

# Watershed-scale forest biomass distribution in a perhumid temperate rainforest as driven by topographic, soil, and disturbance variables

Brian Buma, John Krapek, and Rick T. Edwards

**Abstract:** Temperate rainforests are the most carbon dense forest ecosystem on the planet, with C stocks several times higher than most other forested biomes. While climatic and disturbance drivers of these C stocks are relatively well explored, the spatial distribution of those stocks at the scale of entire watersheds is less well known, particularly in perhumid rainforests where research has been minimal. This study explored biomass distributions across an entire watershed simultaneously, from ocean to glacial icefields, in Southeast Alaska. Utilizing LiDAR and ground surveys, biomass was modelled throughout the landscape and distributions are described statistically. The dominant driver of biomass distributions at this scale (controlling for elevation) was the flow of water through the landscape: areas of higher water accumulation typically had low biomass (often  $<10 \text{ Mg}\cdot\text{ha}^{-1}$ ), whereas well-drained areas supported biomass approaching  $950 \text{ Mg}\cdot\text{ha}^{-1}$ . This relationship was strong at all elevations; only riparian locations (typically well-drained soils) maintained high biomass at low slopes. Exposure to stand-replacing disturbances, often a dominant driver, was only a minor factor. This work emphasizes the importance of water in temperate rainforests and the potentially significant impacts of changes to biomass given changes in precipitation (both increasing and decreasing) due to global climate change.

**Key words:** temperate rainforest, carbon, remote sensing, spatial distribution, biomass.

**Résumé :** Les forêts pluviales tempérées sont les écosystèmes dans lesquels la densité de carbone (C) est la plus élevée sur la planète; les stocks de C y sont plusieurs fois plus élevés que dans la plupart des autres biomes forestiers. Bien que les facteurs climatiques et les perturbations responsables de ces stocks soient relativement bien explorés, leur répartition spatiale de ces stocks à l'échelle des bassins versants est moins bien connue, particulièrement dans les forêts pluviales perhumides qui ont été peu étudiées. Cette étude a examiné la répartition de la biomasse simultanément sur l'ensemble d'un bassin versant, de l'océan jusqu'aux champs de glace dans le sud-est de l'Alaska. À l'aide du lidar et de relevés au sol, la biomasse a été modélisée dans l'ensemble du paysage et sa répartition a été décrite en termes statistiques. Le facteur dominant responsable de la répartition de la biomasse à cette échelle (après avoir éliminé l'effet de l'altitude) était le flux de l'eau dans le paysage : la quantité de biomasse était généralement faible (souvent  $<10 \text{ Mg}\cdot\text{ha}^{-1}$ ) dans les zones où il y avait une forte accumulation d'eau tandis qu'elle atteignait presque  $950 \text{ Mg}\cdot\text{ha}^{-1}$  dans les zones bien drainées. La relation était robuste peu importe l'altitude; seules les zones riveraines (sols typiquement bien drainés) supportaient une quantité élevée de biomasse sur des pentes faibles. L'exposition à des perturbations majeures, souvent un facteur dominant, était seulement une cause mineure. Ce travail fait ressortir l'importance de l'eau dans les forêts pluviales tempérées et les impacts potentiellement significatifs des changements dans la biomasse causés par les variations dans les précipitations (tant augmentation que diminution) dues au changement climatique global. [Traduit par la Rédaction]

**Mots-clés :** forêt pluviale tempérée, carbone, télédétection, répartition spatiale, biomasse.

## Introduction

Temperate rainforests are the most carbon dense forest biome on the planet, sequestering up to  $1800 \text{ Mg C}\cdot\text{ha}^{-1}$  in some locations in aboveground C alone (Keith et al. 2009). The forests of the northwestern North American coast represent approximately half of the remaining temperate rainforests globally ( $\sim 27$  million ha; DellaSala 2011) and high carbon densities (aboveground mean  $334 \text{ Mg C}\cdot\text{ha}^{-1}$ ; Keith et al. 2009). Belowground and soil stocks of carbon are often greater than aboveground stocks; the Tongass National Forest (Southeast Alaska) alone is estimated to contain

$\sim 2.8 \text{ Pg C}$ , equivalent to 8% of the total forest carbon in the conterminous US and 0.25% of global forest carbon (Leighty et al. 2006).

Because of the global significance of these carbon reservoirs and the expectations for substantial physical (e.g., freezing days; Meehl et al. 2004) and biological (e.g., yellow-cedar decline; Hennon et al. 2012) changes due to climate warming, it is important to understand the distribution of those carbon stocks at multiple scales, from stand-level controls on forest productivity (e.g., gap dynamics and stochastic single-tree mortality; Alaback 1996; Ott and Juday 2002) to regional assessments of biomass and change (e.g., latitudinal gradients in climate; Buma and Barrett 2015).

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Here, we assess the distribution of biomass at the landscape scale, from the estuary to the glacial headwaters of an approximately 10 000 ha watershed in the perhumid rainforest of Southeast Alaska. Productive portions of these coastal forests are characteristically dense, with estimates of aboveground biomass densities generally from approximately 700 to 1000 Mg·ha<sup>-1</sup> (Waring and Franklin 1979; Smithwick et al. 2002; Matsuzaki et al. 2013), though most research has been in the southern half of the perhumid rainforest biome (British Columbia and Washington–Oregon) and often focused on average biomass of high-productivity stands. Other studies primarily focused on biomass variability across those landscapes, identifying several important factors. For example, riparian zones are typically associated with relatively high aboveground biomass, often attributed to better drained soils (Viereck et al. 1983; Simard et al. 2007), and the influence of marine-derived nutrients may influence biomass at fine scales (Helfield and Naiman 2003). The decline of biomass with increasing elevation is well known, and in many high-latitude areas, lower average solar radiation (e.g., poleward aspects) is also associated with lower biomass. Disturbance events have a significant, long-term influence on biomass in many systems, especially in areas where disturbances are large relative to the landscape under study (Turner et al. 2003); however, Southeast Alaskan perhumid rainforests are typically dominated by a gap phase – noncatastrophic disturbance regime (e.g., single-tree mortality; Veblen and Alaback 1996; Ott and Juday 2002). Severe disturbances such as wind and landslides can cause substantial mortality and subsequent impacts on biomass (Veblen and Alaback 1996; Nowacki and Kramer 1998), but area potentially exposed to those events is relatively limited (southeastern-facing slopes: wind (Kramer et al. 2001); steep slopes: landslides (Buma and Johnson 2015)) and average canopy turnover time of all aspects is quite long, approximately 575 years (range: 210–920 years; Ott and Juday 2002). In total, while the importance of these various processes to biomass distributions has been well delineated in a variety of systems, their relative importance in the perhumid temperate rainforest is poorly understood and not systematically explored despite the significance of this region to regional, national, and global carbon budgets.

