Spatial and topographic trends in forest expansion and biomass change, from regional to local scales

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Abstract

Natural forest growth and expansion are important carbon sequestration processes globally. Climate change is likely to increase forest growth in some regions via CO_2 fertilization, increased temperatures, and altered precipitation; however, altered disturbance regimes and climate stress (e.g. drought) will act to reduce carbon stocks in forests as well. Observations of asynchrony in forest change is useful in determining current trends in forest carbon stocks, both in terms of forest density (e.g. Mg ha^{-1}) and spatially (extent and location). Monitoring change in natural (unmanaged) areas is particularly useful, as while afforestation and recovery from historic land use are currently large carbon sinks, the long-term viability of those sinks depends on climate change and disturbance dynamics at their particular location. We utilize a large, unmanaged biome (>135 000 km^2) which spans a broad latitudinal gradient to explore how variation in location affects forest density and spatial patterning: the forests of the North American temperate rainforests in Alaska, which store >2.8 Pg C in biomass and soil, equivalent to >8% of the C in contiguous US forests. We demonstrate that the regional biome is shifting; gains exceed losses and are located in different spatio-topographic contexts. Forest gains are concentrated on northerly aspects, lower elevations, and higher latitudes, especially in sheltered areas, whereas loss is skewed toward southerly aspects and lower latitudes. Repeat plot-scale biomass data ($n = 759$) indicate that within-forest biomass gains outpace losses (live trees >12.7 cm diameter, 986 Gg yr^{-1}) on gentler slopes and in higher latitudes. This work demonstrates that while temperate rainforest dynamics occur at fine spatial scales (<1000 m^2), the net result of thousands of individual events is regionally patterned change. Correlations between the disturbance/establishment imbalance and biomass accumulation suggest the potential for relatively rapid biome shifts and biomass changes.

Keywords: climate change, disturbance, forest change, North America, temperate rainforest biome

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Introduction

Forests comprise a significant amount of the global carbon pool (861.1 ± 66.4 Pg) and are currently a significant carbon sink (1.11 ± 0.8 Pg yr^{-1}; Pan *et al.*, 2011a). This sequestered carbon is a critical part of the carbon cycle and potentially an important offset to anthropogenic emissions. Much of this can be attributed to afforestation (e.g. afforestation in China; Piao *et al.*, 2009) and shifting land use practices (e.g. recovery from historic land clearing; Birdsey *et al.*, 2006; Zhang *et al.*, 2012). Global climate change and increasing N deposition are also expected to alter forest biomass substantially (Pan *et al.*, 2011a), although the direction and magnitude of change are difficult to predict due to competing factors. While N deposition and carbon fertilization may increase growth rates in many locations (Hember *et al.*, 2012; Zhang *et al.*, 2012), increased evaporative demand, altered precipitation patterns, and altered disturbance regimes may decrease forest

biomass in others (Van Mantgem *et al.*, 2009). The development of an improved understanding of forest dynamics and forest extent change is vital for supporting accurate assessments of changes in forest biomass and improving future monitoring efforts.

While the overall carbon balance in a forest is a function of afforestation, historic and current management, and natural dynamics, understanding patterns and trends in unmanaged (i.e. 'natural') forests are particularly important. Afforestation may serve to compliment natural forest biomass accumulation, but in some cases may mask a decline: For example, China has seen a net gain in forested carbon stocks via afforestation which mask a slight decline in natural forests (Fang *et al.*, 2001). Similarly, regrowth from historic logging in the United States (Pan *et al.*, 2011b) is currently offsetting a decline due to increasing disturbances in many western states (Zhang *et al.*, 2012). Predicting global and regional carbon balance in the future, understanding how afforestation efforts may fare in the future, and anticipating the sustainability of current efforts requires an improved understanding of how natural forests (e.g.

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forests not managed historically or presently) respond to climate change.

Differences in the relative magnitude of forest disturbance, establishment, growth, and mortality is the mechanism by which unmanaged forest biomass and distributions will shift in response to a warming climate (Dale *et al.*, 2001; Johnson & Miyanishi, 2010; Vanderwel & Purves, 2014). Identifying where ecosystem dynamics are in disequilibrium is a means to determining where change is being manifested on the landscape, its magnitude, and relative rate, and requires understanding the spatial distribution of disturbance and establishment events and field plots which can record the magnitude of change. In a hypothetical stable system, the spatio-topographic distribution and magnitude of those fine-scale disturbance/establishment events would be similar at appropriately broad spatial and temporal scales (large enough to encompass many individual events while still comparable in terms of disturbance drivers, e.g. climate, species composition, Johnson & Miyanishi, 2010), although this requires the assumption that enough observations of change can be made to adequately describe ongoing spatiotemporal dynamics for the system under study (see Materials and methods). Derivations from this hypothetical stable system should be observable as differences in the spatial and topographic distribution of disturbance and recovery events.

