



# Forest structure more important than topography in determining windthrow during Hurricane Juan in Canada's Acadian Forest



Anthony R. Taylor<sup>a,b,\*</sup>, Evan Dracup<sup>a</sup>, David A. MacLean<sup>b</sup>, Yan Boulanger<sup>c</sup>, Sarah Endicott<sup>a</sup>

<sup>a</sup> Natural Resources Canada, Canadian Forest Service – Atlantic Forestry Centre, 1350 Regent Street, PO Box 4000, Fredericton, New Brunswick E3B 5P7, Canada

<sup>b</sup> Faculty of Forestry and Environmental Management, University of New Brunswick, 28 Dineen Drive, Fredericton, NB E3B 5A3, Canada

<sup>c</sup> Natural Resources Canada, Canadian Forest Service – Laurentian Forestry Centre, 1055 rue du P.E.P.S., P.O. Box 10380, Stn. Sainte-Foy, Quebec, QC G1V 4C7, Canada

## ARTICLE INFO

### Keywords:

Windthrow  
Disturbance  
Hurricane  
Stand structure  
Forest dynamics

## ABSTRACT

Wind is an important driver of forest dynamics in eastern Canada, but knowledge of variables that predispose forest stands to windthrow remains unclear. This is of particular concern as climate change is expected to alter the frequency of strong wind events that affect eastern Canada. In this study, we used widescale forest survey data from Nova Scotia, Canada, of wind damage caused by Hurricane Juan, to investigate variables that influence stand vulnerability to windthrow. Juan made landfall as a category SS2 hurricane with sustained winds of 158 km/h and damaged over 600,000 ha of forest. The damage zone was surveyed using aerial photography and satellite imagery, delineated according to level of wind damage, and digitized as a 15 × 15 m resolution spatial raster layer. We selected a random sample of 50,000 cells classified as intact forest and 50,000 cells classified as stand-replacing windthrow from the raster layer and used boosted regression tree analysis to explore the influence of various meteorological, topographic, soil, and forest structural variables on the occurrence of windthrow. Wind speed and forest structure, specifically stand height and species composition, were most influential in determining windthrow. Sustained winds of at least 95 km/h or gusts of 130 km/h caused > 50% probability of windthrow. Taller stands were most vulnerable, especially those dominated by spruce (*Picea* spp.) and balsam fir (*Abies balsamea*), whereas higher hardwood and pine abundance reduced windthrow. Interestingly, topographical exposure (TopeX) ranked low in overall influence; however, a clear relationship between increased exposure and windthrow was observed.

## 1. Introduction

Wind is an important driver of forest dynamics in eastern Canada's Acadian Forest Region (Seymour et al., 2002; Neily et al., 2008), but which variables predispose forest stands to windthrow is not well known, especially for catastrophic wind events, such as hurricanes. Hurricanes are relatively infrequent in this region, making landfall only every 5–10 years (Chenoweth, 2006; Environment and Climate Change Canada, 2016), but have disproportionate and long-lasting effects on the forest landscape, relative to less intense wind storms (Dwyer, 1979; Everham and Brokaw, 1996). The Acadian Forest is part of an ecological transition zone that links conifer-dominated boreal forest to the north with temperate deciduous forests to the south (Rowe, 1972; Loo and Ives, 2003). Although studies have investigated the impacts of hurricanes on nearby, temperate New England forests (e.g., Foster and Boose, 1992), to date, no study has directly examined the effects of

hurricanes on the Acadian Forest. This is of particular concern as climate change is expected to increase the frequency of severe hurricanes that will affect the Acadian Forest over the 21st century (Dale et al., 2001; Knutson et al., 2010; National Oceanic and Atmospheric Administration, 2018), and knowledge of their effects on forest dynamics is critical to the development of future sustainable forest management practices (Dale et al., 1998; Busby et al., 2008).

Windthrow is the result of a balance between applied forces (wind and gravity) and resistance to these forces, such as tree crown and rooting properties (Everham and Brokaw, 1996). Four broad groups of variables are important in determining a forest stand's vulnerability to windthrow: (1) meteorological variables that characterize the nature of the wind force itself; (2) topographical variables that modulate the movement of wind across the land surface; (3) soil variables that influence the anchorage of tree roots; and (4) stand structural variables that affect tree resistance to wind and gravity (Stathers et al., 1994;

\* Corresponding author at: Natural Resources Canada, Canadian Forest Service – Atlantic Forestry Centre, 1350 Regent Street, PO Box 4000, Fredericton, New Brunswick E3B 5P7, Canada.

E-mail address: [anthony.taylor@canada.ca](mailto:anthony.taylor@canada.ca) (A.R. Taylor).

<https://doi.org/10.1016/j.foreco.2018.12.026>

Received 30 October 2018; Received in revised form 6 December 2018; Accepted 14 December 2018

0378-1127/ Crown Copyright © 2018 Published by Elsevier B.V. All rights reserved.

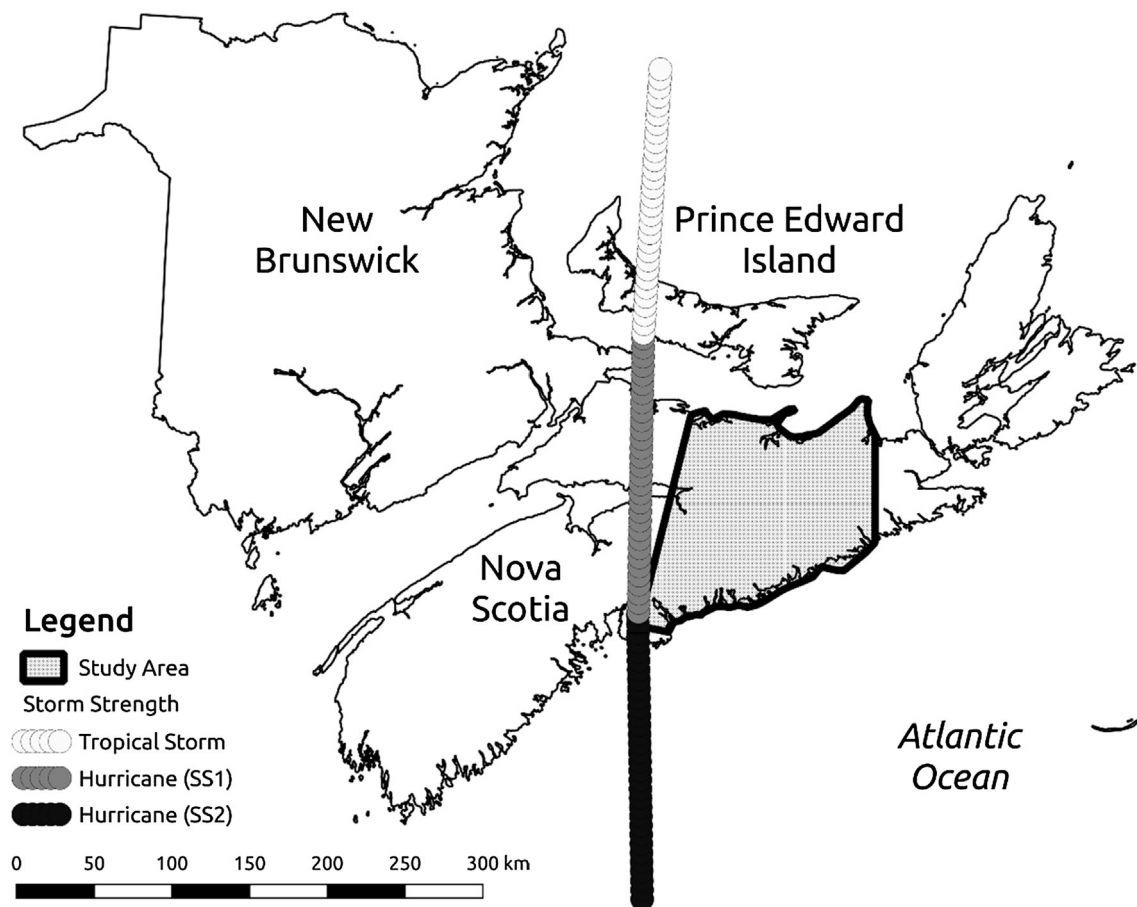


Fig. 1. Map of study area and track of Hurricane Juan through Nova Scotia.