We were interested in assessing topographic, disturbance, and edaphic drivers simultaneously to explore their relative contribution to biomass distribution in an unmanaged watershed. Despite the importance of these forests, previous research on spatial distributions of biomass has been limited due to access. Little of the landscape is accessible by road, necessitating boat or plane transport, and the terrain is steep and heavily wooded, with substantial amounts of downed debris and often inclement weather. Consequently, descriptions of patterns of biomass density at the landscape scale (e.g., in relation to slope, riparian areas, or elevation) are typically indirect and often limited to field-sampled plots, which may then be scaled using multiple plots spread out over the entire region (e.g., Forest Inventory and Analysis (FIA) plots; Peterson et al. 2014). Alternatively, some carbon assessments utilize photointerpreted forest age along with plots to estimate biomass distributions (e.g., Leighty et al. 2006). These methods are valid but suffer from the necessity of making inferences to unsampled areas (“up-scaling errors”; Keith et al. 2010). This creates uncertainty when looking at fine spatial scales such as a single watershed.

LiDAR is an active remote sensing technique that directly measures attributes of forest structure across wide areas at a fine spatial resolution. This direct measurement avoids the issues associated with correlations based on reflectance or photointerpreted patterns, as all points on the landscape are physically measured. While limited in some applications, LiDAR is particularly useful for biomass estimation and mapping in forests (Mitchard et al. 2013), as biomass is tightly coupled to forest structure; LiDAR measures the structural characteristics of a forest stand at a fine

resolution (Wulder et al. 2012). By relating ground truth biomass measurements to the LiDAR, highly accurate maps of forest biomass can be constructed utilizing the wide coverage of the LiDAR structural measurements (e.g., Hudak et al. 2012). Using LiDAR, we mapped biomass over an entire watershed simultaneously, from estuary to glacial headwaters, and examined topodaphic and disturbance-associated controls on biomass distribution at this broad scale. The riparian zone is specifically examined in terms of both its association with overall landscape biomass patterns and how it influences the relationship of other topodaphic–disturbance variables with biomass.

The following questions were asked:

1. How do topodaphic factors and exposure to disturbances influence biomass distribution across an entire watershed?
2. Are the relationships between biomass and topodaphic drivers – disturbance exposure different in the riparian zone compared with the rest of the landscape?

## Methods

### Site

The study area comprises the Cowee Creek watershed, one broad drainage approximately 60 km north of Juneau, Alaska, U.S.A. (58.65° latitude, –134.91° longitude), extending from a broad estuarine landscape on the coast to three large watersheds, one of which contains two glaciers (Davies and Quiet glaciers), one with a single glacier (Cowee Glacier), and one with no glacial influence; the majority of the landscape is designated as the U.S. Forest Service Héén Latinee Experimental Forest (HLEF). Climate is maritime, with yearly precipitation of 1500–3000+ mm (>10% during the summer) and mean temperatures ranging from –5 °C in the winter to ~10–15 °C in the summer (Alaback 1996). Overstory diversity is low, dominated by Sitka spruce (*Picea sitchensis* (Bong.) Carrière), western and mountain hemlock (*Tsuga heterophylla* (Raf.) Sarg. and *Tsuga mertensiana* (Bong.) Carrière), black cottonwood (*Populus balsamifera* L. ssp. *trichocarpa* (Torr. & A. Gray ex Hook.) Brayshaw), and red and Sitka alder (*Alnus rubra* (Bong.) and *Alnus viridis* (Chaix) DC spp. *sinuata* (Regel) Á. Löve & D. Löve), with shore pine (*Pinus contorta* Douglas ex Loudon var. *contorta*) dominating in peatlands. Small populations of willows (*Salix* spp.) and Alaska yellow-cedar (*Callitropsis nootkatensis* (D. Don) Oerst. ex D.P. Little) occur in isolated locations.

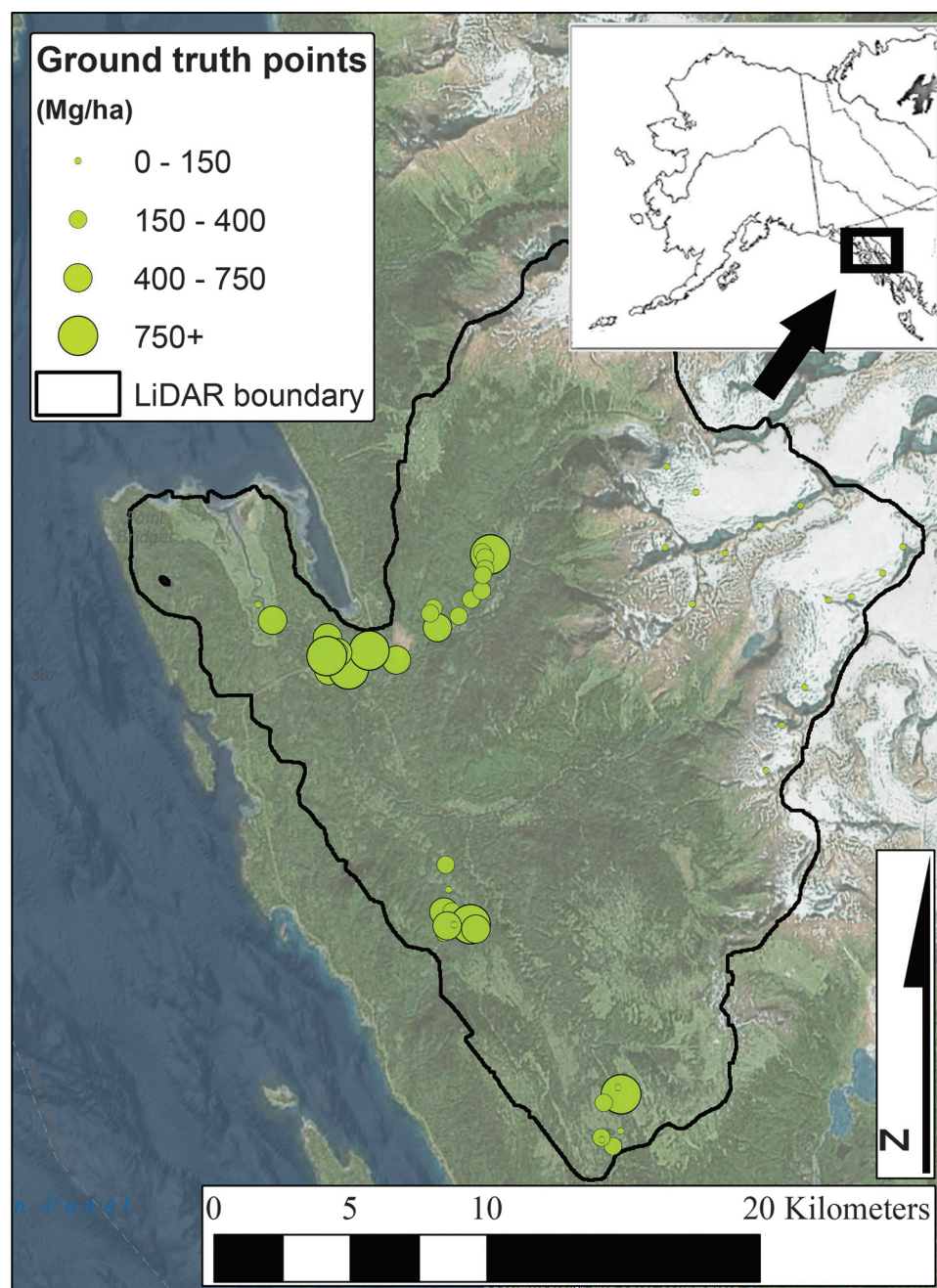
The Cowee Creek and Davies Creek drainages have not been subjected to widespread timber harvest. During the 1940s, approximately 80 ha of timber was clear-cut along Cowee Creek in the lower watershed near the present road (Carstenson 2013). In 1999, approximately 20 ha of timber was clear-cut on the northern side of Davies Creek in the lower watershed, and trees were removed by selective harvest on an adjacent area northeast of the clearcut. Some timber was likely removed for mine roads and structures along the western edge of Cowee Creek in approximately 1890–1920, but no evidence of such logging is detectable. No evidence of logging was observed on any of the calibration plots (below).

