Abiotic controls on windthrow and forest dynamics in a coastal temperate rainforest, Kuiu Island, southeast Alaska
by Marc G Kramer

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Biological Sciences
Montana State University

Abstract:
The pristine coastal temperate rainforests in southeast Alaska present a unique opportunity to study natural patterns disturbance relatively devoid of human influence. We investigated the role of 4 abiotic factors in controlling patterns of long-term windthrow on the forested landscape. Our objectives were to 1) test the hypothesis that long-term patterns of windthrow can be predicted spatially at the landscape scale using four abiotic factors; exposure to prevailing storm direction, slope, elevation and soil stability; and 2) compare stand age and structural characteristics in windthrow-prone and windthrow-protected landscapes. We used photointerpretation to identify forest patches that were of windthrown origin on Kuiu Island, southeast Alaska. A. spatially-explicit logistic model was then built from the windthrow data, and other GIS data layers, based on elevation, slope, exposure to prevailing storm winds and soil type. Landform influence on patterns of windthrow was examined by evaluating model classification error rates by landform type. The model was validated by extrapolating the Kuiu model coefficients to nearby Zarembo Island, and comparing model predictions to an independent large-scale windthrow data set. The model correctly classified 72% of both windthrown and non-windthrown forest. Field plots collected in most and least windthrow-prone landscapes on Kuiu suggest that structural and age characteristics as well as forest development stages (stem-exclusion, understory-reinitiation, or gap-phase forests) vary with probability of windthrow occurrence across the landscape. We conclude that small-scale (partial-canopy) disturbance processes predominate in areas least-prone to windthrow, and that large-scale stand-replacement disturbance processes predominate in areas most-prone to windthrow. Our work suggests that a long-term wind damage gradient exists on Kuiu Island, which can be predicted spatially. Previous to this research forest dynamics in coastal temperate rainforests were thought to be regulated primarily by gap-phase disturbance processes. We conclude there is less naturally occurring old-growth forest regulated by gap-phase succession than previously believed. To date, more than 50% of the timber harvest on Kuiu Island has been located in areas where gap-phase processes (old-growth forests) predominate, only 14% has been in areas where stand-replacement processes predominate. Future management activities should be tailored to consider long-term natural disturbance patterns to better maintain ecosystem function. In areas least-prone to catastrophic storm damage, individual tree or group tree selection may be more appropriate. Two-aged management may be more appropriate in areas most-prone to catastrophic storm effects.

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TABLE OF CONTENTS

TABLE OF CONTENTS--Continued

LIST OF TABLES

Table

LIST OF FIGURES

Figure

LIST OF FIGURES --Continued

ABSTRACT

The pristine coastal temperate rainforests in southeast Alaska present a unique opportunity to study natural patterns disturbance relatively devoid of human influence. We investigated the role of 4 abiotic factors in controlling patterns of long-term windthrow on the forested landscape. Our objectives were to 1) test the hypothesis that long-term patterns of windthrow can be predicted spatially at the landscape scale using four abiotic factors; exposure to prevailing storm direction, slope, elevation and soil stability; and 2) compare stand age and structural characteristics in windthrow-prone and windthrow-protected landscapes. We used photointerpretation to identify forest patches that were of windthrown origin on Kuiu Island, southeast Alaska. A spatially-explicit logistic model was then built from the windthrow data, and other GIS data layers, based on elevation, slope, exposure to prevailing storm winds and soil type. Landform influence on patterns of windthrow was examined by evaluating model classification error rates by landform type. The model was validated by extrapolating the Kuiu model coefficients to nearby Zarembo Island, and comparing model predictions to an independent large-scale windthrow data set. The model correctly classified 72% of both windthrown and non-windthrown forest. Field plots collected in most and least windthrow-prone landscapes on Kuiu suggest that structural and age characteristics as well as forest development stages (stem-exclusion, understory-reinitiation, or gap-phase forests) vary with probability of windthrow occurrence across the landscape. We conclude that small-scale (partial-canopy) disturbance processes predominate in areas least-prone to windthrow, and that large-scale stand-replacement disturbance processes predominate in areas most-prone to windthrow. Our work suggests that a long-term wind damage gradient exists on Kuiu Island, which can be predicted spatially. Previous to this research forest dynamics in coastal temperate rainforests were thought to be regulated primarily by gap-phase disturbance processes. We conclude there is less naturally occurring old-growth forest regulated by gap-phase succession than previously believed. To date, more than 50% of the timber harvest on Kuiu Island has been located in areas where gap-phase processes (old-growth forests) predominate, only 14% has been in areas where stand-replacement processes predominate. Future management activities should be tailored to consider long-term natural disturbance patterns to better maintain ecosystem function. In areas least-prone to catastrophic storm damage, individual tree or group tree selection may be more appropriate. Two-aged management may be more appropriate in areas most-prone to catastrophic storm effects.