While the importance of forests as a carbon sink is well recognized, understanding how that carbon is changing in response to climate change at multiple scales (both in terms of forest extent and biomass density) is difficult. Here, we explore the relationships between latitudinal and topographic patterns of forest change (disturbance and recovery) and forest biomass change in a significant carbon storehouse, the North Pacific temperate rainforests. If similar drivers are controlling each process, then natural systems may respond rapidly to climate change (e.g. an increase in biomass density and an increase in extent in areas where the warming climate favors forests). If not, then forest carbon stock response to climate change may be attenuated (e.g. a warming climate favors denser forests but also more disturbance/less recovery). As the strength and direction of this relationship may vary by location, such an analysis must be carried out in a spatially explicit fashion. Here, we address the following questions:

1 Are spatial patterns of forest change similar to spatial patterns of biomass change?

2 Are the topographic distributions of forest change similar to the topographic distributions of biomass change?

3 How are the temperate rainforests of the North Pacific changing in terms of aboveground, live biomass,

and where are those changes most significant? Do these changes correspond with previous hypotheses about the effects of climate change on this substantial carbon pool?

Materials and methods

Study region

Southeast Alaskan temperate rainforests provide the unique opportunity to look at a consistent system, in terms of species, climate, and disturbance regimes across a broad latitudinal gradient, which allows us to explore the relationship between disequilibrium in forest change and forest biomass changes. In addition, they are ecologically significant. Temperate rainforests contain the world's densest stocks of carbon (Leighty *et al.*, 2006; Keith *et al.*, 2009), a variety of important ecosystem services (Brandt *et al.*, 2014), and a multitude of endemic species (Cook *et al.*, 2001). They are also experiencing (and will experience) profound changes due to climatic warming (Meehl *et al.*, 2004; Wolken *et al.*, 2011; Orians & Schoen, 2013). Alaskan temperate rainforests contain an estimated $>2.8 \pm 0.5$ Pg C in biomass and soil, equivalent to $>8\%$ of the C in all the forests of the contiguous United States (Leighty *et al.*, 2006). Despite the broad latitudinal gradient, the climate and species composition are similar across the region, facilitating a regional analysis (DellaSala, 2011). Temperatures are mild and precipitation uniformly high (cool maritime, Köppen climate classification Cfb) due to the moderating oceanic influence. Species diversity is relatively low and composition is similar across the region as well, primarily *Picea sitchensis* – *Tsuga heterophylla* forests. *Pinus contorta* var. *contorta*, *Thuja plicata,* and *Cupressus nootkatensis* are found in boggy locations throughout the region, and *Alnus viridis* is often found in recently disturbed locations. Critically, disturbance drivers are consistent across the region: predominately fine-scale, non-episodic mortality events, primarily a function of small gaps forming through stem decay, wind, or snow damage (Ott & Juday, 2002; Hennon & McClellan, 2003). There are no indications of historic fire or large-scale insect outbreaks (including in the paleo record), and major windstorms (Harris, 1999; Kramer *et al.*, 2001; Orians & Schoen, 2013) and landslides (Swanston, 1974; Buma & Johnson, 2015), also rare, affect limited spatial regions (exposed southerly slopes and steep terrain) consistently across the region. Because the small-scale gap dynamics are relatively frequent when considering the entire region, using a space-for-time conceptual framework a good description of the spatial-topographic distribution of the regional disturbance regime can be constructed. This assumption and generalization allows us to draw empirically based conclusions regarding the biomass trajectory of this large region while also incorporating disturbances, a task which would be difficult in other systems where disturbance patterns, species, and change are more variable (e.g. infrequent, severe fires).

Current expectations for the region (excluding historic or currently harvested areas) are expansion and accretion of biomass (Wolken *et al.*, 2011), with the region operating as a potentially significant carbon sink. This is expected because of

observed increases in temperature driving increased growth, declining snowpacks allowing for expansion of forests at treeline, a lack of drought stress due to continuous, high precipitation, and the absence of fire. Testing these expectations, however, is difficult, because of the inaccessible nature of the terrain and the lack of infrastructure (the majority of the region is not on a road system). Here, we use a combination of remotely sensed resources and repeat plot measurements to determine where forest change is occurring and the magnitude of that change in terms of biomass.