### Plot network

Forty-seven 20 × 20 m plots were established throughout the HLEF. Location was determined semi-randomly, constrained by access due to the rough terrain of the watershed. After a point was placed, a preliminary 5 × 5 m tree height map derived from the LiDAR was used to locate four plots around that point; one point was located in each of the following tree height classes: the lowest 25% of tree heights, the 25%–50%, the 50%–75%, and the 75%–100%. Because the LiDAR sampling covered the entire watershed, the goal in the plot selection process was to sample the entire range of LiDAR response values. This ensured that although the location of the plots within the landscape was only semi-random and constrained by access and logistical limitations, there was a similar



Fig. 1. Study area, estimated biomass (Standish allometrics), and biomass sampling points. (This figure is available in colour online.)



(and comprehensive) range in aboveground biomass in each general area visited, which spanned much of the elevational range present in the forested part of the watershed (maximum elevation = 588 m). Each plot was completely surveyed for aboveground biomass. Diameter, species, and health status of all trees >1.4 m tall were recorded; a subset also had their height measured using an inclinometer. Stumps and snags (standing dead trees) were recorded; if tops were broken, the height of the breakage was noted and used to adjust biomass estimates (below). Snag species were recorded whenever possible; if unknown, they were assumed to be Sitka spruce, the most common overstory species, for biomass calculations. All seedlings were counted by species and grouped into height classes (0–10, 10–20, 20–30, 30–40, 40–50, and 50+ cm). Coarse woody debris (CWD) loading was estimated via two 20 m Brown's lines (a line intercept method; Brown 1974)

limited to the LiDAR pixel footprint (see below); sound and rotten debris were tallied separately. Because the watershed contains a substantial amount of unvisited glacial area, 16 points were randomly located on the bare rock – snow – icefield at the top of the watershed; these sites were assigned zero biomass. In total, the final set of ground data used to create the LiDAR biomass map contained 63 sites (Fig. 1).

These measurements were converted to aboveground biomass utilizing allometrics derived for this ecosystem. Two allometric regression groups (ARGs) were used to check for sensitivity of biomass to different diameter–height–biomass relationship equations, either Standish et al. (1985) or Ter-Mikaelian and Korzukhin (1997). Equations were from Ung et al. (2008) for alder and from Brown (1976) for willow; both are minor components of the landscape and were used for both of the ARGs. Biomass estimates for

**Table 1.** Variables used in distribution models (elevation was removed via statistical partialling; see Supplementary data 2<sup>1</sup>). See source for information on derivation.

| Variable                                                             | Units                                   | Source                                                                                                        |
|----------------------------------------------------------------------|-----------------------------------------|---------------------------------------------------------------------------------------------------------------|
| Aspect                                                               | 0 (north), 1 (south)                    | ASTER digital elevation model (DEM)                                                                           |
| Slope                                                                | 0–90, degrees                           | ASTER DEM                                                                                                     |
| Potential solar radiation                                            | 0+, W·m <sup>-2</sup>                   | ASTER DEM (yearly average based on topographic shading and latitude)                                          |
| Contributing area                                                    | 0+, m <sup>2</sup>                      | ASTER DEM                                                                                                     |
| Topographic index                                                    | 0+, log(catchment area / tan gradient)  | ASTER DEM                                                                                                     |
| Exposure to stand-replacing windstorms                               | 0–9 (relative scale): 0 = low, 9 = high | Methods from <a href="#">Kramer et al. (2001)</a> , as implemented by <a href="#">Buma and Johnson (2015)</a> |
| Exposure to landslides                                               | 0.0–1.0 (slide suitability)             | Methods from <a href="#">Buma and Johnson (2015)</a>                                                          |
| Hydric soils (soils typically waterlogged; from photointerpretation) | Yes or no                               | Tongass National Forest Soil Inventory, <a href="#">U.S. Forest Service 2013</a>                              |
| Riparian area (alluvial soils; from photointerpretation)             | Yes or no                               | Tongass National Forest Soil Inventory, <a href="#">U.S. Forest Service 2013</a>                              |

broken trees were adjusted based on observed breakage height and stem taper equations from [Kozak et al. \(1969\)](#). Seedling biomass was estimated by averaging biomass estimates for each size class using data from [Keyser \(2008\)](#) and D'Amore (unpublished data).

### LiDAR acquisition

LiDAR data were acquired using a Leica ALS50 Phase II system on two dates, 21 September and 26 October 2012, by Watershed Sciences Inc., Corvallis, Oregon. Average first-return point densities were 7.2 and 7.7 points·m<sup>-2</sup> on the two dates, respectively. Ground-classified point densities were 0.81 and 1.73 points·m<sup>-2</sup>, respectively. Average absolute vertical accuracy was 3 mm on both dates. RMSE accuracy was 36 mm. The LiDAR coverage included the entire watershed, and a small buffer extending into neighboring watersheds to avoid edge complications (which was excluded from the final results).

### LiDAR processing

The LiDAR data were aggregated at a 20 m resolution into 61 statistical descriptions of the point cloud, similar to [Hudak et al. \(2012\)](#). For example, in a given 20 × 20 m pixel, there are approximately 4000 LiDAR returns. For the median height raster, the median vegetation height value was rasterized, resulting in the median height raster for the entire study region. For the 90th percentile height raster, the 90th percentile vegetation height value was rasterized. Five additional datasets potentially related to biomass were used: forest type, land cover, precipitation, wind exposure, and landslide susceptibility. For more details and a complete list of metrics, see Supplementary data 1<sup>1</sup>.