INTRODUCTION

The role of disturbance in regulating forest dynamics is a widely recognized (Pickett and White 1985, Reice 1994) emergent theme in forest ecology. Disturbances such as fire, catastrophic windthrow, and insect outbreak may result in disturbance histories that interact both synergistically and stochastically with edaphic and climatic gradients to produce complex vegetation mosaics over the landscape (Foster 1988a, Romme and Knight 1982, Peet 1988, Veblen et al. 1992, Hadley 1994, Veblen et al. 1994). Differences between past studies that have emphasized a steady-state gap-phase dominated model of forest development (Bray 1956, Bormann and Likens 1979a) and those that stress the role of broad-scale catastrophic processes in regulating forest dynamics (Franklin and Dryness 1973, Heinselman 1973) are now attributed largely to differences in the rate, scale and severity of disturbance processes over space and time (Picket and White 1985, Reice 1994). Yet few studies have explicitly examined how these disturbance parameters (rate, scale and severity) vary across the landscape (Boose et al. 1994) or explicitly used abiotic factors to predict and understand actual long-term disturbance dynamics over large spatial scales (Bergeron and Brisson 1990).

Abiotic factors may control the expression of disturbance rate, scale and severity across large spatial and temporal scales. This, in turn, could result in a long-term difference in forest structure and dynamics across the landscape (Dale et al. 1986). If portions of the landscape are subject to more frequent severe disturbance events, this could also result in differences in ecosystem processes such as soil development, nutrient cycling, and forest productivity (Vitousek 1985, Bormann and Sidle 1991, Vasenev and Targul'yan 1995). Seral trajectories could be different as well which could effect old-growth dependent species (Carey 1985, Kirchhoff and Shoen 1987, Boyle 1996). These factors in turn have important implications for forest management.

In this study we investigate the role of four abiotic factors in controlling long-term patterns of windthrow on two islands in the coastal temperate forests of southeast Alaska. The coastal temperate rainforests of southeast Alaska are dominated by a single disturbance type, wind (Harris 1989), and are thus well suited for investigation into abiotic controls on long-term temporal and spatial disturbance dynamics. Our questions are 1) what generalizations if any can be made regarding the role of topography, edaphic conditions and prevailing storm direction in controlling long-term storm effects across the landscape and 2) if long-term storm windthrow patterns vary across the landscape and can be predicted spatially, what are the consequences for forest development (age, structure characteristics).

Many studies have recognized that forest dynamics are influenced by a wind disturbance continuum ranging from small gap openings in the forest canopy to catastrophic stand-replacement events (Harmon et al. 1983, Runkle 1990, Spies et al. 1990, Frelich and Graumlich 1990, Deal et al. 1991), but few have explicitly addressed this on a landscape-scale (Boose et al. 1994). The impact a given storm event has on a forested landscape depends on a combination of biotic factors (species composition, canopy structure, size, age, and vigor) and abiotic factors (precipitation, wind intensity and direction, soil and site properties, and orographic effects of windflow patterns) (Harris 1989, Mayer 1989). The interaction among biotic and abiotic factors is complex, making wind disturbance particularly difficult to characterize and predict (Fosberg et al. 1976, Harris 1989, Attiwill 1994, Everham 1996).

While storm intensity, frequency, topography, and soil conditions have long been known to influence patterns of storm damage on forested landscapes (Smith 1946, Anderson 1954), few generalizations regarding long-term landscape-scale storm susceptibility can be drawn from the literature (Everham 1996). Recent work by Boose et al. (1994) suggests relatively simple assumptions regarding topographic exposure to storm direction, wind behavior over complex terrain, and a knowledge of stand history show good agreement with landscape-level patterns of forest damage that resulted from a 1938 hurricane that struck the Harvard forest in New England.