Mitchell, 2013). How these variables affect wind firmness of trees is well studied for small-scale wind events, but much less is known about their relative importance during hurricanes, which vary greatly in the intensity, direction, turbulence, and duration of wind forces generated (Everham and Brokaw, 1996; Mitchell, 2013). Generally, unidirectional sustained winds (i.e., average wind speed measured 10 m above the ground over a 10-min period; World Meteorological Organization 2018) stronger than 90 km/h are considered to cause windthrow, with few tree species capable of withstanding wind speeds above 100 km/h for more than 10 min (Stathers et al., 1994; Nicoll et al., 2008). However, during a hurricane, multidirectional bursts of turbulent, high speed winds (i.e., gusts lasting less than a minute) often exceed these values, but their influence on windthrow is poorly understood, particularly when experienced over long durations (e.g., several hours) and wide areas (Everham and Brokaw 1996).

In addition to characteristics of wind events, many variables can influence stand vulnerability to windthrow (Stathers et al., 1994; Everham and Brokaw, 1996; Mitchell, 2013). Topographical position may be especially important as it can expose or shelter stands of trees from wind (Ruel et al., 1998; Xi et al., 2008; Waldron et al., 2013). Surface winds flow over and around hills and can change direction by as much as 90% as they are funneled through valleys and around mountains (Stathers et al., 1994; Ruel et al., 2001). The windward side of a ridge, hill, or mountain will generally experience stronger winds than the leeward side (Everham and Brokaw, 1996). The combined interaction of meteorological variables and topography is referred to as “wind exposure,” which can be developed into a topographic wind exposure index called “TopeX” (cf., Ashcroft et al., 2008). Although the importance of wind exposure on stand vulnerability to windthrow is well known (e.g., Ruel et al. 2000), its influence relative to other site

and stand structural variables remains unclear, especially during strong wind events and across diverse forest types (e.g., Foster and Boose, 1992; Dobbertin, 2002; Kupfer et al., 2008).

Soil directly contributes to soil–root resistance to windthrow by providing anchorage (Everham and Brokaw, 1996; Mitchell, 2013). The physical properties of soil that govern root morphology and overall size and shape of the soil–root mass (i.e., the root ball) are the most important determinants of anchorage, with well-drained, deep soils of low bulk density and stoniness promoting deep, robust root networks (Nicoll et al., 2006; Waldron et al., 2013). However, soil properties may have minimal influence on windthrow severity in forests dominated by shallow-rooted tree species, such as spruce (*Picea* spp.) and balsam fir (*Abies balsamea* [L.] Mill.), which comprise greater than 40% of the Acadian Forest, because these species are unlikely to fully exploit deep soils (Waldron et al., 2013). Additionally, poorly drained, wet soils have low shear strength, and wetness decreases soil-to-root adhesion forces, both contributing to reduced anchorage (Stathers et al., 1994; Nicoll et al., 2006). This may be particularly problematic during hurricanes, which are often associated with high rainfall and localized flooding.

Stand structural variables, such as age, height, density, and species composition have each been linked to wind firmness (Mitchell, 2013), but their relative importance during hurricanes is unclear. Young stands are more windfirm than older stands (e.g., Kupfer et al., 2008; Bouchard et al., 2009) as age controls tree height and taper, and taller trees with greater height-to-diameter ratio are more vulnerable to overturning (Xi et al., 2008; Valinger and Fridman, 2011). Higher stem density promotes wind firmness as interlocking root systems and adjacent stems help absorb sway and movement caused by wind, and crown closure can reduce wind drag over the canopy, elevating

turbulence and eddies (Scott and Mitchell, 2005). However, trees grown in high density stands tend to allocate more growth to crown and fine roots, thereby making them more susceptible to turnover if the stand is opened up by natural or commercial thinning (McGrath and Ellingsen, 2009; Mitchell, 2013). Furthermore, trees that have developed under more open stand conditions can become acclimatized to wind through continued wind exposure and allocation of resources to stem thickening and thickening and lengthening of lateral roots (Nicolli and Ray, 1996). Species vary considerably in wind firmness due to differences in canopy and rooting architecture, leaf shape and texture, and stem strength and elasticity (Everham and Brokaw, 1996). Generally, trees with small, less dense crowns composed of leaves and flexible branches produce less wind drag, and trees with strong stem wood and deep rooting habit are less prone to stem breakage and uprooting (Xi et al., 2008; Valinger and Fridman, 2011; Waldron et al., 2013). However, whether individual species adaptations are important during a hurricane is unclear as differential adaptations may be overcome by the strength and variability of wind generated by a hurricane.

In this study, we provide the first investigation of variables that predispose forest stands to windthrow during a catastrophic wind event in the Acadian Forest Region of eastern Canada. To do so, we made use of a natural experiment created following the landfall of Hurricane Juan on 29 September 2003, near Halifax, Nova Scotia. Juan made landfall as a category 2 Saffir Simpson (SS) hurricane with sustained winds of 158 km/h, and gusts of up to 185 km/h (Fogarty, 2004). As the system traversed northward, across the central portion of Nova Scotia (Fig. 1), it lost strength and was downgraded to a tropical storm by the time it passed into the Northumberland Strait, providing a wide gradient in wind conditions that affected a wide variety of forest and site types. Overall, the storm lasted approximately 3 h and damaged over 600,000 ha of forest. The damaged area was surveyed using aerial photography and satellite imagery immediately following the storm (Fall of 2003), which provided the opportunity to determine the importance of variables controlling windthrow during an infrequent, severe wind event. We hypothesized that wind speed would be the most important variable affecting stand windthrow, but that this effect would vary according to topography, soils, and stand structural variables. More specifically, we predicted that (1) topography would be the second most important variable affecting windthrow as topographic position has the potential to substantially expose or protect forest stands from prevailing winds; (2) well-drained, less stony soils would be more resilient to windthrow because they promote deeper rooting habit and anchorage; and (3) stands composed of wind-tolerant species would be less prone to windthrow because they possess traits that make them less susceptible to wind drag and uprooting.

## 2. Methods

### 2.1. Study area and natural disturbances

The study area covers approximately 1.5 million hectares of central Nova Scotia, Canada (corner coordinates: SW –63.787, 44.564; NW –63.362, 45.791; NE –61.899, 45.871; SE –61.861, 45.040), and includes most of the area damaged by Hurricane Juan (Fig. 1). This area is part of the Acadian Forest Region and includes a wide range of vegetation communities created from diverse climatic and geographic conditions (Rowe, 1972; Neily et al., 2013). Inland, the terrain becomes hilly and elevation rises to 300 m. Precipitation generally ranges from 1100 to 1500 mm per year with variable amounts of snow, depending on elevation and distance to the coast (Neily et al., 2013).