Forest change map

Using 30 m resolution forest loss and gain maps (Hansen et al., 2013), the distribution of forest loss events was contrasted against establishment events (where 'events' are contiguous patches) over the entire temperate rainforest biome of southeast Alaska (135 000 km^2; regional scale) and by 1° latitudinal bands (subregional scale). To isolate natural dynamics, areas of historic and current logging were removed prior to analysis. Maps were built from available satellite imagery (2000–2012) and represent either the loss or gain of forest cover over that time period. This layer was then limited to locations within the defined perhumid temperate rainforest biome (Ecotrust, 1995) between latitude 54.7° (Alaska–Canada border) and 59° where harvest maps were available; harvested areas (either active loss or regrowth from historic harvesting) were not considered in this analysis (USFS, 2013). Private lands (a minor component of the landscape) do not consistently track forest harvest spatially and were excluded. Spatially contiguous gain or loss pixels were combined into single polygonal 'events;' note that a single patch expanding over multiple years is considered a single event. Accuracy of the forest change map was assessed manually via high resolution remote sensing (overall accuracy 91%), see Data S1.

Spatio-topographic data

Topographic variables were calculated from the ASTER Global DEM V2 dataset. The ASTER dataset has reasonable accuracy (NASA, 2011), with a mean error of 0.94 m for evergreen forest. Aspect was transformed to 0 N, 180 S (E/W equivalent) to avoid circularity. Exposure was calculated for the entire study area using methodology calibrated in southeast Alaska (Kramer *et al.*, 2001) and represents topographic sheltering to regional prevailing winds [southeast, south, southeast, (Harris, 1999)]. 2001 landcover maps (Homer *et al.*, 2007) were used to correspond to the beginning of the observation period. A resolution of 30 m was used throughout, which while useful for disturbances at meso- and broad scales, limits our ability to identify small, subpixel single-tree mortality; this is addressed using FIA data.

FIA Data

To investigate change at finer scales (e.g. single-tree mortality) and tie observed spatial patterns to biomass change, US Forest Service Forest Inventory and Analysis (FIA) data within the region were investigated (*n* = 1465 plots, with 759 forested plots; ~500 m^2). FIA plots are established on a regular grid across all locations (regardless of ownership), provide repeated measurements of biomass accumulation and mortality at regular intervals, and are designed to provide an unbiased assessment of forest biomass change at regional scales, along with appropriate measures of uncertainty. FIA plots were partitioned according to their spatio-topographic position to assess changes in biomass in the same fashion as changes in forest extent and disturbance patterns from the remote sensing analysis.

Remeasured inventory data include all trees above 12.7 cm diameter; biomass change is calculated based on increases in size on trees within each plot, observed mortality, and recruitment of smaller trees into the >12.7-cm diameter pool. Soil and dead material was not remeasured and thus not available for this spatially explicit design. Plots were revisited between 2004 and 2010; only plots with no history of management were included here. Wilderness areas were only visited once and thus not used for biomass difference calculations; rather observed change was scaled by relative area to include wilderness areas for the final net totals. Estimates were produced using the standard national method (Bechtold & Patterson, 2005).

The use of remeasured FIA plots allows us to: (1) characterize the implications of observed forest disturbance by directly tying change to biomass totals, (2) infer causal agents by noting species differences, and (3) observe single-tree mortality events, which would likely be missed by the 30-m resolution satellite record. Thus, we can monitor the entire spatial spectrum of forest change, from single tree to large events, and compare spatio-topographic patterns across multiple scales of investigation.

All statistical and geospatial analyses were conducted in R. Significance of any skew in the distribution, indicating topographic bias in disturbance or gain, was calculated using D'Agostino K^2 tests (D'Agostino *et al.*, 1990). It should be noted that complex relationships (e.g. bimodal distributions) are not well suited to statistical and significance summaries and distribution results should be interpreted primarily via the histograms/density plots.

Results

Results indicate that the temperate rainforests of southeast Alaska are growing, shifting their distribution and density at large spatial scales through thousands of small events (loss: >17 400 patches; gain: >27 107 patches; Fig. 1). This change can be observed in three ways: (1) more spatially extensive establishment events than loss events, (2) differing spatial and topographic patterns in loss vs. gains, and (3) biomass accumulation within forested areas outpacing mortality.