Wind-generated disturbance is the principal disturbance affecting coastal temperate rainforest dynamics (Harris 1989). The forests are low in tree species diversity, relatively devoid of human influence and of significant fire disturbance (Noste 1969). Catastrophic wind disturbance has been known to occur in the region (Harris 1989, Deal et al. 1991), but evidence of long-term catastrophic storm damage has been scant, and no known quantitative studies have occurred on the subject. Small-scale gap dynamics were thought to be the dominant disturbance process controlling and maintaining forest structure over much of the forested landscape (Alaback and Tappenier 1991, Boyle 1996, Lertzman et al. 1996), punctuated by infrequent catastrophic wind events (Deal et al. 1991).

Our objectives in this study were to 1) test the hypothesis that long-term windthrow patterns can be predicted spatially at the landscape scale using four abiotic factors; exposure to prevailing storm direction, slope, elevation and soil stability; and 2) compare stand age and structural characteristics in most and least windthrow-prone areas around Kuiu Island.

Study Area

The coastal temperate rainforest biome found in the Alexander Archipelago of southeast Alaska, is unique in the world (FIG. 1a). Twenty-nine percent of the worlds unlogged coastal temperate rainforest can be found there. While some 3 million hectares of rainforest are thought to remain, this forest is distributed among 7 million hectares of total area, located on over 1000 islands of diverse geology and topography (Conservation International 1992). Soils throughout the region are characteristically young and shallow due to recent glaciation (Kissinger pers. comm.). Paludification is common in many soils in the absence of catastrophic soil mixing disturbance (Ugolini and Mann 1979) due primarily to year-round precipitation and characteristically cool maritime temperatures (Harris 1989).

Tree species diversity in the coastal temperate forests of southeast Alaska is low. Four dominant tree species are common in the region. On well drained sites, western hemlock (*Tsuga heterophylla*) and Sitka spruce forests (*Picea sitchensis*) are predominant, with some mixture of Alaska yellow cedar (*Camaecyparis nootkatensis*). At higher elevations (above 400 m), mountain hemlock (*Tsuga martensiana*) occurs, typically replacing western hemlock. Mixed conifer scrub forests which can occur extensively on the landscape along with muskeg (non-forest), typically occur on lower site hydric soils or wetlands (Alaback 1996).

Cyclonic storms that affect this region begin in the Pacific Ocean, southwest of the Alexander Archipelago and follow a north-northeast track to the west coast of North America (Harris 1989). These storms are characteristically accompanied by high levels of precipitation as they occur during the fall and winter months (Harris 1989). The frequency of these cyclones, which occur throughout the Gulf of Alaska region, are reported to be the highest in the northern hemisphere during the months of October to April (Klien 1957).

Kuiu and Zarembo Islands are located in the middle of the Alexander Archipelago, southeast Alaska in the Tongass National Forest (FIGS. 1a,b) and are approx. 197,000 and 30,000 hectares in size respectively. Kuiu is located 160 km from the coast and is exposed to directly to cyclonic storms that originate south to southwest off the Pacific Ocean. Zarembo Island is located 90 km from the coast and is juxtaposed between four large island masses but is still exposed to storms over open water from the south and southwest. Timber harvest has occurred on both islands since as early as 1910 (McCallum pers. comm.), but began primarily in 1956 with long-term timber contracts initiated by the USDA forest service (USFS 1991). Less than 10% of the forested area on Kuiu Island has been affected by timber harvest, while 25% of the forests on Zarembo have been harvested. Kuiu Island is large (197,000 ha) with diverse geology, landforms and patterns of soil and vegetation distribution. Four broad landform categories with unique topographic, geologic, soil and plant community associations exist on the island (FIG. 2a, Table 1). A description of each of these was included because we were interested in determining the relative effect of landform type on patterns of windthrow. Delineations of these landforms were created by Kissinger (1995a)

Table 1. Summary statistics from each landform type.

Geophysical Region	Total Size (ha)	Percent Forested	Percent Hydric Soil	Percent Scrub/NonForest
Plutonic Mtns	36,857	52	10	48
Sedimentary Hills	53,491	85	20	15
Limestone Cliffs	8,192	83	18	17
Greywacke Hills	98,368	59	49	41

Plutonic Mountains

This area consists of all of the major mountains on Kuiu Island (FIG. 2b). Landforms here are typically smooth mountain slopes below relatively extensive alpine areas. Mountain slopes are generally steep, frequently dissected, and shallowly incised. Elevation ranges from sea level to about 1105 meters. Vegetation is dominantly western hemlock/blueberry/shield fern plant associations (Martin 1989). Large alluvial fans (Tuxekan series) on mountain toeslopes are characteristic of this geophysical area. Muskegs are a very small part of these landscapes, and are found infrequently on lower slopes and in valley bottoms.