The study area is 81% forested, 14% wetlands/barrens/water covered, 3% urban (including the greater Halifax area), and 2% agricultural (Nova Scotia Department of Natural Resources, 2016). There are 32 common tree species throughout the study area. White spruce (*Picea glauca* [Moench] Voss) and shade-intolerant hardwood species, such as red maple (*Acer rubrum* L.) and white birch (*Betula papyrifera*

Marsh.), are most common along coastal areas. Further inland, red (*Picea rubens* Sarg.) and black (*Picea mariana* [Mill.] BSP) spruce predominate and are often associated with balsam fir. Although spruce dominates many areas, shade-tolerant hardwoods are common on hillsides and tops, typically comprising of sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britt.), and American beech (*Fagus grandifolia* Ehrh.). Red pine (*Pinus resinosa* Ait.), white pine (*Pinus strobus* L.), and eastern hemlock (*Tsuga canadensis* [L.] Carr.) are scattered throughout the landscape, but seldom form pure stands (Loucks, 1962; Neily et al., 2013). All hardwoods were still fully leafed prior to Hurricane Juan making landfall.

Small canopy gap-forming disturbances ( $\approx 10\text{--}1000\text{ m}^2$ ) are the most common form of natural disturbance driving forest dynamics in the study area and are primarily caused by wind, pathogens, and insect herbivory, with average return intervals of 50–200 years (Seymour et al., 2002; Neily et al., 2008). Wildfire and strong wind events (e.g., hurricanes) are the two dominant natural stand-replacing disturbances. The return interval of stand-replacing fire is estimated to be > 1000 years in the study area (Wein and Moore, 1979). The return interval of stand-replacing windthrow is unknown. Historically, Nova Scotia has experienced more hurricanes and wind storms than any other Canadian province, with 35 hurricanes from 1850 to 2016 (28 SS1 and seven SS2 strength) (Environment and Climate Change Canada, 2016; National Oceanic and Atmospheric Administration, 2018). Most of these hurricanes caused thousands of hectares of low severity forest damage along their track, but some SS2 class hurricanes, such as Hurricane Juan, have caused extensive and severe forest damage (Boose et al., 2001; Lorimer and White, 2003).

### 2.2. Sampling design and response variable

We used wind damage survey data collected by the Nova Scotia Department of Natural Resources (NSDNR) following Hurricane Juan to explore variables that control forest vulnerability to windthrow. Immediately following Juan, NSDNR conducted an aerial photograph (1:24,000 scale) survey covering the full spatial extent of Hurricane Juan's damage path through central Nova Scotia. All areas interpreted from the aerial photos as sustaining severe, stand-replacing windthrow (> 75% of all trees overturned) were delineated as polygons and digitized into a geographic information system (GIS) file. Subsequently, NSDNR also purchased Landsat 5 satellite imagery of the study area from before (August 2002) and following (August 2004) the storm and used multi-spectral band analysis and supervised training-classification procedures (based on known areas of windthrow identified from the aerial photo survey and local forest sample plot data) to further discriminate areas of partial windthrow and salvage harvests from intact (non-windthrown) forest. Results from the Landsat imagery analysis and aerial photo interpretation were combined into a single rasterized windthrow data layer of the entire study area, which included 42,482,217  $15 \times 15\text{ m}^2$  cells delimiting forest areas as partially damaged, severely damaged, or intact (i.e., non-wind damaged).

We selected a random sample of 50,000 cells classified as intact forest and 50,000 cells (herein referred to as points) classified as stand-replacing windthrow from the post-Hurricane Juan windthrow raster data layer. Due to uncertainty in the procedures NSDNR used to classify forest cells as partially damaged (personal communication: James Bruce, NSDNR, April 2017), we excluded these points from the analysis. The original windthrow raster layer was ground-validated in 2004 by NSDNR using their extensive network of forest permanent sample plots. We further validated our sample point data set by comparing it with data for 22 ground plot surveys of windthrow sites from Taylor et al. (2017a).

### 2.3. Explanatory variables

Four groups of explanatory variables were selected based on their

**Table 1**  
Description of variables used in final boosted regression tree model.

Variable Name	Units	Description
Windthrow	Categorical (presence/absence)	Indicator of windthrow
Sustained Wind	Continuous (km/h)	Average wind speed during storm
Wind Gust	Continuous (km/hr)	Maximum wind speed during storm
Topex	Continuous (log of altitudinal degree)	Topographic exposure (0 = high)
Drainage	Categorical (W, I, P) <sup>a</sup>	Dominant soil drainage conditions
Stoniness	Categorical (low, high) <sup>b</sup>	Abundance of rock fragments on soil surface
Texture	Categorical (C, M, F, O) <sup>c</sup>	Dominant soil texture class based on relative abundance of sand, silt, clay or organic material
Crown Closure	Continuous (%)	Dominant canopy layer crown closure
Height	Continuous (m)	Dominant canopy layer height
Hardwood	Continuous (%)	Relative abundance of hardwood species
Pine	Continuous (%)	Relative abundance of pine species
Spruce–Fir	Continuous (%)	Relative abundance of spruce species and balsam fir

<sup>a</sup> W = well drained, I = imperfectly drained, P = poorly drained.

<sup>b</sup> low = < 3% of soil surface covered in stones, high = > 3% of soil surface covered in stones.

<sup>c</sup> C = coarse, M = medium, F = fine, O = organic soil.

hypothesized influence over forest vulnerability to windthrow: (1) meteorological, (2) topographic, (3) soil, and (4) forest structure. Data for each variable were acquired as spatial vector or raster layers and were spatially intersected with the 100,000 sample points using QGIS version 2.18.17. More detail on the acquisition and construction of each explanatory variable is provided below, and the final set of modeled variables is described in Table 1.

### 2.3.1. Meteorological variables

Meteorological data were collected from 63 weather stations within and neighboring the study area between 11:00 pm September 28 and 11:00 am September 29, 2003 (Environment and Climate Change Canada <http://climate.weather.gc.ca>) and used to create spatial raster layers of maximum sustained wind (2-min average), maximum wind gust speed (sudden increase in wind speed lasting < 20 sec), wind direction (which was used to develop the topographic exposure variable – see topographic variables), and precipitation. However, not all data were available from all stations. Of the 63 total stations, 52 collected precipitation, 33 collected sustained wind speed and direction, and 32 collected maximum wind gust speed. Therefore, weather station data were imported into QGIS as point vector files, and each weather variable was converted into a continuous raster using the Inverse Distance Weighted tool in the QGIS Spatial Analysis toolbox.

### 2.3.2. Topographic variables

Digital elevation model (DEM) data (1 m resolution) of the study area was acquired from the Nova Scotia Geomatics Centre (<https://nsgi.novascotia.ca/gdd/>) and used to construct a Topex raster layer (Ashcroft et al., 2008) using the QGIS hillshade tool. Topex is considered an important predictor of windthrow risk as it takes into consideration the topographical condition (i.e., elevation, slope, aspect) of each sample point relative to its surrounding topography and the direction of the predominant wind (Kramer et al., 2001). Dominant wind direction along the track of Hurricane Juan ranged from 130°–138° (southeast), so an azimuth of 135° was used to calculate Topex. Separate aspect and slope raster layers were also created from the DEM using the QGIS Terrain Models tool. Although the Topex variable uses DEM, aspect, and slope in its formulation, we tested for possible individual effects of DEM, aspect, and slope on windthrow.