To create the landscape-scale biomass map, multivariate adaptive regression splines (MARS; [Friedman 1991](#)) was employed. Observed biomass was modeled based on the observed LiDAR metrics at each point. MARS is a nonparametric modeling framework suitable for high-dimensional data where relationships are not necessarily linear and has been shown to be superior to comparable methods in similar floodplain forests at a 30 m scale ([Gunalp et al. 2014](#)). It produces a continuous, nonlinear response to the data. However, as the number of terms increases, the potential for overfitting also increases. The MARS model was therefore pruned based on 10-fold cross-validation to avoid overfitting. In this process, a portion of the dataset is left out of model building and used to test model fit. This was done 10 times using a random subsample of plots for validation each time; the optimal tree size was determined from mean  $r^2$  on the validation points. The final model was then built from all the data points and pruned to that optimal tree size.

### Distributional analyses

We then explored how that biomass was distributed over the landscape in relation to 10 topographic variables. Six were related to topography (aspect, slope, solar radiation, contributing area, topographic index, and elevation; data from the NASA ASTER mission), two were related to soil (hydric soils, which are locations that are often water saturated, and riparian areas, assumed to be predominately coarse, well-drained soil; data for both from U.S. Forest Service maps derived from aerial photographs), and two were related to disturbance exposure (exposure to the prevailing storm track and exposure to landslides; [Buma and Johnson 2015](#); [Buma and Barrett 2015](#)). These variables were chosen to assess drivers of biomass distribution hypothesized to be relevant to aboveground biomass—CWD at this scale: elevation, drainage, disturbance, and solar radiation.

For units and references, see Table 1. Two thousand points were randomly distributed across the study area in R ([R Core Team 2015](#)). Preliminary analyses indicated that elevation was the most significant predictor variable of biomass (from sea level to ice-field), so we regressed the biomass estimates via a cubic linear model, limited the data points to below the tree line (<900 m), and conducted subsequent analyses on the residuals of that relationship (for further details, see Supplementary data 2<sup>1</sup>). This subsetting focused the analysis on variables associated with higher or lower biomass values (i) than would be expected based on elevation alone and (ii) excluding the zero biomass points on the ice-field, a statistically conservative approach to lower the chance of type I errors. From this point onward, the term “biomass” refers to this residual biomass number after removing the elevational trend.

To identify drivers of biomass across the landscape, classification and regression trees (CART; [Breiman et al. 1983](#)) were used. Regression trees are useful in describing nonlinear relationships and complex interactions between variables and appropriate for non-normally distributed response data. The trees were pruned using 10-fold cross-validation, with tree size being limited by the point where increasing complexity returned minimal (<0.5%) error reduction. Finally, to explore potential interactions between the riparian zone and the other variables on biomass, we used ANCOVA models (transformed variables where appropriate) to compare how the various potential drivers of biomass were modified by being inside or outside the riparian zone.

## Results

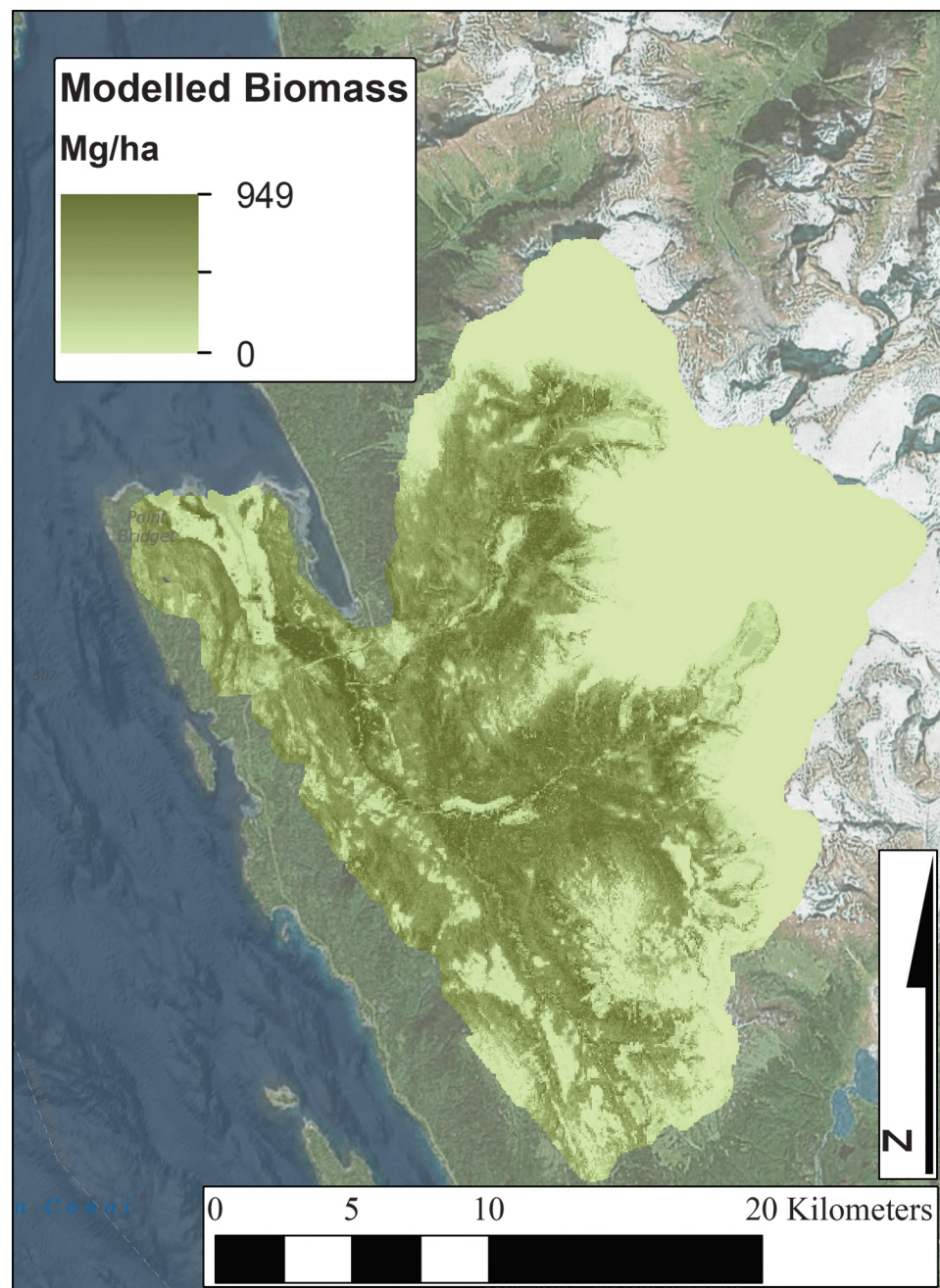
### Biomass mapping and LiDAR

Final ground data ranged from 0 Mg·ha<sup>-1</sup> to 1115 Mg·ha<sup>-1</sup> using the Standish ARG. The LiDAR data successfully modeled observed

<sup>1</sup>Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2016-0041>.