Sedimentary Hills

This landform type is characterized by long, smooth, forested hillslopes bisected by broad 'U'-shaped glacial valleys (FIG. 2C). Hill summits are well rounded and most are less than 700 meters in elevation. Nearly all of the well-drained hillslope positions are occupied by the highly productive western hemlock /blueberry /shield fern plant associations (Martin 1989). Alpine ecosystems are rare, however hilltops commonly have subalpine (mountain hemlock) plant communities. Muskegs and muskeg-scrub forest complexes are extensive in the broad glacial valleys.

Limestone Ridges

Landforms are characterized by gently sloping to moderately steep hills that are abruptly broken by prominent limestone cliffs (FIG. 2d). The cliffs are generally parallel to each other, giving the landscape the appearance of a series of parallel ridges oriented in a NW-SE direction. The landscape has been severely modified by glaciation. Thick glacial till covers much of the moderately sloped areas, especially at lower elevations, however the white limestone cliffs remain the prominent landscape feature. Vegetation is dominantly western hemlock/blueberry/shield fern plant associations (Martin 1989).

Greywacke Lowlands

The landscape is characterized by a series of low-lying rolling hills (typically less than 300 meters) (FIG. 2e). Hillslopes are typically short, broken and irregular in shape, with well-rounded summits typical of glaciated terrain. Forested hillslopes are dominantly western hemlock and western hemlock-Alaska yellow cedar plant communities (Martin 1989). Muskegs and mixed conifer plant communities (scrub timber) on excessively wet sites occupy extensive areas.

METHODS

Overview of study design

The extent to which long-term windthrow patterns and consequently forest dynamics are mediated by physiography and regional weather patterns was explored using a combination of remotely-sensed data, statistical modeling and field based measurements. Remotely-sensed data were used to construct and validate a spatially-explicit predictive windthrow model. Field plots were used to validate and determine storm dates from a windthrow map that was created and compare forest structure and age characteristics in windthrow-prone and windthrow-protected landscapes based on model results. Our approach included seven steps (FIG. 3); 1) Quantify past windthrow on Kuiu Island through photointerpretation and field validation. 2) Assemble the database necessary to construct a predictive windthrow model 3) Construct the windthrow model, 4) Account for spatial autocorrelation 5) Evaluate and validate the model 6) Quantify stand dynamics based on model results and 7) Evaluate timber harvest on Kuiu Island relative to probability of windthrow occurrence.

Quantify past windthrow on Kuiu Island

We used Kissinger's (1995b) photointerpretation of 1:32000 high-altitude infra-red photographs (1979) to identify and delineate forest patches that appeared to be even-aged that were possibly of windthrown origin on Kuiu Island. Oliver's model of stand development (Oliver 1981) was used to describe stand conditions. Forests that have experienced a stand-replacement disturbance generally undergo three distinct stages of development before achieving true old-growth stage based on this approach; stand-initiation stem-exclusion and understory-reinitiation forests -all of which are characteristically even or multi-aged stands. Forests in the old-growth stage are a true all-aged forest (Runkle 1990) and have undergone complete turnover since the last catastrophic event. To avoid the confounding effects of timber harvest on windthrow dynamics, only blowdowns that occurred prior to 1956 when the effects of timber harvest were minimal (McCallum pers. comm.) were mapped. Blowdowns that occurred subsequent to this date are minimal, and are believed to comprise less that one percent of known natural blowdowns on the island. Each even-aged patch was digitized into a geographic information system, in Alaska state plane coordinates.

Field sampling was then focused in areas identified as even-aged from the photointerpretation exercise. Eighty-one plots were distributed among the even-aged patches throughout the island, as logistics permitted. Plot locations are shown in FIG. 4. At each plot evidence that dominant canopy trees originated from one or more catastrophic wind events was collected. Seral stage (stand initiation, stem-exclusion, early understory-reinitiation, late understory-reinitiation, or old-growth, Oliver 1981) was visually estimated based on light conditions, and structural and size characteristics. The plot was classified as confirmed windthrow if dead and downed trees that appeared synchronously root-thrown or snapped were present. Downed stems showing consistency in direction of fall was also used as evidence of windthrow (Gastaldo 1990).