Total area

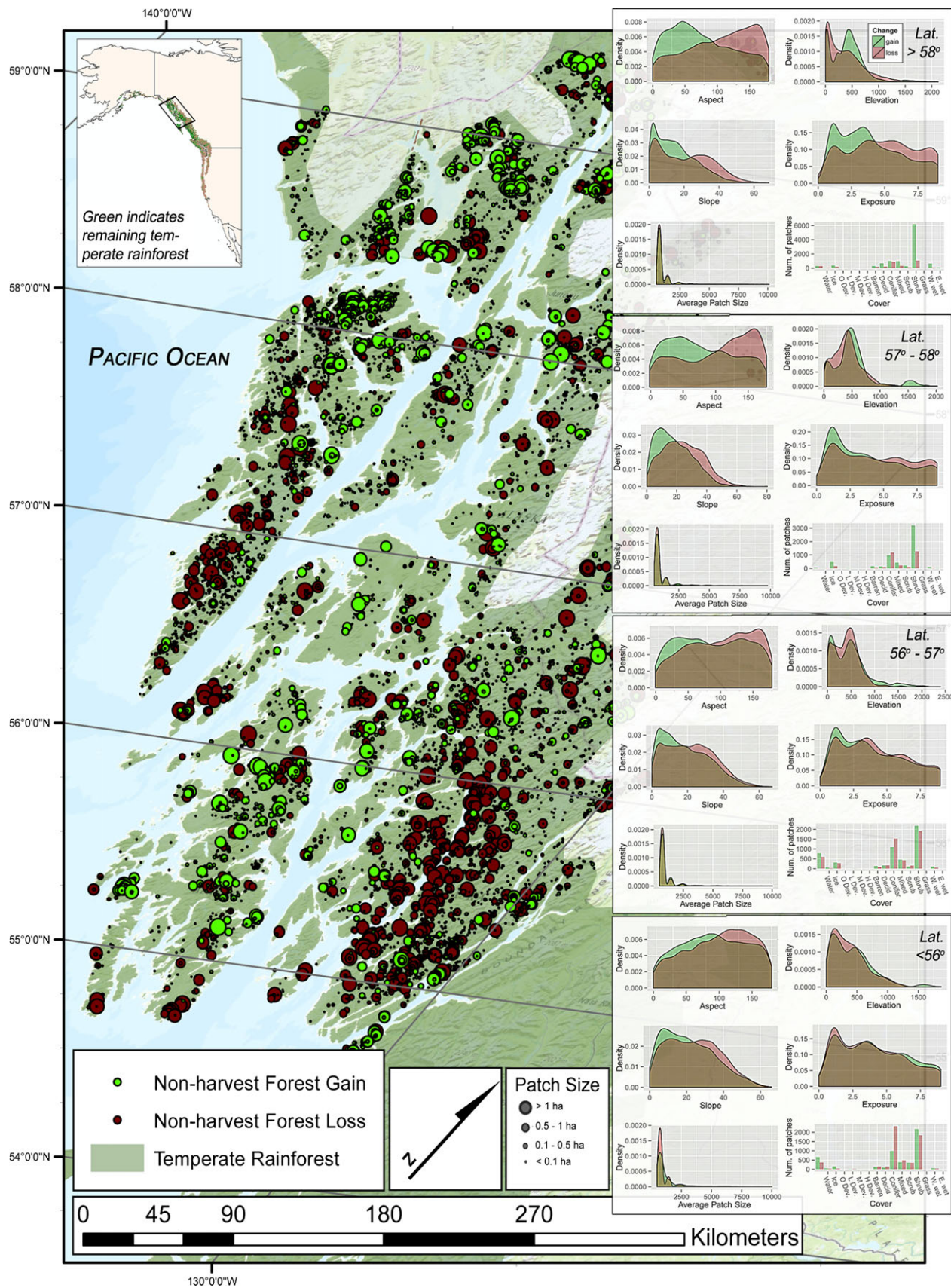At the regional scale, ~25% more area was gained than lost, although that difference was not distributed

Fig. 1 Distribution of forest loss/gain events and topographical distributions of gain and loss. The North Pacific perhumid rainforest zone of SE Alaska, with gain and loss events. Events located in harvested area, or private land, are not shown. Density plots: Subregional density plots (corresponding to latitudinal bands in main map) are shown for each topographic variable. Topographic disequilibrium can be seen by non-overlapping distributions, such as in the north, where forest gain is skewed toward northerly facing slopes (note aspect transformation, see Materials and methods); loss toward southerly. Cover abbreviations: O/L/M/H Dev: Open, low, medium, high developed; Decid: Deciduous; Mixed: Mixed forest, W. Wet: Woody wetlands; E. Wet: Emergent herbaceous wetlands. Unlabeled column is undefined cover types, primarily located along the US–Canadian border.

evenly, with more gains in the north. Losses are, in general, evenly distributed, although a slight skew toward the south is apparent, where they slightly outweigh gained forest (Fig. 2). The relative difference peaks sharply in the north, where gained areas greatly outpace losses and are concentrated primarily in shrubland (such as above treeline, areas exposed by receding glaciers, and floodplains; Fig. 3). In all cases, the average patch size (for both losses and gains) is small, on the order of 1000 m^2 (Table 1).