**Fig. 2.** Modeled aboveground biomass (live, dead, CWD) utilizing the Standish set of allometric equations. The discrete patches of low biomass at low elevation correspond to peatlands found in areas of very low slope throughout the region (compare with Fig. 1). Area around the boundary faded to provide contrast. (This figure is available in colour online.)



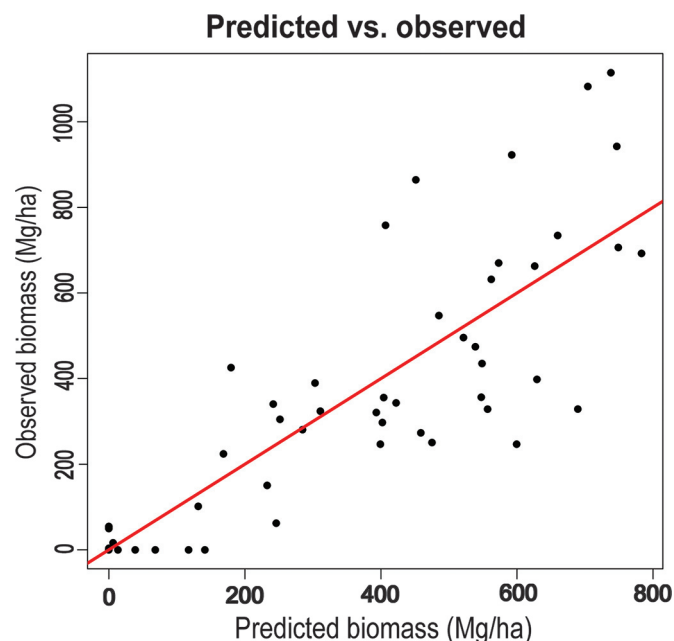
total aboveground biomass throughout the landscape for both sets of allometric equations ( $r^2$ : Standish, 76% (Fig. 2); Ter-Mikaelian, 73%). Error was normally distributed around zero with no bias, supporting the subsequent use of the map to estimate watershed-scale controls on biomass distribution. Mean errors relative to the ground plots (predicted – observed) were  $2.03 \text{ Mg}\cdot\text{ha}^{-1}$  (Standish; Fig. 3) and  $-11.6 \text{ Mg}\cdot\text{ha}^{-1}$  (Ter-Mikaelian). The MARS model and variable selection procedure isolated vegetation density and the 90th percentile of vegetation height as the most useful predictors (both allometric sets) and discarded the remaining coefficients. The MARS modeling approach was also successful for individual components of that total biomass, though fit was less than the cumulative biomass value. For standing biomass (live and dead), the

Standish allometrics were a slightly better fit after cross-validation ( $r^2 = 0.70$ ) than the Ter-Mikaelian ( $r^2 = 0.66$ ). For CWD alone (excluding standing live and dead), the MARS technique was less successful ( $r^2 = 0.58$ ). Because the overall results are relatively insensitive to the ARGs, only those for the Standish set of equations are reported here. In addition, we focus on the cumulative biomass (standing live, standing dead, and CWD). See Appendix A for a comparison of the two allometric sets.

#### Biomass distribution modeling

Analysis of the distribution of biomass across the landscape highlighted drainage-relevant variables as the main controls on aboveground biomass after partitioning out elevational relation-

**Fig. 3.** Predicted aboveground biomass (live, dead, CWD) vs. observed ( $r^2 = 0.76$ ,  $n = 63$ ) utilizing the Standish set of allometric equations and histogram of the residuals. Error was normally distributed, with errors  $<10\%$  for the majority of the plots sampled.



ships (Fig. 4). Both topography and soils were relevant: slope was the primary driver, as was contributing area (log transformed), both strong influences on drainage and water accumulation, with biomass increasing as drainage rates would be expected to increase. Hydric soils (predominately saturated and often dominated by *Sphagnum* spp.) were also important, with lower biomass found on hydric soil types. Low slopes were associated with low biomass; even low slope areas not identified with hydric soils had lower biomass than would be expected from elevation alone (though substantial variance does exist). Residual variance for biomass was high ( $r^2$ : Standish = 0.32). This low  $r^2$  value is conservative in that a more complex regression tree increases the  $r^2$  value; however, it increases cross-validated error rates. As a result, the more general and conservative, highly pruned tree (minimal splits) is reported.

The riparian zone was not an indicator chosen in the regression tree models, and there were no significant differences between riparian and nonriparian zones in terms of detrended biomass. However, the ANCOVA analyses indicated that the relationships between slope, wind exposure, and slide suitability and biomass were significantly influenced by being in the riparian zone. This is apparent in the slope vs. residual biomass plot (Fig. 5). At low slopes, riparian zones are approximately normally distributed with respect to biomass, whereas nonriparian areas at low slopes have substantial negative values, indicating much less biomass than what would be expected based on elevation alone.

## Discussion

This study investigated the distribution of total aboveground biomass (standing (live) and dead) in a complete per-humid temperate rainforest system, from the estuary to glacial headwaters, at a high spatial resolution. The use of LiDAR and the particular nature of the study area, which progresses from marine tidal areas to glaciers in a short horizontal distance, allows for a synoptic view of the entire watershed landscape and simultaneous evaluation of a variety of drivers of biomass distribution. Areas with the highest density of aboveground biomass (live, standing dead, and CWD) on the landscape (e.g.,  $\sim 750$ – $949$  Mg·ha $^{-1}$ ; Fig. 2) were