### 2.3.3. Soil variables

We used the Nova Scotia Ecological Land Classification system (NSEL; <https://novascotia.ca/natr/forestry/ecological/ecolandclass.asp>; Neily et al., 2017) for soil variable data. The NSEL provides hierarchical mapping of Nova Scotia's ecosystems. Ecosystems are the smallest mapped homogeneous units, ranging in size between 1 and 10,000 ha, and represent areas of similar edaphic conditions (Neily

et al., 2017). Soil drainage and texture values identified for each ecosystem represent the dominant (> 60% of area) soil drainage and texture conditions. Drainage was classified as well (W), imperfect (I), or poorly (P) drained (Neily et al., 2017). Texture is an indicator of the relative percentage of sand, silt, and clay in the soil and was classified as coarse, medium, fine, or organic, with “organic” referring to soils dominated by decomposing plant material rather than mineral substrate (Neily et al., 2017).

A measure of soil surface stoniness, defined as the abundance and distribution of rock fragments > 25 cm, was acquired from the Canadian Soil Information Service, a section of Agriculture and Agri-Food Canada (<http://sis.agr.gc.ca/cansis>) as spatial vector files. Stoniness was measured as the percentage of surface soil covered by stones, with values < 3% indicating low stoniness and > 3% indicating high stoniness.

Lastly, a depth-to-water index was acquired from the NSDNR wet areas mapping spatial layer (<https://novascotia.ca/natr/forestry/gis/wamdownload.asp>). This spatial vector layer shows the modeled depth-to-water table based on digital elevation and known locations of surface water bodies and wetlands in Nova Scotia.

### 2.3.4. Forest variables

Forest stand inventory data describing tree species composition, height, and crown closure of the dominant canopy layer were obtained from the NSDNR provincial forest stand inventory GIS layer (<https://novascotia.ca/natr/forestry/gis/forest-inventory.asp>). The forest inventory was based on aerial photo interpretation of forest stands delineated as polygons and provided as a continuous spatial vector layer. Each year a subsection of stands are ground-truthed using the Nova Scotia forest ground plot measurements. We used the most recent forest inventory data prior to Hurricane Juan, which ranged between 1997 and 2003. The forest inventory included relative abundance of 32 tree species; however, we grouped all species into three species groups focusing on species traits that affect susceptibility to windthrow: spruce–fir, pine, and hardwood.

## 2.4. Data analysis

### 2.4.1. Statistical model

We analyzed windthrow response against our pool of explanatory variables using a generalized boosting model (GBM; Ridgeway, 2017), also referred to as boosted regression tree analysis (BRT), which is an ensemble regression tree method in which many simple regression trees, generated using recursive binary splits based on the explanatory power of a single variable (or predictor) at each split, are fitted in a step-wise manner (Elith et al., 2008). Boosted regression tree analysis accommodates many of the violations of conventional, parametric



**Table 2**

Results of the boosted regression tree (BRT) analysis of windthrow. The relative influence of each explanatory variable indicates its proportional contribution to the accounted-for variation of the BRT model.

Model Performance Diagnostics	Value
Prediction Accuracy	0.88
Cohen's Kappa Score	0.75
AUC	0.95
<b>Variable Relative Influence (%)</b>	
Sustained Wind <sup>a</sup>	80.6
Height	9.2
Stoniness	3.0
Hardwood	2.6
Spruce–Fir	1.8
Drainage	1.0
Topex	0.9
Crown Closure	0.6
Pine	0.4
Texture	0.3

<sup>a</sup> Wind Gust was also ranked the most influential variable, with a score of 81.4%, in the BRT model in which ‘Sustained Wind’ was replaced by ‘Wind Gust’.

statistics (e.g., multiple linear regression) that are common to observational data, including missing data, departures from normality and homogeneity of variance, and strong collinearity among explanatory variables, and is considered well suited to analyzing ecological data (Elith et al., 2008; Zhang et al., 2014). Furthermore, BRT has been demonstrated to outperform, in predictive abilities, all other forms of tree-based regression methods, including the Random Forest algorithm (Caruana and Niculescu-Mizil, 2006).

All BRT models and supporting analyses were performed using R version 3.4.4 (R Core Team, 2017) and the R gbm package (Ridgeway, 2017). A BRT model was first built using all available explanatory variables (i.e., full model). Because the response variable was binomial, we selected a bernoulli response distribution. The default 0.5 bag fraction was used for analyses. Optimal model hyperparameters for the full model were manually searched by running a grid of alternative models using different hyperparameter settings and using cross-validation (with 10 folds) to evaluate model performance. Based on recommended optimal settings for ecological modeling (Elith et al., 2008), we varied learning rate by 0.1–0.001, tree complexity by 2–5, and number of trees by 1000–30000 to find the combination of hyperparameters that provided a balance of high performance, minimal computational cost, and model simplicity. A final model based on 4000 trees, a learning rate of 0.01, and tree complexity of 3 was selected.

#### 2.4.2. Simplifying model explanatory variables

Variable selection in BRT is achieved because the model largely ignores non-informative variables when fitting trees. However, model simplification (removing variables) can be useful as redundant or unimportant variables can degrade model performance, interfere with variable interpretation, or be helpful if users are uncomfortable with inclusion of unimportant variables (Strobl et al., 2008; Dormann et al., 2013; Gregorutti et al., 2017).

Elith et al. (2008) describe a method for model simplification that uses variable importance to choose which variables to remove in a backwards stepwise procedure. We followed a similar strategy, but used a combination of correlation between explanatory variables and expert judgment (meaning that, even if a pair of variables were highly correlated, we considered retaining both if it supported testing our hypotheses; see Results section for further explanation) to consider whether a variable should be dropped from the model. Correlation between all pairs of variables was calculated and, starting with the most correlated pair of variables, the model was refitted without each variable in turn. Each model was run using a training data set (80% of original

data) and compared using change in AUC, with change in AUC of > 0.1 considered significant. The reduced model with the best performance was selected, so long as performance was not significantly less than that of the full model, and used as the base model for the next comparison, until all variable pairs with a correlation coefficient greater than 0.75 were tested.

Lastly, because we chose a tree complexity level of 3 in our final BRT model, there is the possibility of observing important interactions between explanatory variables. To test for potential 2-way interaction effects, we relied on the `interact.gbm` function provided in the `gbm` package, which computes the dimensionless Friedman's H-statistic to assess the strength of pair-wise variable interactions. Interpretation of the H-statistic is somewhat arbitrary, but lies on a scale between 0, indicating no interaction, and 1, denoting a strong interaction. There is currently no universally agreed upon value of H-statistic that signifies significant interaction, therefore we chose to investigate any 2-way interactions that resulted in an H-statistic > 0.1.

### 3. Results

Several variables with high variable importance in the full model were removed because of correlation with other variables: (1) Precipitation was highly correlated (87%) with Sustained Wind and Wind Gust; (2) DEM, Aspect, and Slope were correlated with Topex, but consistently ranked lower in importance; and (3) Depth-to-Water and Drainage were correlated (48%) but Depth-to-Water consistently ranked lower in importance. However, several correlated variables were retained in the analysis. Sustained Wind and Wind Gust were highly correlated (98%), but both were consistently the strongest predictors of windthrow, so we created separate models for each variable, within which the wind variable ranked highest in importance with all other variables following similar rankings. The species composition variables Hardwood, Spruce–Fir, and Pine were all inversely correlated, with Hardwood and Spruce–Fir being most correlated (91%), but given our interest in the potential effects of tree species composition and abundance on critical windthrow thresholds, we retained all three composition variables in the final BRT model. The final set of explanatory variables, along with variable importance rankings and model performance diagnostics, is shown in Tables 1 and 2, respectively.