Topographic differences

Forest losses and gains are distributed differently for the topographic variables considered ($P < 0.05$), with the strongest differences seen in aspect and slope (subregionally: Fig. 1; regionally: Fig. 3). Forest gains are essentially uniformly distributed with respect to aspect in the south, but take on a skew toward northerly aspects in the northerly portions of the rainforest. In contrast, forest loss events are skewed toward southerly aspects across the region, although the effect is strongest in the north. Gains and losses are distributed similarly across elevation; regional medians: 391 m (loss), 441 m (gain) except in the far north, where gained area is distributed biomodally, with most occurring either at sea level or around 500-m elevation (Fig. 1). Gains were typically seen on lower slopes throughout the region (median = 15.7 deg), and losses more uniformly distributed across slopes (median 22.1 deg). Establishment and losses relative to wind exposure were broadly similar except in the north, where gains were skewed toward sheltered locales and loss toward exposed areas.

Biomass change

Within the previously forested areas on the landscape, there was an estimated net increase in biomass of 0.24 Mg ha^{-1} yr^{-1} (SE 0.19 Mg ha^{-1} yr^{-1}), or approximately 985.5 Gg per year across the preexisting forest (4 403 000 ha; Table 2). Fine-scale, single-tree mortality occurred (~1.371 Mg ha^{-1} yr^{-1}, SE: 0.156 Mg ha^{-1} yr^{-1}), but was more than compensated for by growth of remaining individuals (1.523 Mg ha^{-1} yr^{-1}, SE:
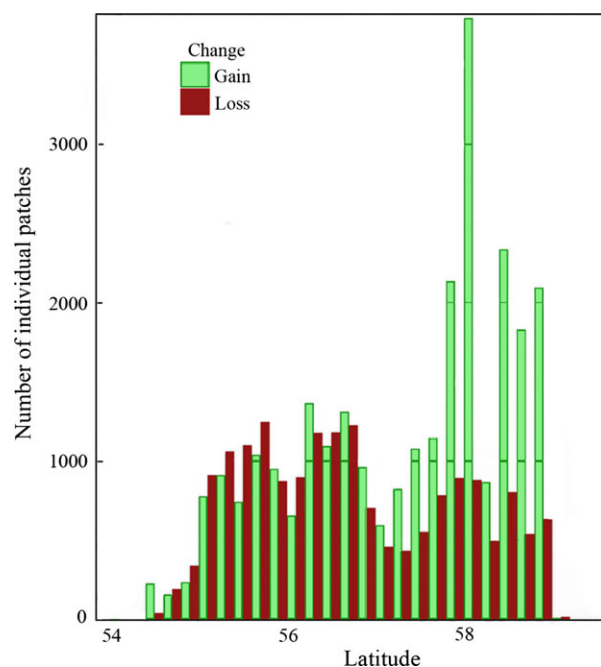

Fig. 2 Summary of latitudinal distributions of losses and gains in the North Pacific perhumid rainforest. In sum, there are 17 400 individual patches of forest loss and 27 107 patches of forest gain (excluding harvest and private landholdings). While forest loss is spread across the latitudinal range, a sharp skew in forest gain to the north indicates forest expansion in that region. Patch areal and topographic statistics given in Table 1; topographic distributions in Fig. 3.

0.12 Mg ha^{-1} yr^{-1}) and recruitment of smaller individuals into the measured pool (0.095 Mg ha^{-1} yr^{-1}, SE: 0.006 Mg ha^{-1} yr^{-1}). This estimate does not include forest expansion in previously non-forested areas (which was not measured in the FIA system) and thus is a conservative estimate of biomass accumulation.