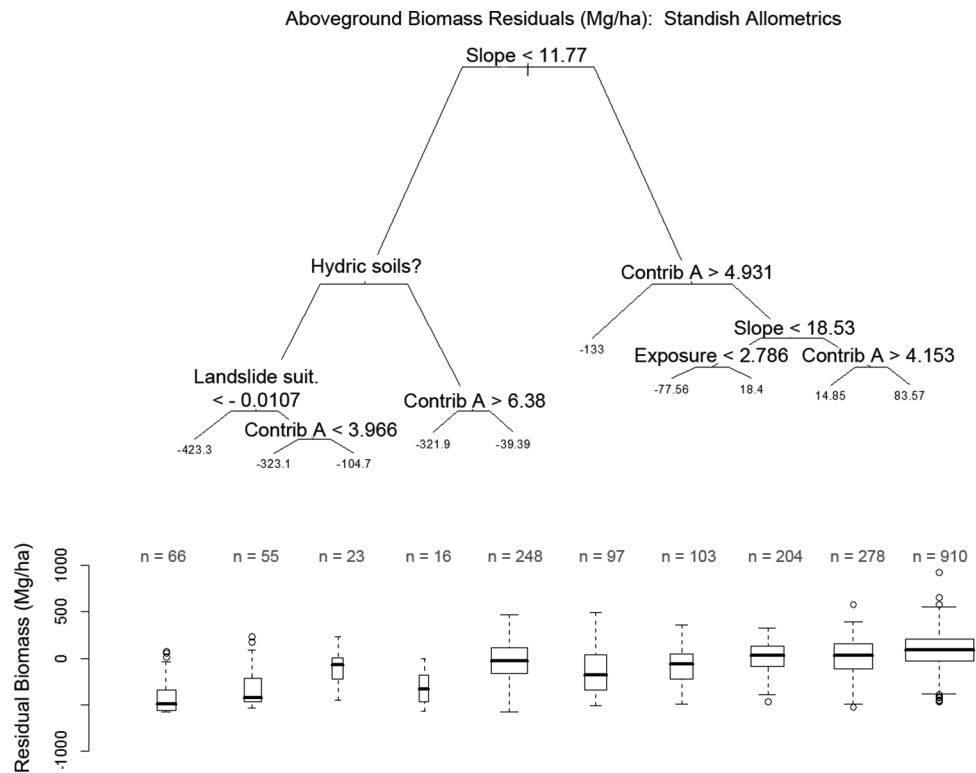
similar to values from previous research in the same species assemblages further south in the biome (examples: 690 Mg·ha $^{-1}$  (Matsuzaki et al. 2013, assuming biomass  $\sim 50\%$  C), 789 Mg·ha $^{-1}$  (Waring and Franklin 1979), 815 Mg·ha $^{-1}$  (Trofymow and Blackwell 1998), 956 Mg·ha $^{-1}$  (Smithwick et al. 2002, assuming biomass  $\sim 50\%$  C)), confirming the expectation that aboveground biomass is generally dense in productive, old stands. Variation in that value, however, was apparent at the 20 m scale across the watershed (Fig. 2). Unsurprisingly for a study area that covers sea level to glaciers, the major correlate of biomass distribution within the watershed was elevation (Fig. 2). Peak biomass on well-drained slopes began to decline above  $\sim 400$  m and dropped to near zero above 850 m (Supplementary data 2 $^{\circ}$ ). This roughly corresponds to a switch from Sitka spruce and western hemlock dominance to mountain hemlock dominance, although all species can be found across most of the elevational gradient.

Analysis of both allometric maps (Fig. 4; Appendix A, Fig. A1) suggests that the dominant control on aboveground biomass in perhumid rainforests, after controlling for elevation, is how long water is retained in the soil. Slope, hydric soils (predominately peatlands and signifying areas where water accumulates), and contributing area were the dominant drivers of biomass variation, with steeper slopes, nonhydric soils, and lower contributing area all leading to higher biomass totals. This confirms expectations that in regions of high precipitation (e.g.,  $>2000$ + mm·year $^{-1}$ ), drainage and water accumulation are critical to aboveground carbon balance (Bisbing et al. 2016). This is likely due to decreased productivity in wet areas (lower NPP due to waterlogging). A comparison of old-growth stands in British Columbia on well-drained and poorly drained soils also found slightly higher biomass in better draining soils, despite being in an area with much less precipitation (930 mm vs. 1500–3000+ mm; Fredeen et al. 2005). Alternatively, it could result from increased mortality (e.g., anoxic conditions, less windfirmness, more stem rots); however, increased wind exposure was associated with higher rather than lower biomass, and areas that had topographic shelter from the storms had lower biomass. This is consistent with the drainage hypothesis, as wind disturbance results in soil disruption (e.g., tip-up mounds), which can increase soil drainage and alter nutrient cycling (Kimmins 1996; Kramer et al. 2004). Increasing landslide suitability likewise resulted in increased biomass. This could be due to disturbance but must be interpreted cautiously; most of the landscape has a relatively low landslide suitability score and that score is directly related to both slope and drainage metrics (Buma and Johnson 2015) and so the confounding influence with those variables is possible. In the case of landslide suitability, the difference was, in any case, relatively minimal.

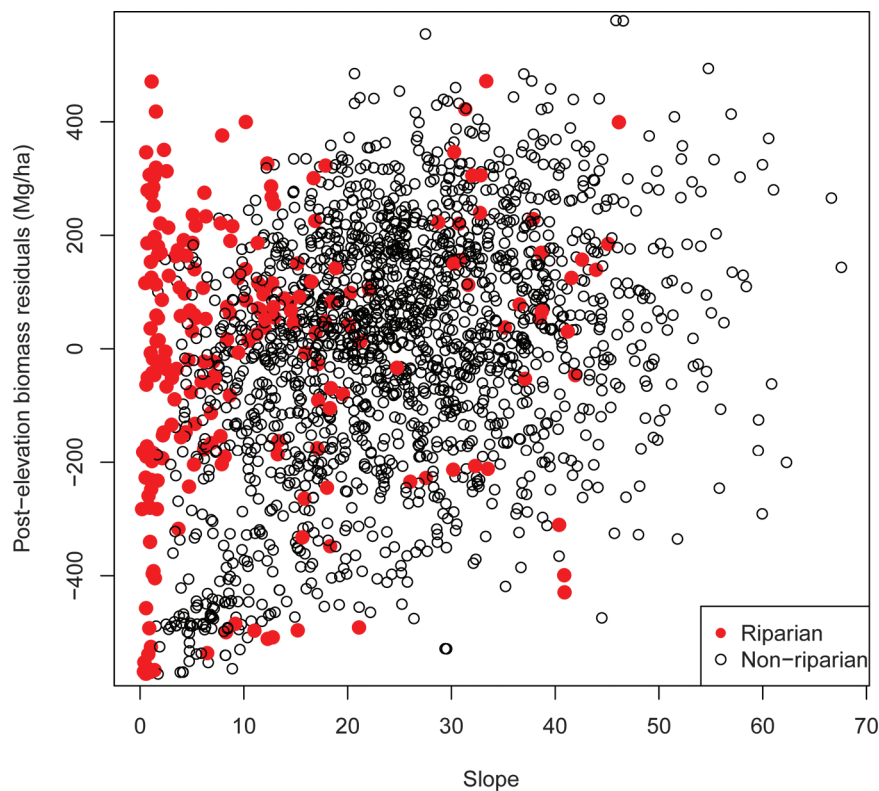
Overall, the topographic and disturbance variables only explained a portion of the variance in the biomass residuals (Fig. 2). This can be explained in two ways, one statistical–methodological and one ecological. Statistically, the regression trees are conservative and seek to avoid overfitting by limiting the number of splits via cross-validation. A more complex tree would fit the data more closely (resulting in more splits, with smaller numbers of points in each terminal node) and thus return higher  $r^2$  values but would decrease the generalizability of the results. The similarity of results between the ARGs (Appendix A) indicates that the results are an accurate representation of general biomass patterns.