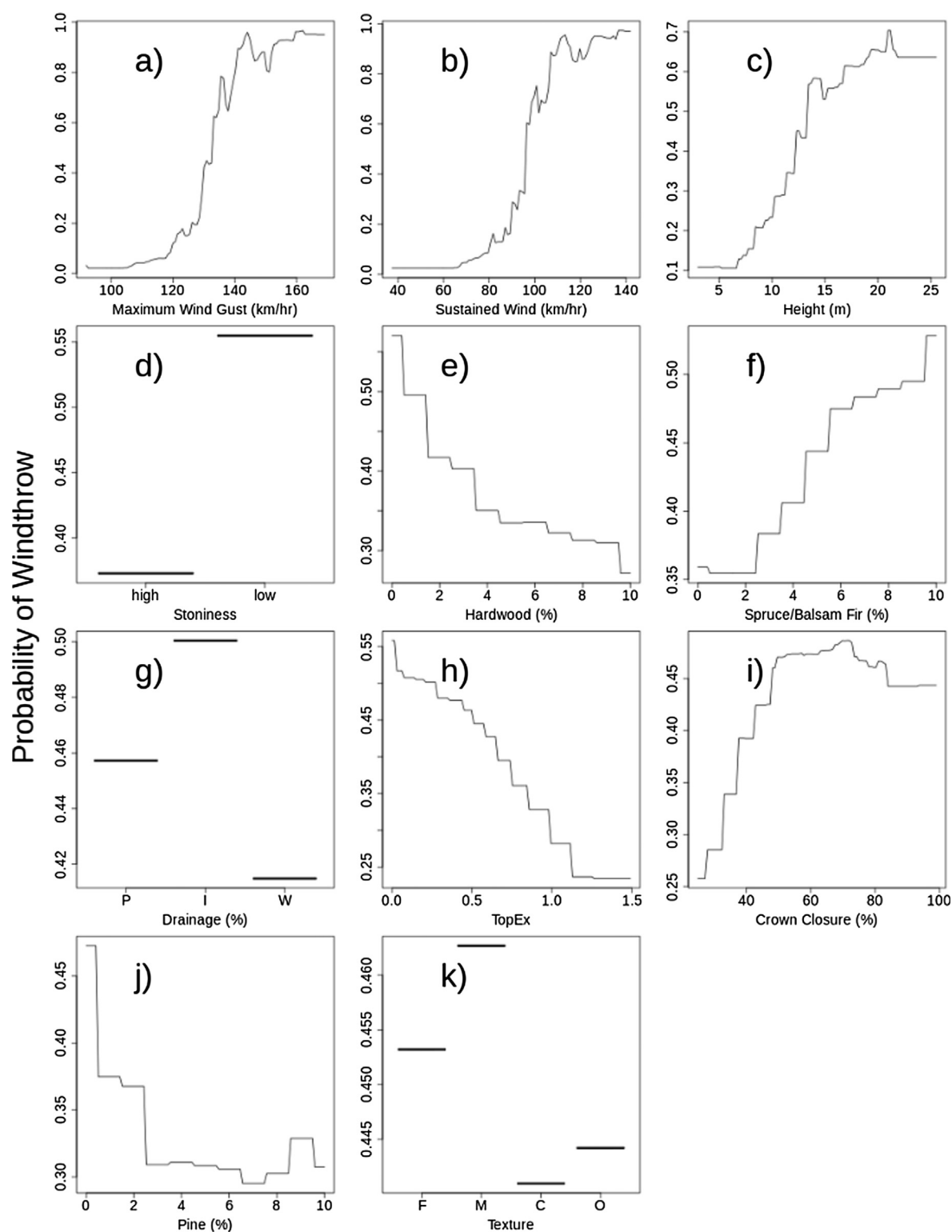
The final BRT model had a prediction accuracy of 89%, a Cohen's Kappa score of 0.75, and an AUC of 0.95 on a withheld set of test data (20% of original data) (Table 2). Kappa is a commonly used metric for evaluating the performance of machine learning algorithms and is a particularly useful measure of performance of prediction accuracy as it accounts for imbalances in the proportion of observations in each class of response data. Kappa scores lie between –1 to 1, with values > 0.70 indicating excellent performance (Landis and Koch, 1977). Similarly, AUC scores > 0.90 suggest high agreement between model predictions and test data.

#### 3.1. Wind speed

Sustained Wind and Wind Gust were, overwhelmingly, the most influential variables affecting stand vulnerability to windthrow, with both variables individually contributing > 80% of accounted-for variation in the BRT model (Table 2). Each wind variable demonstrated a clear sigmoidal relationship between increasing wind speed and risk of windthrow (Fig. 2a, b). Partial dependence plots (Fig. 2a, b) showed that, after averaging out the effects of all other variables in the model, Wind Gust of 130 km/h or Sustained Wind of 95 km/h caused a > 50% probability of windthrow.

#### 3.2. Forest structure

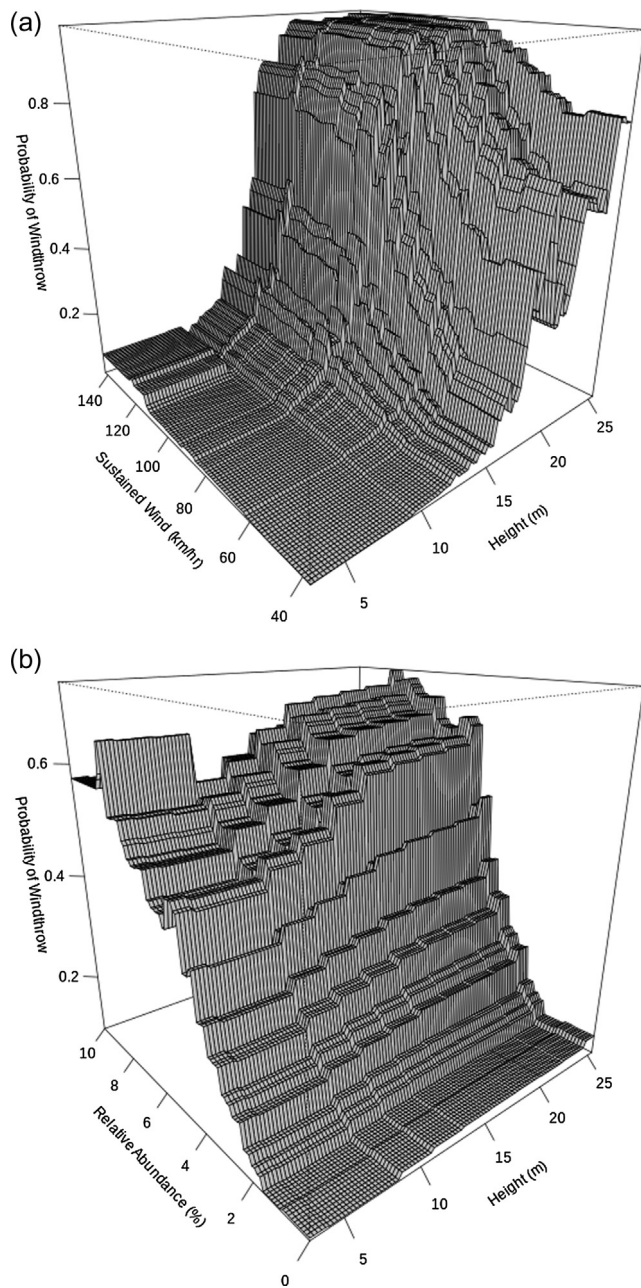
Forest structure, including stand height and species composition,



**Fig. 2.** Partial plot (a–k) results of the boosted regression tree analysis of windthrow comparing the probability of windthrow with each explanatory variable. Refer to [Table 1](#) caption for all class abbreviations.

were the next most influential variables affecting forest vulnerability to windthrow. Height was the second most influential variable, and abundance of Hardwood and Spruce–Fir were the fourth and fifth most influential variables, respectively ([Table 2](#)). Crown Closure had minimal influence on windthrow ([Table 2](#), [Fig. 2i](#)), but, interestingly, showed that more open stands (crown closure < 50%) had a lower risk of windthrow.