The date of the storm event was approximated based on the age of the 5-15 new cohorts located on windthrow mounds (if present) at breast height. This method of estimation may bias storm dates due to mortality since catastrophic disturbance (Fox 1989), so storms were dated in 25 year intervals. Understory-reinitiation forests over 150 years old (mature forests) were not classified as confirmed windthrow because decomposition made identification of dead and downed stems as well as pit and mound characteristics difficult. In these mature forests the plot was classified as probable windthrow if no evidence for landslide activity could be found. Alternative stand-replacement causes include insect or pathogen outbreak. If evidence of timber harvest was found based on the presence of cut stumps, the cause of disturbance was identified as timber harvest.

Assemble data base

To construct a spatially-explicit windthrow model, additional digital data delineating all forest lands on Kuiu was required. Only forests not affected by timber harvest in the last 100 years were considered in the model. These forests comprised 90% of the forest lands on Kuiu Island. Scrub forest and non-forest on the landscape were not included in the analysis. These areas were thought to be minimally affected by catastrophic storms, and did not show any identifiable evidence of catastrophic windthrow.

A digital map delineating all non-harvested forest lands was obtained from the USDA Forest Service (USFS unpublished data). All forest lands on the island were then converted into 0.8 ha grid cells. A new digital layer was then created using the windthrow GIS layer, and the forest lands cover. Each forested cell was classified as being windthrown or non-windthrown using binary classification based on presence or absence of windthrow (FIG. 5). A cell size of 0.8 hectares was selected because it represented coarsest scale of available GIS data, and was computationally efficient.

Slope, elevation, soil type and storm exposure categories were then created for each 0.8 ha forested cell on Kuiu. Biotic factors (stand age, site) were not included in the model because, while these may influence damage patterns from a single storm (Foster 1988b), we assumed they are less important in long-term storm damage patterns. Slope categories were created using the LATTICEPOLY command in Arc/Info software (Version 7.0.1), and a 1:200,000 DEM (USFS unpubslished data) of Kuiu Island (FIG. 6). Soil stability classes were obtained from existing digital USFS maps (USDA 1992), and converted to a 0.8 ha cell grid size (FIG. 7). Elevation classes were calculated using the RECLASS command in Arc/Info GRID from a 1:200,000 DEM (FIG. 8).

Storm exposure was calculated using a modification of the EXPOSE model (Boose et al. 1994), and a 1:200,000 USGS DEM of Kuiu. The EXPOSE model simulates simple wind flow over terrain from a specified oncoming storm direction. A specified inflection angle allows wind to bend (in the vertical plane) as it passes over any protruding surface (i.e. a ridge or peak). Each 0.8 ha cell in a DEM is then classified as exposed or protected (binary state) as wind approaches the topographic surface from the horizon. To create a range of exposure values over the Kuiu Island, the EXPOSE model was modified to run iteratively increasing the inflection angle by 2 degrees (FIG. 9) up to maximum inflection angle of 14 degrees, resulting in 9 degrees of exposure. Because storm data was unavailable for Kuiu Island, and the exact direction of prevailing storms was unknown, a range of southeast (160 deg.) and southwest (220 deg.) prevailing storm directions were used based on prevailing storm directions known to occur in the region (Harris 1989). The average exposure from these two prevailing wind directions was then used to calculate a final exposure score for each forest 0.8 ha cell on the island (FIG. 10). Ordinal values that resulted for each class for elevation, slope, soil stability and storm exposure are shown in Table 2.

Table 2. Ordinal categories (from lowest to highest) for slope, elevation, soil and exposure. All possible values are covered in the categories used.

Ordinal Category (increasing value)	**Percent Slope (Percent)**	**Elevation (meters)**	**Soil Stability** (stability class)	**Storm Exposure (by inflection angle)**
1	0	0	0	Never Exposed
2	1	62	1	14
3	2.15	124	2	12
4	4.6	186	3	10
5	10	248	4 (highest)	8
6	21.5	310	--	6
7	46.4	372	--	4
8	100	434	--	2
9	1000 (steepest)	1112 (highest)	--	0 (Most Exposed)

Model construction

We selected a multiple logistic regression model to estimate model coefficients, and generate a probability of windthrow occurrence for each forested cell on Kuiu Island. Logistic regression belongs to a family of generalized linear models that most commonly use maximum likelihood estimation (MLE) based on iteratively reweighted least squares to estimate model coefficients (Neter et al. 1996, Hosmer and Lomeshow

