitting statistical models to relative growth rate of basal area without explicit consideration of the covariance between time and intrinsic factors, including stand age and size. Tree size needs to be a covariate in models of growth, regardless of whether one works with absolute or relative growth rates. Thus, we question whether decrease in relative growth rate within broad age classes reflects change in tree size, given that growth efficiency consistently decreases in perennial plants.

Here we attempted to account for intrinsic variation that emerges from the combined effect of competition and succession, ontogeny of the survivors, and sample instability. The former two components describe natural stand dynamics, while the latter represents artificial variation that is attributed to addition and removal of plots from the (incomplete) sample, which can affect temporal trends if plot additions and/or removals alter the average site quality or climate of the sample through time. We additionally recognized that the forcing imposed by competition for resources can fundamentally differ between the plot samples and landscapes. For example, consider the sample for the Pacific Maritime ecozone, where stand biomass increased substantially over time (Figure 4a). Inferring the influence of competition on NEBP from $\beta_{Bt,\text{plot}} \times \lambda_{M,B}$ gives a false impression that competition has a strong impact on transient variability. However, it arises only because mean sample properties, including stand age and biomass, were allowed to drift over time by the measurement program. The age class distribution of landscapes is not changing by the same magnitude but rather at a rate dependent on disturbance regimes [*Kurz et al.*, 1995; *Kurz and Apps*, 1999; *Williams et al.*, 2012]. Based on applications of the dynamic model, in which stand biomass is governed by both environmental change and realistic landscape-scale disturbances, we argue that significant temporal variability of regional forest growth, mortality, and NEBP was fundamentally driven by environmental change and secondarily mediated by negative feedback mechanisms likely involving the intensity of competition for site resources and finite limits on the maximum size and longevity of survivors.

5. Conclusions

Taking the most conservative approach we could devise and considering an unprecedented number of field plot remeasurements, statistical models indicated that environmental changes accelerated the rate at which biomass accumulates in intact forest stands across southern ecozones of Canada by 90% over 1951–2012. This anthropogenic biomass sink was confined to wet regions where a combination of warming and increasing carbon dioxide concentration drove enhancement of growth and suppression of mortality. The biomass sink in dry regions of western Canada decreased, suggesting that large expanses of boreal and temperate forest biomes, historically located at the boundary between wet and dry climates, may be at high risk of decline under continued increases in evaporative demand. These results have important implications for stand management and the greenhouse gas balance of Canada's forest sector.

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