Taller stands had a higher windthrow risk from Hurricane Juan, with stands greater than 14 m tall having a > 50% probability of windthrow ([Fig. 2c](#)). In addition, a significant interaction (H-statistic = 0.2) between Height and wind (both Sustained Wind and Wind Gust) occurred ([Fig. 3a](#)). Shorter stands required higher wind speeds to be blown over, relative to taller stands. Indeed, even with sustained winds of 140 km/h, stands < 10 m tall had < 10% probability of



**Fig. 3.** Interaction plots displaying probability of windthrow compared with (a) sustained wind speed (km/h) and height (m), and (b) relative abundance of softwood (%) and height (m).

windthrow (Fig. 3a).

Stands with a greater abundance of Hardwood were less likely to experience windthrow than Spruce–Fir dominated stands (Fig. 2e, f). Hardwood-dominated stands (e.g., > 80% hardwood species) had a < 30% chance of windthrow, whereas Spruce–Fir dominant stands had a > 50% probability of windthrow. However, a significant interaction ( $H$ -statistic = 0.2) between Height and Spruce–Fir abundance occurred (Fig. 3b), whereby stands that contained little Spruce–Fir (< 20%) had a low probability of windthrow, even when tall. In contrast, stands that contained higher proportions of Spruce–Fir, even short stands (e.g., < 10 m tall), had a > 50% probability of windthrow.

### 3.3. Topographic and soil conditions

Of the topographic and soil-related variables tested, Stoniness had

the greatest influence on windthrow from Hurricane Juan, but counter to our expectations, sites with low stoniness had a higher probability of windthrow than those with high stoniness (Table 2, Fig. 2d). Similarly, coarse-textured soils had lower probability of windthrow than fine or medium-textured soils (Fig. 2k). Drainage was the second most influential soil variable, with imperfectly drained soils having the highest risk of windthrow (Fig. 2g). Interestingly, both Texture and Drainage demonstrated a convex relationship versus windthrow risk, with moderate levels of either Texture or Drainage having the highest probability of windthrow. Although Topex did not rank highly in overall variable importance, a clear relationship between site exposure to wind and risk of windthrow was evident, with more protected (less exposed) sites having a lower probability of wind damage (Fig. 2h).

## 4. Discussion

As expected, wind speed was the most influential variable affecting windthrow from Hurricane Juan, supporting our first hypothesis. However, contrary to our second hypothesis, topography (i.e., Topex), was less important than anticipated. Rather, stand structure, specifically Height and the species composition variables, were most important following wind speed, similar to previous studies that have examined predictors of forest damage from hurricanes in eastern North America (e.g., Foster and Boose, 1992; Dobberty, 2002; Kupfer et al., 2008). Although soil variables also had influence over windthrow, their effects were primarily contrary to our expectations: stony, coarse textured, and wet soils showed the lowest probability of windthrow.

### 4.1. Interactions between wind and stand height

On average across all site and stand conditions, maximum sustained wind speeds > 95 km/h (26 m/sec) or gust speeds > 130 km/h (36 m/sec) increased the probability of stand-replacing windthrow by > 50%. These results align with previous reports indicating average hourly wind speeds of > 90 km/h (25 m/sec) or gust speeds > 100 km/h (28 m/sec) can lead to catastrophic wind damage to forests (Stathers et al., 1994; Nicoll et al., 2008).

However, as we hypothesized, the effect of wind speed varied with stand height, whereby windthrow of taller stands required substantially less wind force than in shorter stands. The effect of tree height on wind firmness is well documented (Stathers et al., 1994; Xi et al., 2008; Valinger and Fridman, 2011) and stand height (or age, which may be considered as a proxy for height) has been reported as an important predictor of stand damage during hurricanes and strong wind storms (e.g., Foster and Boose, 1992; Dobberty, 2002; Kupfer et al., 2008; Bouchard et al., 2009). Taller trees provide a longer ‘lever’ on which the applied forces of wind and gravity can act: i.e., the longer the lever, the less force required to overturn a tree (Mitchell, 2013). Moreover, taller trees, especially those grown in dense stands, tend to have higher height-to-diameter ratios, and slender stems are more prone to breakage than shorter, thicker stems (McGrath and Ellingsen, 2009). However, our study also detected an interaction between stand height and the relative abundance of spruce–fir, with the positive relationship between height and windthrow varying according to stand composition. Tall stands with less spruce–fir were less likely to blow over than spruce–fir dominated stands, and even short spruce–fir stands (< 10 m tall) had a greater probability of windthrow.

### 4.2. Importance of stand composition and crown closure

Although our hypothesis regarding the importance of species composition was supported, the overall influence of composition on windthrow from Hurricane Juan was stronger than expected, but did corroborate previous reports (e.g., Foster and Boose, 1992; Kupfer et al., 2008). Higher hardwood abundance substantially reduced the risk of stand-replacing windthrow, whereas spruce–fir content increased the

probability of windthrow. Previous studies have also found that mixed species stands, especially those with high hardwood abundance, are more resistant to windthrow (Valinger and Fridman, 2011). Spruce spp. and balsam fir are highly susceptible to windthrow because their crowns of dense branches and foliage are inflexible to wind, causing considerable wind drag, and their shallow rooting also impedes anchorage (Stathers et al., 1994; Valinger and Fridman, 2011; Waldron et al., 2013).

Although the influence of pine abundance on windthrow from Hurricane Juan was not as strong as for spruce–fir, higher pine abundance did increase resistance to windthrow. White pine is the predominant pine species in the study area, but seldom occurs in pure stands and is most often found mixed with spruce and balsam fir (Neily et al., 2013, 2017). Indeed, many firsthand accounts of the storm's aftermath describe softwood stands > 75% blown flat except for the white pine component, where the wind acted as a selective thinning agent, as observed by Rich et al. (2007). Similar to hardwood species in the study area (e.g., red maple and yellow birch), white pine canopies are generally less dense than spruce and balsam fir and comprise fewer, larger branches. Furthermore, pine needles are long, narrow and very flexible, which substantially reduces wind drag. Combined with their strong stem wood and deep rooting habit, stands with high white pine and hardwood proportions are less vulnerable to windthrow.

Crown closure had only a minor influence on windthrow, and its effect was contrary to our expectations. Whereas studies have found that higher crown closure decreases stand vulnerability to windthrow, due to the buffering effects of neighboring tree stems (e.g., Scott and Mitchell, 2005), our results indicated the opposite, with stands of < 50% crown closure having the lowest risk of windthrow. However, this may be because primarily natural stands were sampled in our study, not subjected to commercial thinning or partial cutting. Therefore, stands of lower crown closure likely developed naturally, over time, and the trees within them have acclimated to open-grown conditions (Mitchell, 2013). Indeed, open-grown trees, including plantations raised at lower stocking densities, are exposed to more wind from a young age and allocate more resources to stem thickening and lengthening of lateral roots (Stathers et al., 1994; Nicoll et al., 2008). Other research conducted within our study area has shown that reducing crown density of mature stands through harvesting significantly increases risk of windthrow, especially in spruce- and balsam fir-dominated forests (McGrath and Ellingsen, 2009).