Patterns in biomass accumulation were roughly similar to broad scale forest disturbance and establishment spatio-topographic patterning, although more variable and less significant, as heterogeneity increased at finer scales. Net accumulation was most significant in the north (0.79 Mg ha^{-1} yr^{-1}, SE 0.36 Mg ha^{-1} yr^{-1}), similar to the observed expansion patterns. Lower latitudes showed mortality roughly balanced with biomass
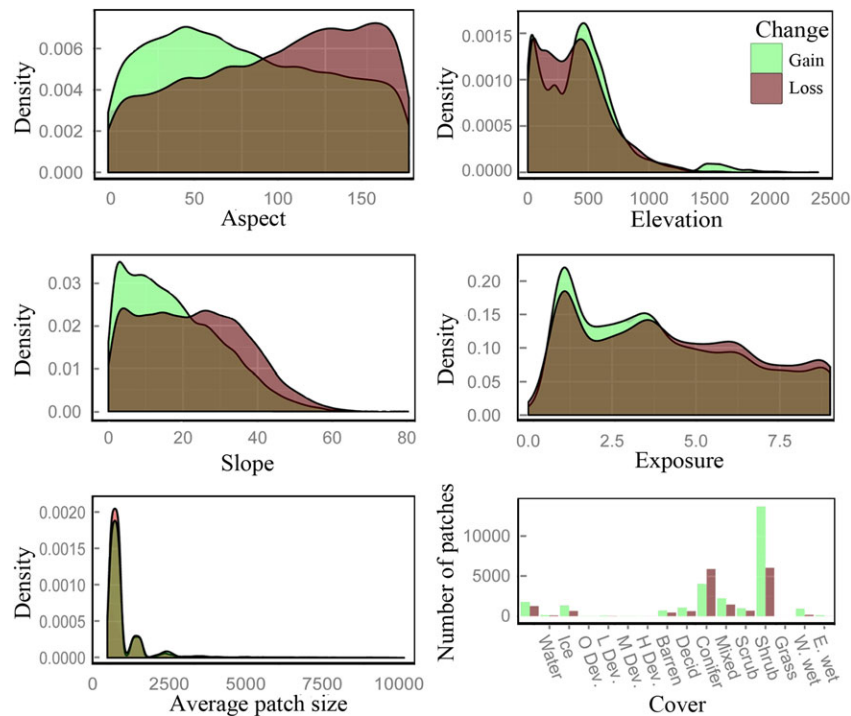
Fig. 3 Regional-scale relationship between topographic variables and forest change. Data include all points in Fig. 1. Forest loss is strongly skewed to steeper, southerly slopes, whereas gains are skewed toward shallow, northerly slopes. There is little difference in the distributions in relation to exposure or elevation at the regional scale, although a slight skew toward higher elevations is apparent in forest gain locations. A majority of the gains occur in shrublands, which includes lowlands, postglacial landscapes, and above tree-line.

Table 1 Change in forest extent and patch sizes by region and subregion

	Latitude range				
	<56°	56°–57°	57°–58°	>58°	Regional
Loss area (ha)	728	576	339	362	2006
Gain area (ha)	534	503	525	1088	2650
Patches lost	5754	5182	3116	3348	17 400
Mean patch size (ha)	0.13	0.11	0.11	0.07	0.12
Median patch size (ha)	0.07	0.07	0.07	0.11	0.07
Patches gained	5027	5386	5773	10 921	27 107
Mean patch size (ha)	0.11	0.09	0.11	0.07	0.1
Median patch size (ha)	0.07	0.07	0.07	0.1	0.07

accumulation, although variance was high. At the regional scale, biomass accumulation was biased toward low elevations (<350 m) with an estimated net change of +0.37 Mg ha^{-1} yr^{-1} (SE 0.25 Mg ha^{-1} yr^{-1}) and low slopes (<20 deg.) where biomass is increasing at a rate of 0.64 Mg ha^{-1} yr^{-1} (SE 0.19 Mg ha^{-1} yr^{-1}). In the northerly portions of the region, accumulation was highest on north slopes (Table S1), although that pattern was not significant at the regional scale (Table 2).

Discussion

Forest change is driven by disturbance, establishment, and growth. Disturbances happen at multiple scales, from single-tree mortality events at the plot scale which open up resources to the understory and reduce standing live biomass, to larger, patch-forming events which are easily discernable from the satellite record, often driven by winter storms or landslides. Establishment of forests in non-forested locations