Ecologically, the forest is dominated by a gap dynamic regime (Alaback 1996; Ott and Juday 2002; Buma and Barrett 2015), with single-tree mortality occurring via stem rot and snapping. While we considered exposure to stand-replacing events in our modeling, background mortality from this single-tree death (e.g., senescence, heart rot, etc.) cannot be accounted for. Because the trees are large ( $>1$  m DBH,  $>60$  m height), they comprise a significant portion of any given pixel. Thus a single tree dying or falling will have a substantial impact on observed biomass at any given point (regardless of topographic position) as a function of individual-tree

**Fig. 4.** Regression tree results for the Standish allometrics. Both allometrics produced trees that are broadly similar, highlighting the importance of water and drainage throughout the landscape, primarily as a function of slope, soils, and contributing area. Disturbance exposure was included in the trees, although only explaining a minor component of the variation. Landslide suit. = slide suitability ( $\log_{10}$ ); Contrib A = contributing area ( $\log_{10}$ ); Exposure = wind exposure.



**Fig. 5.** Slope vs. residual biomass values after controlling for elevation. Areas of low slope are generally associated with lower biomass than would be expected from their elevation (negative residuals); areas of steeper slope have higher biomass; that pattern is altered in riparian zones. (This figure is available in colour online.)





age; this is essentially “inherent variability” at fine scales. While this mortality should be partially captured by our estimates of CWD biomass, which is incorporated into the total aboveground biomass estimates, the LiDAR data were very limited in their ability to model CWD alone (data not shown). This is likely due to the characteristically thick surface organic component and often thick and continuous understory layer, with moss and rapid humus formation obscuring the CWD from the LiDAR (in other words, the CWD surfaces may be confused for the ground). One alternative would be carrying out the analyses at a coarser resolution (e.g., 50 m pixels) to further reduce the influence of single-tree mortality. However, this would reduce spatial precision, especially on significant boundaries such as the edges of peatlands, the bottoms of slopes, and at the tree line. Therefore we opted to retain the variance (box plots in Fig. 4) and propose that much of that residual variance is explained by site-to-site variation in single-tree mortality surrounding the mean values driven by the topographic and disturbance exposure values that we modeled (the nodes of the tree in Fig. 4).

The lack of major influence of the riparian zone on biomass residuals directly (at this scale) was unexpected. Both main streams support strong salmon runs within the areas considered riparian, with several species of salmon making yearly migrations. Salmon, and their associated influx of marine-derived nutrients (MDN) into forested systems, have long been hypothesized as drivers of riparian productivity and biodiversity (e.g., Helfield and Naiman 2003; Muehlbauer et al. 2014). There was no evidence of a significant MDN–productivity relationship at this scale, which would be expected to result in substantially higher biomass in riparian zones. Flooding disturbance is also a potential issue, as there could be higher productivity but also higher biomass turnover rates. As CWD was measured, any dead material would need to be removed from the system to have not been included in estimates. The relatively small size of the watershed and river (mean annual flow rate of  $8 \text{ m}^3 \cdot \text{s}^{-1}$  at the mouth), however, make that hypothesis less likely, although an investigation of relative growth rates is needed to conclusively address that possibility. In the end, the lack of inclusion of riparian zonation in the CART regression indicates that biomass changes with elevation similarly in riparian and nonriparian areas. The riparian zones in the study region are all at relatively low elevation, however, and it is unknown if the relationships would be similar at higher elevations.

Riparian zones did, however, change the relationship between other topographic predictors and biomass. Biomass was higher in riparian areas relative to nonriparian areas in areas of lower slopes and higher wind–landslide exposure ( $p < 0.05$ ). The difference was seen in low-slope areas ( $<10$  degrees), which typically had low biomass (Fig. 5), resulting from excess water and often poor drainage, and resultant low growth and (or) peatland presence (Bisbing et al. 2016). Riparian areas, with characteristically coarse alluvial soils, are typically well drained, reducing the potential for hypoxic conditions even at low slopes (Kimmins 1996; Alaback 1996). This characteristic together with our observations of low biomass in most low slope areas further supports the hypothesis that biomass is primarily controlled by drainage. The coarser soils allow for deeper rooting, allowing for more biomass in wind and potential landslide areas by increasing forest resistance to disturbance (Ray and Nicoll 1998; Mitchell 2013). Analysis of tree ages would be necessary to determine if the riparian zone is, in this case, increasing forest resistance to disturbance and would need to be coupled with estimations of mortality by other factors (e.g., fungal infections). However, that we observed low biomass in nonriparian low-slope areas protected from storm winds and landslides suggests that drainage is more significant.

### Uncertainties

As with all remote sensing based studies, several caveats exist. Plot locations were located according to a semi-random design

intended to sample the range of potential biomass totals and across the range of elevations. This minimizes any extrapolation with unsampled LiDAR distributions. However, plot locations were limited by accessibility to areas that could be visited on foot, and there was not a truly independent verification dataset (rather, 10-fold cross-validation was used). Because of the low tree species diversity and the wide range sampled, this is likely a minor source of error. Similarly, hydric soils and the riparian zone were delineated via photointerpretation based on morphology and reflectance. Given the remoteness of the region, this is the only feasible approach without relying on modeling products, which entail assumptions that would interfere with the statistical analysis here. Informal observations at each plot supported the soil classifications. Finally, single-tree mortality is expected to cause significant random variation at the pixel scale due to variations in tree age and background tree death. This is not a limitation of the LiDAR-derived biomass map, which can accommodate those gaps at this scale ( $400 \text{ m}^2$ ), but does likely add variability to the subsequent evaluation of biomass distributions, as a plot may have low biomass because of topography (for example) or because of a recent tree fall. As this is assumed to be both relatively common given the large landscape and randomly distributed spatially throughout the watershed, this would not bias the distribution analysis towards any particular descriptor variable (though it would be expected to lower final  $r^2$  values; e.g., in Fig. 3).

### Conclusions

Temperate rainforests are unique landscapes comprised of thick forests with very high precipitation rates and little to no history of fire. As a result, biomass (above- and below-ground) accumulates and carbon stocks reach densities higher than in any other global biome (Keith et al. 2009). Understanding how that biomass is distributed at multiple scales is important for a variety of reasons, including anticipating how climate change will affect these forests and better informing management decisions (e.g., prioritizing certain areas of high biomass accumulation for carbon storage). This study used a synoptic approach, analyzing the entire forest from glacial headwaters to estuarine mouth simultaneously to explore landscape-scale drivers of aboveground biomass distributions. Elevation was, unsurprisingly, strongly correlated with biomass, likely by influencing growing season length and temperature. Beyond that, drainage rates and water accumulation appear to control where biomass is located on the landscape: areas with high water accumulation and (or) poor drainage have little aboveground biomass, whereas better drained locations have higher aboveground biomass. Stand-replacing disturbances appear to have had little influence on current biomass distributions, but the data suggest that small-scale gap formation (single-tree mortality) plays a large role in point-to-point variation at this resolution (20 m). A better understanding of future water balance is therefore needed to successfully anticipate aboveground forest biomass changes due to the shifting climate in this region.