#### 4.3. Role of topography and soil conditions

Despite the reported importance of wind exposure on windthrow (e.g., Ruel et al., 2000, 2001; Xi et al., 2008), it did not have a major influence on stand vulnerability to windthrow during Hurricane Juan. One possibility for its low ranking in variable importance may be because the wind variables included in our study inherently include variation in wind speed attributed to the effect of Topex. However, because the wind data were interpolated at a resolution of 2.5 km<sup>2</sup> and the Topex layer at 10 m<sup>2</sup>, it is unlikely that the coarse-scale wind data would capture much variation in wind speed caused by topography. Another possibility is that, although the dominant wind direction along the track of Hurricane Juan was approximately 135° (southeast), wind generated from hurricanes is often multidirectional and turbulent (Everham and Brokaw, 1996), with anecdotal accounts of microburst and tornadoes reported, but not confirmed, during Juan (McGrath and Ellingsen, 2009). Our Topex model was unlikely to account for these fine-scale variations in wind conditions, which would confound the effect of Topex on windthrow. Nonetheless, a relationship between Topex and windthrow was detected, corroborating previous studies that show highly exposed stands do have a higher risk of windthrow (Ruel et al., 2000, 2001).

Of the soil variables tested, Stoniness ranked highest in importance; however, counter to Nicoll et al. (2006, 2008), stony soils had the

lowest probability of windthrow. A similar trend occurred for Drainage and Texture, whereby imperfectly drained, medium textured soils (i.e., mesic site types) had the highest risk of windthrow, in contrast to expectations that such conditions promote root anchorage and resistance to wind (Nicoll et al., 2006, 2008). However, less stony sites with deep, fertile soils have been reported as more windthrow prone than shallow, less fertile sites (e.g., Dobberty, 2002; Bouchard et al., 2009) as rich soils promote higher tree growth, inter-tree competition and mutual shelter, which limit acclimative growth toward wind resistance (Mitchell, 2013). Further explanation may be related to the species composition of our study area in relation to soil type. Although no significant difference in the relative abundance of Spruce–Fir or Hardwoods was detected between high or low Stoniness soils, stony soils had a significantly higher relative abundance of white pine (two-sample *t*-test, *p* < 0.01), and coarse-textured soils had the highest mean abundance of pine and hardwoods, both of which are comparatively wind firm. Spruce–fir occurred more on well-drained, medium-textured soils (Taylor et al., 2017a). Given the higher susceptibility of spruce and balsam fir to windthrow, and its propensity for mesic sites, it is not unreasonable to expect higher instances of windthrow on such sites. Similarly, Dobberty (2002) and Waldron et al. (2013) observed that presence of shallow-rooted conifers distorted the expected relationship between mesic site conditions and greater resistance to windthrow, as these species are unable to fully exploit the higher anchorage capacity provided by mesic soils.

## 5. Conclusions

Hurricane Juan was unusual in its strength and trajectory across the province of Nova Scotia, but such events may become more common with projected global climate change (Dale et al., 2001; Knutson et al., 2010; National Oceanic and Atmospheric Administration, 2018), underlining the important opportunity Hurricane Juan provided to study variables controlling the effects of a catastrophic wind event on windthrow in the Acadian Forest Region.

Overall, wind speed was the most influential variable affecting windthrow from Hurricane Juan, but contrary to our expectations, stand structural variables, specifically stand height and composition, were more important predictors of windthrow than topographical exposure. Taller stands, especially those dominated by shallow-rooted spruce and balsam fir were most susceptible to windthrow, whereas higher proportions of pine and hardwood species substantially reduced windthrow risk. This has implications for the local forestry sector who actively promote management strategies that encourage spruce–fir abundance for the production of softwood lumber and pulp and paper. However, climate change is projected to increase the abundance of hardwood and pine species across the Acadian Forest over the 21st century (Taylor et al., 2017b), which may help increase the resilience of these forests to higher incidences of catastrophic wind events.

## Acknowledgments

We thank James Bruce and the Nova Scotia Department of Lands and Forestry for providing data for this project. We also thank Caroline Simpson and the anonymous reviewers, who provided useful comments on an earlier version of this manuscript. This study was funded by Natural Resources Canada and by a Natural Sciences and Engineering Research Council grant to DAM.

## Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2018.12.026>.