Table 2 Change in regional biomass within existing forest across topographic context. Totals estimated from remeasured FIA plots within each group

| Group | Observed change | | | | | | | | Forest area total |
	Growth total	SE	Ingrowth total	SE	Mortality total Gg	SE	Net total*	SE	1000 ha
Elev < 350 m	2440	290	140	12	2002	276	1086	386	3170
Elev 350–700 m	1212	120	69	9	1286	275	−5	273	1001
Elev > 700 m	35	11	5	2	32	16	20	18	232
Slope < 20 deg	2200	211	121	12	1391	197	1427	272	2421
Slope > 20 deg	1487	231	93	10	1929	329	−675	375	1982
Flat – no aspect	613	101	22	5	248	67	741	102	552
South aspect	1582	230	114	12	1670	302	42	360	1922
North aspect	1492	194	78	8	1402	240	282	282	1928
All forest	3687	301	214	14	3320	380	985	469	4403

*Final net change (total growth–mortality) scaled from observed plot data to total unmanaged forested area including wilderness areas (see Materials and methods).

allows for the accumulation of new biomass in woody material, and growth of existing forests, if not balanced by ongoing mortality, increases biomass density within the biome.

Differences in spatial distributions suggest ongoing change in the total area and spatial location of the forest, occurring via small, isolated patches. Forest extent appears to be exhibiting a slight decline in the south, and expanding in the north on northerly facing, low angle, sheltered slopes. This is potentially a signal, in part, of lower snowpacks and earlier melt dates resulting in longer growing seasons in previously short-season areas (Barrett & Christensen, 2011; Wolken et al., 2011). The similar skew toward areas of lower exposure would correspond with this hypothesis, as higher success in sheltered areas would be expected if amelioration of environmental limitations is the driving factor in the observed forest gains, as opposed to declines in the intensity of disturbance drivers (higher exposure) or changes in solar energy inputs potentially driven by changes in cloud patterns (southerly slopes). Observed gains are also consistent with the hypothesis that climate change is allowing for colonization of previously non-forested locations, including above treeline and low elevation, recently deglaciated land (Fastie, 1995; Wolken et al., 2011). Wetland encroachment, found in all subregions (Fig. 1), could also explain much of the biomass and spatial gains at low slopes. Because some of these shifts are reinforcing (establishment skewed to northerly aspects, mortality skewed to southerly), relatively rapid changes in forest distributions are possible.

These broad spatial patterns were somewhat reflected in the finer-scale plot-level changes, which include subpixel forest mortality, although variance was high due to the relatively small sample size (759 forested plots). Broadly, plots are accumulating biomass in the north (similar to expansion) while remaining neutral in the south. At present, this increase in biomass is relatively modest at fine scales (0.24 Mg ha^{-1} per year), but because of the substantial area, total biomass accretion is large, on the order of 986 Gg per year; assuming 50% C, approximately 0.5 Tg C yr^{-1} in natural, unmanaged forest. The observed increases in biomass are an underestimation of carbon/biomass accumulation, as a change in inventory methods prevented the inclusion of biomass accretion in newly forested areas (e.g. treeline or periglacial areas) or soil/detrital pools. Increases in forest extent are apparent in the comparison of change by landcover types (subregional: Fig. 1) and on the change map, such as in the Glacier Bay region (59°N, 136°W), which has seen extensive glacial retreat and forest establishment (Fastie, 1995). We refrain from extrapolating observed biomass accumulation within forested areas to the observed and potential future expansion outside of forested areas as it is outside the scope of our questions and would be highly speculative; however, given the large amount of coastal, periglacial, and treeline in the region, the amount could be significant depending on the rate of change. Forest expansion has implications for albedo and absorbed solar radiation in formerly treeless areas (~1.7x increase across these latitudes), a substantial potential feedback mechanism which appears to enhance subsequent growth (Sturm et al., 2005). However, increases in precipitation in the future may decrease growth if soils become waterlogged, although slower

decomposition may balance that decrease in terms of overall ecosystem carbon balance (Orians & Schoen, 2013). Further research on biomass trends during a shrub-to-forest transition in the region (for example) as well as the potential for future precipitation increases and its effect on growth is needed to resolve these potential feedbacks and magnitudes.

The pattern of both increased extent and plot-level biomass was primarily a northern phenomenon, less apparent in the south. An emerging disturbance, yellow cedar mortality, may be driving much of this spatial pattern. Currently affecting >250 000 ha and resulting in >70% mortality in mainly southerly locations, this mortality is a result of early snowpack melting and shallow rooting in wet soils, predisposing fine roots to freezing (Hennon et al., 2012). FIA data do not show an overall decline in yellow cedar biomass, although biomass increases for yellow cedar are highest on steeper, north facing slopes (which are likely to be better drained and hold snow longer) and nonexistent on south facing, shallow slopes, contrary to the other major tree species and the overall trends of higher mortality at higher slopes (Table S2). Successional trends following this large-scale morality are relatively unknown; one study indicated a shift to western hemlock dominance (Oakes et al., 2014), although that study was in an area with a relatively small tree species pool. This represents a climatic shift that explicitly disfavors one species while favoring other tree species, and thus expansion and increased biomass accumulation in the forest may proceed while certain species are lost.