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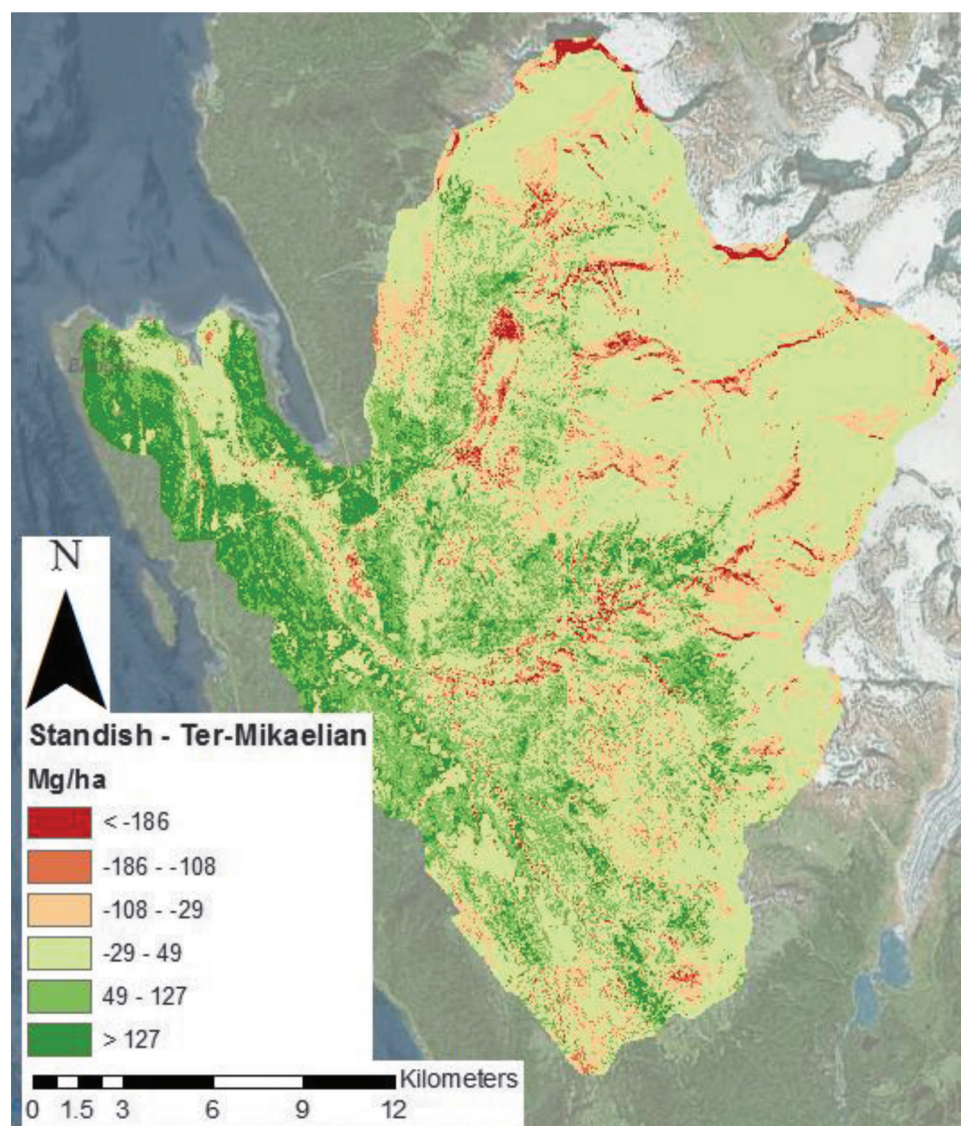
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## Appendix A. Allometric equation comparisons and sensitivity test

Any study with allometric scaling must consider the sensitivity of the conclusions to different allometric equations, especially those using equations not derived on the site. To do so, we utilized two independent sets of regression equations and conducted identical analyses, including creating a MARS model and a CART analysis (as described in the main text). Below is an analysis of the differences between the two ARGs demonstrating minimal differences between the two and the CART regression model for the alternate set of equations.

The Standish and Ter-Mikaelian allometrics were quite similar (mean difference 11.6 Mg·ha<sup>-1</sup>, with Standish being larger). This difference was not evenly distributed, with Standish typically predicting higher biomass on hillsides and Ter-Mikaelian predicting higher biomass on flat ground (Fig. A1), and the dominant variables identified using the alternative allometrics were very similar (Fig. A2). There was also error in areas of smaller trees such as along the edges of peatlands. This is likely because allometric models are historically biased towards high biomass (and commercially valuable) forest stands and do not accurately handle small trees or noncommercial, peatland species such as shore pine. Both ARGs resulted in some anomalous areas of higher biomass at very high elevations, above the tree line. This resulted from cliffs, glacial crevasses, and other rock topography appearing as vertical heterogeneity. This could be removed by analyzing the data at a finer spatial resolution, which would introduce problems in the forest (where tree size and spatial heterogeneity re-

**Fig. A1.** Differences between the two biomass maps; positive values show higher estimation by Standish allometrics, negative values show higher estimation by Ter-Mikaelian. Mean value of 11.6 Mg·ha<sup>-1</sup>, groups are 1 SD each. (This figure is available in colour online.)



quire larger units of analysis); using a variable resolution of analysis (finer scale in nonvegetated locations); or simply eliminating or masking high-elevation areas from further consideration, as was done here.

As many areas in temperate rainforests are entering protected status, or are already designated for noncommercial use, future allometric development should likely focus on areas of low biomass to resolve these discrepancies. Although this will not dramatically change estimates of total landscape biomass, mostly controlled by high-volume areas of the landscape, it will increase spatial precision of those estimates.

To confirm that the conclusions were not sensitive to the choice of allometrics, an identical CART analysis was conducted on the secondary allometric dataset. The most important variables were again related to drainage: slope and soils. Wind exposure was the final split retained after tree pruning. Similar to landslides identified in the Standish model, wind exposure is a measure of disturbance potential. The similarity in variable selections between the CART models, despite the independent allometrics, lends support to the conclusion that drainage is the primary variable controlling biomass distribution at the watershed scale.

**Fig. A2.** CART analysis of the Ter-Mikaleian derived biomass map. Similar to the primary analysis, slope and drainage appear to be the main factors driving biomass distribution across the landscape.