## References

- Ashcroft, M.B., Chisholm, L.A., French, K.O., 2008. The effect of exposure on landscape scale soil surface temperatures and species distribution models. *Landscape Ecol.* 23, 211–225.
- Boose, E.R., Chamberlin, K.E., Foster, D.R., 2001. Landscape and regional impacts of hurricanes in New England. *Ecol. Monogr.* 71, 27–48.
- Bouchard, M., Pothier, D., Ruel, J.C., 2009. Stand-replacing windthrow in the boreal forests of eastern Quebec. *Can. J. For. Res.* 39, 481–487.
- Busby, P.E., Motzkin, G., Boose, E.R., 2008. Landscape-level variation in forest response to hurricane disturbance across a storm track. *Can. J. For. Res.* 38, 2942–2950.
- Caruana, R., Niculescu-Mizil, A., 2006. An empirical comparison of supervised learning algorithms using different performance metrics. In: *Proceedings of the 23rd International Conference on Machine Learning*, pp. 161–168.
- Chenoweth, M., 2006. A reassessment of historical Atlantic basin tropical cyclone activity, 1700–1855. *Clim. Change* 76, 169–240.
- Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R.P., Ayres, M.P., Flannigan, M.D., Hanson, P.J., Irland, L.C., Lugo, A.E., Peterson, C.J., Simberloff, D., 2001. Climate change and forest disturbances: climate change can affect forests by altering the frequency, intensity, duration, and timing of fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or landslides. *AIBS Bulletin* 51, 723–734.
- Dale, V.H., Lugo, A.E., MacMahon, J.A., Pickett, S.T., 1998. Ecosystem management in the context of large, infrequent disturbances. *Ecosystems* 1, 546–557.
- Dobbertin, M., 2002. Influence of stand structure and site factors on wind damage comparing the storms Vivian and Lofar. *Forest Snow Landscape Res.* 77, 187–205.
- Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münckmüller, T., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36, 27–46.
- Dwyer, D., 1979. Woodlands shaped by past hurricanes. Nova Scotia Department of Lands and Forests, *Forest Times*. November.
- Elith, J., Leathwick, J.R., Hastie, T., 2008. A working guide to boosted regression trees. *J. Anim. Ecol.* 77, 802–813.
- Environment and Climate Change Canada. 2016. A climatology of hurricanes for eastern Canada. <https://www.ec.gc.ca/hurricane/> (accessed April 10, 2016).
- Everham, E.M., Brokaw, N.V., 1996. Forest damage and recovery from catastrophic wind. *Bot. Rev.* 62, 113–185.
- Fogarty, C., 2004. Hurricane Juan Storm Summary. [http://www.novaweather.net/Hurricane\\_Juan\\_files/Juan\\_Summary.pdf](http://www.novaweather.net/Hurricane_Juan_files/Juan_Summary.pdf) (accessed March 18, 2016).
- Foster, D.R., Boose, E.R., 1992. Patterns of forest damage resulting from catastrophic wind in central New England, USA. *J. Ecol.* 80, 79–98.
- Gregorutti, B., Michel, B., Saint-Pierre, P., 2017. Correlation and variable importance in random forests. *Statist. Comput.* 27, 659–678.
- Knutson, T.R., McBride, J.L., Chan, J., Emanuel, K., Holland, G., Landsea, C., Held, I., Kossin, J.P., Srivastava, A.K., Sugi, M., 2010. Tropical cyclones and climate change. *Nat. Geosci.* 3, 157–163.
- Kramer, M.G., Hansen, A.J., Taper, M.L., Kissinger, E.J., 2001. Abiotic controls on long-term windthrow disturbance and temperate rain forest dynamics in southeast Alaska. *Ecology* 82, 2749–2768.
- Kupfer, J.A., Myers, A.T., McLane, S.E., Melton, G.N., 2008. Patterns of forest damage in a southern Mississippi landscape caused by Hurricane Katrina. *Ecosystems* 11, 45–60.
- Landis, J.R., Koch, G.G., 1977. The measurement of observer agreement for categorical data. *Biometrics* 33, 159–174.
- Loo, J., Ives, N., 2003. The Acadian forest: historical condition and human impacts. *For. Chronicle* 79, 462–474.
- Lorimer, C.G., White, A.S., 2003. Scale and frequency of natural disturbances in the northeastern US: implications for early successional forest habitats and regional age distributions. *For. Ecol. Manage.* 185, 41–64.
- Loucks, O.L., 1962. A forest classification for the Maritime provinces. *Proc. Nova Scotian Inst. Sci.* 25, 86–167.
- McGrath, T., Ellingsen, J., 2009. The effects of hurricane Juan on managed stands commercially thinned in central Nova Scotia. Nova Scotia Department of Natural Resources. Report FOR 2009-4.
- Mitchell, S.J., 2013. Wind as a natural disturbance agent in forests: a synthesis. *Forestry* 86, 147–157.
- National Oceanic and Atmospheric Administration (NOAA). 2018. Global Warming and Hurricanes. <https://www.gfdl.noaa.gov/global-warming-and-hurricanes/> (accessed September 25, 2018).
- Neily, P.D., Basquill, S., Quigley, E., Stewart, B., Keys, K., 2017. Ecological land classification for Nova Scotia. Nova Scotia Department of Natural Resources. Report FOR 2017-13.
- Neily, P.D., Keys, K., Quigley, E., Basquill, S., Stewart, B., 2013. Forest Ecosystem Classification for Nova Scotia. Nova Scotia Department of Natural Resources. Report FOR 2013-1.
- Neily, P.D., Quigley, E., Stewart, B., 2008. Mapping Nova Scotia's natural disturbance regimes. Nova Scotia Department of Natural Resources. Report FOR 2008-5.
- Nicoll, B.C., Gardiner, B.A., Rayner, B., Peace, A.J., 2006. Anchorage of coniferous trees in relation to species, soil type, and rooting depth. *Can. J. For. Res.* 36, 1871–1883.
- Nicoll, B.C., Gardiner, B.A., Peace, A.J., 2008. Improvements in anchorage provided by the acclimation of forest trees to wind stress. *Forestry* 81, 389–398.
- Nicoll, B.C., Ray, D., 1996. Adaptive growth of tree root systems in response to wind action and site conditions. *Tree Physiol.* 16, 891–898.
- Nova Scotia Department of Natural Resources. 2016. State of the forest. [https://novascotia.ca/natr/forestry/reports/State\\_of\\_the\\_Forest\\_2016.pdf](https://novascotia.ca/natr/forestry/reports/State_of_the_Forest_2016.pdf) (accessed February 24, 2018).
- R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Rich, R.L., Frelich, L.E., Reich, P.B., 2007. Wind-throw mortality in the southern boreal forest: effects of species, diameter and stand age. *J. Ecol.* 95, 1261–1273.
- Ridgeway, G., 2017. gbm: Generalized Boosted Regression Models. R package version 2.1.3. <https://CRAN.R-project.org/package=gbm>.
- Rowe, J.S., 1972. Forest regions of Canada. Natural Resources Canada, Canadian Forest Service, Ottawa, Canada.
- Ruel, J.C., Pin, D., Cooper, K., 1998. Effect of topography on wind behavior in a complex terrain. *Forestry* 71, 261–265.
- Ruel, J.C., Pin, D., Cooper, K., 2001. Windthrow in riparian buffer strips: effect of wind exposure, thinning and strip width. *For. Ecol. Manage.* 143, 105–113.
- Ruel, J.C., Quine, C.P., Meunier, S., Suarez, J., 2000. Estimating windthrow risk in balsam fir stands with the Forest Gales model. *For. Chronicle* 76, 329–337.
- Scott, R.E., Mitchell, S.J., 2005. Empirical modelling of windthrow risk in partially harvested stands using tree, neighbourhood, and stand attributes. *For. Ecol. Manage.* 218, 193–209.
- Seymour, R.S., White, A.S., DeMaynadier, P.G., 2002. Natural disturbance regimes in northeastern North America—evaluating silvicultural systems using natural scales and frequencies. *For. Ecol. Manage.* 155, 357–367.
- Stathers, R.J., Rollerson, T.P., Mitchell, S.J., 1994. Windthrow Handbook for British Columbia Forests. B.C. Ministry of Forestry, Victoria, B.C. Working Paper 9401.
- Strobl, C., Boulesteix, A.L., Kneib, T., Augustin, T., Zeileis, A., 2008. Conditional variable importance for random forests. *BMC Bioinf.* 9, 307.
- Taylor, A.R., MacLean, D.A., McPhee, D., Dracup, E., Keys, K., 2017a. Salvaging has minimal impacts on vegetation regeneration 10 years after severe windthrow. *For. Ecol. Manage.* 406, 19–27.
- Taylor, A.R., Boulanger, Y., Price, D.T., Cyr, D., McGarrigle, E., Rammer, W., Kershaw, J.A., 2017b. Rapid 21st century climate change projected to shift composition and growth of Canada's Acadian Forest Region. *For. Ecol. Manage.* 405, 284–294.
- Valinger, E., Fridman, J., 2011. Factors affecting the probability of windthrow at stand level as a result of Gudrun winter storm in southern Sweden. *For. Ecol. Manage.* 262, 398–403.
- Waldron, K., Ruel, J.C., Gauthier, S., 2013. The effects of site characteristics on the landscape-level windthrow regime in the North Shore region of Quebec, Canada. *Forestry* 86, 159–171.
- Wein, R.W., Moore, J.M., 1979. Fire history and recent fire rotation periods in the Nova Scotia Acadian Forest. *Can. J. For. Res.* 9, 166–178.
- World Meteorological Organization (WMO). 2018. Guidelines for converting between various wind averaging periods in tropical cyclone conditions. [https://www.wmo.int/pages/prog/www/tcp/documents/Doc2.3\\_WindAveraging.pdf](https://www.wmo.int/pages/prog/www/tcp/documents/Doc2.3_WindAveraging.pdf) (accessed September 25, 2018).
- Xi, W., Peet, R.K., Decoster, J.K., Urban, D.K., 2008. Tree damage risk factors associated with large, infrequent wind disturbances of Carolina forests. *Forestry* 81, 317–334.
- Zhang, Y., Chen, H.Y., Taylor, A., 2014. Multiple drivers of plant diversity in forest ecosystems. *Glob. Ecol. Biogeogr.* 23, 885–893.