1989). Logistic regression is well suited for ordinal independent variables, large numbers of observations and a binary response (i.e. windthrown vs non-windthrown forest) (Hosmer and Lomeshow 1989, Neter et al. 1996). Each variable was then centered around 0 based on subtraction of the midpoint value and was then univariately transformed. The transformation that would best linearalize the relationship between independent and dependent variables was selected. Second order and interaction terms were added, resulting in fourteen terms considered for inclusion in the model. An exploratory stepwise approach based on Akaike Information Criteria (AIC) (Akaike 1973) was used to select the best-candidate model (SAS 1988). AIC minimizes information criteria from the data to select a model (from a set of nested models) that best approximates the theoretically correct model. Final model coefficients were standardized for relative comparison. For diagnostic purposes a comparison between the AIC value and a probability surface map of this best candidate model was made with AIC values, a probability surface map generated from two other models; a single variable **(EXPOSE)**, and four variable model (all four abiotic factors). Variance inflation factors (VIF) were calculated for each independent variable to detect for the presence of multicollinearity in the independent variables. Generally a VIF less than 10 suggests moderate multicollinearity influence on least squares estimates (Neter et al. 1996).

Spatial autocorrelation

Statistical inference and parameter estimation is a difficult problem in spatially-explicit modeling because assumptions regarding independence are difficult to meet

(Cressie 1991). The presence of spatial autocorrelation in dependent and independent model variables may influence parameter estimates and prediction estimates (Manly 1991) and make interpretation of spatial data through model coefficients difficult. New methods have recently emerged to account for spatial autocorrelation in spatial data so that inferential assumptions are met, however few have been applied and used in ecological modeling problems. (Manly 1991). Distance sampling has been used by numerous authors (Pereira and Itami 1991, Sinton 1996) to account for spatial autocorrelation, however this typically results in elimination of most of the data in estimating model coefficients and is not recommended (Legendre 1993). A more sophisticated and difficult approach involves the use of markov chains in autologistic models (Cressie 1991) to incorporate spatial autocorrelation as a term in the model. This technique has proven especially useful in cases where spatially-dependent processes (such as animal dispersal) are being modeled (Augustin et al. 1996). Resampling of lattice data has been recently suggested by numerous authors as a technique to cross-validate prediction estimates, and obtain confidence intervals for model coefficients that account for spatial autocorrelation present in lattice data (Manly 1991, Cressie 1991, Lele 1991). While resampling has been recognized in the statistical literature (Cressie 1991, Manly 1991, Sherman 1996, Lele 1991), techniques such as the jackknife or the bootstrap have not been applied to spatially-explicit ecological problems yet, and the method is not widely understood or used (Heagerty and Lele, In Press).

Resampling techniques such as the jackknife or bootstrap may be appropriate if prediction is the primary goal in constructing a spatial model, and assumptions regarding independence of each observation (or cell) in the model can be relaxed. The degree to which spatial dependence is influencing model predictions is still an important consideration, to ensure that spatial dependence is not unduly influencing coefficient and prediction estimates.

In this study our primary modeling objective was to develop a predictive windthrow model to make predictions of long-term windthrow susceptibility on the forested landscape. We employed a jackknife cross-validation resampling approach to determine the degree to which high spatial autocorrelation was influencing our model predictions. For 256 individual cells, model coefficients and a prediction for each cell was generated using only data that were not highly spatially autocorrelated to that cell. Ninety-five percent prediction and coefficient confidence intervals for both windthrown and non-windthrown forests were then calculated based on these results. Because a spatial error (dependence) term was not included in the model, the 95% confidence intervals obtained from resampling represents a conservative estimate both on our predictions and coefficient estimates.

Spatial autocorrelation in windthrown forest cells was measured using semivariance (Carr 1987). Semivariance (Gamma h) is inversely related to spatial autocorrelation (Carr 1987). Spatial dependence is determined by the lag (or distance) at which maximum semivariance is attained (Robertson 1987). A program VGRAM was used to compute the semivariance (Marks 1995). The results from the semivariogram were then used to create a block based on the distance at which windthrown data were found to be highly spatially autocorrelated in two directions; N-S and E-W (FIGS. 11a,b). This block was then centered on a single forested cell randomly selected from Kuiu. All forested cells contained within that block were then eliminated from the analysis (FIG. 12a). The remaining data were used to estimate model coefficients and compute a probability of windthrow occurrence for that individual cell. The block was then centered on each forested cell that would result in non-overlapping blocks on the forested landscape (FIG. 12b) in an iterative fashion.