Because the FIA plots used here were only remeasured once, it is impossible to estimate changes in rates, for example, if the observed increase in plot-scale biomass is due to increased growth rates, decreased mortality rates, or both. Regional disturbance patterns suggest that decreased mortality is at least partially responsible, as growth is outpacing mortality at both the plot scale and in terms of disturbance events. An alternate explanation would be a decrease in disturbance events in the recent past; however, there has been no apparent change in high-speed wind events (driving blowdown) or extreme cold events (driving yellow cedar mortality; Fig. S1) or in precipitation totals, an important driver of landslide likelihood (Buma & Johnson, 2015). Thus, it appears the signal is likely more from changes in growth and endogenous mortality, rather than external disturbances. Because of the need for spatially explicit, repeat measurements, results are limited to a subset of the ecosystem (live trees >12.7 cm DBH) for which those data were available. Total ecosystem accumulation in the region is likely significantly higher, as mature forests typically sequester more carbon in slowly decomposing dead material and the soil, especially in the relatively cool and wet temperate rainforest region. Unforested areas, including muskeg bogs, also sequester immense amounts of carbon belowground, and harvested areas are a strong and potentially accelerating carbon sink in these forests (Hember et al., 2012), although limited temporally. Overall all cover types and forest age classes, estimated carbon sequestration in the study region is >2.8 Pg C in total biomass and soil (Leighty et al., 2006).

The data used here are remotely sensed and empirical, intended to test expectations related to forest growth and expansion and explore the spatio-topographic distribution of those changes. This work also represents the first spatially explicit estimate of change in this large carbon sink. The results presented in this study indicate that regional carbon sink is not only driven by afforestation and historic harvest, but also expansion and densification of mature forest, along spatio-topographic patterns expected from a warming climate. Certain aspects, elevations, slopes, and contexts are favored over others, indicating the ongoing shifts are not following historic drivers. Ongoing monitoring, attributing observations to location-specific mechanisms, and following the implications for other cover types will be important over subsequent decades. True equilibrium (e.g. complete balance between growth and loss) can be a useful theoretic concept, although unlikely over short-time periods and small spatial scales due to stochastic variation in growth/loss processes. However, the nature of the perhumid temperate rainforest (similar climate and species, gap-dominated disturbance regime) makes them particularly amenable to this conceptual framework, although rare large events in the future could disrupt the observed patterns. Ongoing work is needed to determine whether the observed imbalance is maintained, increases, or decreases, especially if novel (e.g. fire) or large-scale disturbances affect the region as the climate shifts. Nonetheless, the data presented here represent an imbalance over a decadal time period and an important first data point on regional (spatial) response to climate change.

Generally, spatio-topographic trends in forest extent change are similar (though not identical) to spatio-topographic trends in forest biomass change, representing two independent datasets which support the hypothesis that climate change is causing directional change at the regional scale, although spatial and topographic variation is significant. The temperate rainforests of North America represent one of the globe's great storehouses of ecological diversity (Brandt et al., 2014), endemic flora and fauna (Cook

et al., 2001; Orians & Schoen, 2013), and carbon stocks (Leighty *et al.*, 2006; Luyssaert *et al.*, 2008; Keith *et al.*, 2009). Any change or directionality to their dynamics is important to consider. Overall, the significant differences in total forested area and the spatial/topographic distributions of growth and loss, consistent with expectations of altered forest dynamics due to a warming climate, suggest a directional shift due to climate influences. The process is playing out via small, subhectare scale patches non-randomly distributed across the landscape; unremarkable in isolation but significant in aggregate, these events represent a large, interesting shift in forest dynamics.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Changes in live biomass within existing forest by latitude and topographic context.
Table S2. Regional changes in live biomass by species across all topographic contexts.
Figure S1. Reconstructed extreme wind events for study region from 1958 to 2010. Drivers of disturbance – high winds and low temperatures – are shown for the northern and southern portions of the region, as reconstructed using CMIP5 GCM daily data for the time period. Data indicates no general trend in disturbance drivers which may influence results. Data and visualizations provided by Matthew Leonawicz and SNAP (Scenarios Network for Arctic Planning).
Data S1. Accuracy Assessment. Accuracy assessment of remotely sensed dataset for the region using high resolution imagery.