E-W semivariance nugget values suggest the data are highly spatially autocorrelated to a distance of up to 1500 meters (FIG. 11a). Semivariance plots in the N-S direction suggest high spatial autocorrelation up to 3000 meters (FIG. 11b). The windthrow data are spatially autocorrelated to different degrees in these two directions and are therefore anisotropic. A block 3000 meters x 6000 meters was created based on these anisotropic semivariance results. We jackknifed out a 3000x6000 meter rectangle of data centered on each prediction cell (FIG. 12a,b). From this jackknife cross-validation, 95% confidence intervals for the model coefficients, and prediction estimates were calculated.

Model evaluation and validation

The best-candidate model was evaluated on the island as a whole as a diagnostic, and by each landform type, to determine the relative effects of landform on patterns of windthrow susceptibility over the island. Landform type can influence storm damage patterns in many ways, including channeling wind (i.e. through valleys), impeding windflow (topographic protection), and influencing patterns of vegetation which in turn may influence patterns of storm damage over the landscape (Swanson et al. 1988). Landform type was not considered as a variable in the model due to the diverse form of landform types (both geologic and geomorphic) between and within other islands which would make extrapolation to other areas difficult.

Equal classification error rates between each response state (windthrown and non-windthrown forest) and the corresponding probability cut-off value were reported to compare our model with a random model. Equal classification error rates were used as a diagnostic because equal weight is given to each prediction of both windthrown and non-windthrown forest. Percent improved over random is a measure of improvement over a model that could correctly classify 50 percent of both the windthrown and non-windthrown simply through random selection. A model that correctly classified 60 percent of both windthrown and non-windthrown data would represent a 20 percent improvement over such a random model. These criteria were chosen because our primary objective in developing this model was to predict windthrow occurrence on the landscape.

An assessment of the fit of our best-candidate model was performed via external validation (Hosmer and Lomeshow 1989). Our model was validated on nearby Zarembo Island, using an independent windthrow data set. The digital data construction techniques described for Kuiu Island (step 2) were repeated for Zarembo Island on all forest lands not subject to timber harvest. The coefficients derived from Kuiu Island were then extrapolated to Zarembo, to generate a probability of windthrow occurrence map for every 0.8 intact forested hectare on the island. An independent windthrow data set was then developed using IR photography (using identical methods to those from Kuiu Island). Classification error rates, and a percent improved over random by cut-off specification for both windthrown and non-windthrown forest were used to validate the model.

Stand structure

We used field plots to compare forest structure and age characteristics found in windthrow-prone and windthrow-protected areas on Kuiu Island. The forty two plots (located in areas most-prone to windthrow; probability of occurrence>.2) used to validate the windthrow data set on Kuiu Island were included in this comparison. An additional forty-one 0.1 ha fixed radius field plots were collected on Kuiu in areas both most and least-prone to catastrophic winds (based on Kuiu model results) to obtain more detailed stand and age information. The fixed-radius plots were located primarily throughout the north portion of the island as logistics permitted (FIG. 13). Collection of forest plots was facilitated by a road network present on this portion of the island. Each plot was located randomly in a 15 ha or greater region most or least-prone to windthrow. In each of the 41 plots, diameter at breast height, tree species, and estimated canopy position (dominant/codominant, intermediate, suppressed) of all standing trees (dead or alive and > 12 cm diameter) were recorded. Prominent rootwads (mineral mounds) and stumps (organic mounds) were counted. Ten to twenty codominant trees of representative diameter classes were cored at breast height in each plot for age determination. Cores were stored in a plastic core holder, and counted in the lab using a dissection microscope. Cores that were difficult to count were mounted, sanded, then counted.

A probability of windthrow occurrence (based on the logistic model results) was calculated for each of the forests plots (both windthrow validation plots and 0.1 ha fixed radius plots). For each plot, mean and standard deviation of tree age and diameter was calculated. Standard deviation of tree age and diameters per plot was regressed against probability of long-term storm damage for all plots collected. A regression of mean age to diameter was performed separately for plots most and least susceptible to windthrow. No hypothesis tests or P-values were reported from these regressions. The comparison between forest structure in windthrow-prone and -protected areas was purely exploratory because plots located in known even-aged patches were included in the comparison. Six plots randomly located in windthrow-prone areas not identified as even aged from the photointerpretation exercise were collected. The results from these plots are reported but no inferential statistics were used due to the small sample size. A cluster analysis was performed on summary statistics from the fixed radius plots. Representative plots were used to examine structural and age characteristics from each cluster.

Evaluation of timber harvest on Kuiu Island

Areas of known timber harvest on Kuiu Island were excluded from the model construction portion of the study (FIG. 14). To evaluate the probability of windthrow occurrence in these areas, had they not been harvested, model coefficients were extrapolated to known timber harvest patches, and a probability of windthrow occurrence based on model coefficients was calculated for each 0.8 hectare of known timber harvest. The elevation class for each 0.8 ha cell of known timber harvest was reported as well to determine if harvest patches were distributed primarily in valley bottoms or upland areas.

RESULTS

Identification of windthrown patches on Kuiu Island

Photointerpretation identified twenty percent (20,000 ha) of the forested landscape as stem-exclusion, understory-reinitiation, even-aged forest (FIG. 5). Forty-three percent of the field plots in these even aged forests were identified as confirmed windthrow, while 98% were identified as either confirmed or probable windthrow. We were able to eliminate landslides and fire as alternative causes for disturbance in probable windthrow plots. It is still possible that these forests originated from alternative causes such as catastrophic insect outbreak. However no evidence of insect outbreak was found in any of the more recently originated forests sampled, and aside from localized spruce budworm outbreaks associated with islands located just off the mainland, no catastrophic outbreaks have been reported in the southeast Alaska region (Pawuk pers. comm.). Five forest plots were classified as not windthrown. In these plots either evidence of a landslide or clear-cut activity was found or catastrophic storm evidence was not discernible from forest structure and age characteristics.

Forests that originated from a storm event that occurred 110 years ago comprised 40% of our forest plots (FIG. 15). Age estimates provided evidence of at least 4 other major storms that occurred between 50 and 400 years age (FIG. 15). The direction of downed stems from confirmed windthrow plots suggests our assumption regarding prevailing storm direction, (southeast to southwest) coincides with storm damage patterns that may have been caused by recent storms (in the last 150 years) traveling in these directions (FIG. 16).

Model construction

The primary objective in constructing the logistic model was to make spatially-explicit predictions of windthrow across the landscape. Statistical inference and interpretation of model coefficients was limited due to spatial autocorrelation in the data. However, we examined each variable individually to confirm that it should be considered for inclusion in the model and to make exploratory interpretation of the relative influence of each of the four abiotic factors in predicting the occurrence of windthrow.

Univariate relationships between **EXPOSURE** and occurrence of windthrown and non-windthrown forest on Kuiu suggest this variable is a strong predictor of windthrow occurrence on Kuiu (FIG. 17a). The proportion of windthrown forest increases with higher exposure values. **SLOPE**, **SOIL** and **ELEV** all show a general increase of windthrow occurrence with increasing values (FIG. 17b,c,d), however the rate of windthrow increase is not as strong as with **EXPOSURE**. The univariate results suggests all four independent variables selected may be appropriate for inclusion.

All four first order variables were selected, and second order and interaction terms were included in the best candidate model. The positive values of the first order value for exposure is consistent with results from univariate diagnostics. All interaction terms included the **EXPOSURE** term, again suggesting that **EXPOSURE** is one of the stronger predictors in the model. AIC distance values and differences in the probability surface map suggests this best candidate model represents a considerable improvement over either a single variable model (using **EXPOSURE**) or the four variable model (using the four abiotic factors alone) (FIG. 18a). VIF values for each value in the model were all less then 10 which suggests multicollinearity effects are not unduly influencing our coefficient estimates (Table 3). Prediction error due to spatial autocorrelation was less than .3% for both windthrown and non-windthrown forest. The tight range of 95% prediction confidence intervals and coefficient estimates (Table 3) suggest high spatial autocorrelation is not unduly influencing model predictions.

Table. 3. Final model variables selected in the best candidate model with 95% confidence intervals and VIF values for first order terms.

Model Variable	Lower 95% Limit	Upper 95% Limit	VIF
Intercept	-1.65762	-1.65491	--
Expose	0.32057	0.32142	5.4
$Elev^3$	-0.02441	-0.02423	7.5
$Slope^3$	0.04675	0.04718	3.3
Soil	-0.90812	-0.90463	7.2
$Elev^4$	-0.00478	-0.00471	--
$Slope^4$	0.02316	0.02331	--
$Soil^2$	0.52016	0.52177	--
Exp_El^3	0.01964	0.01980	--
Exp_Sl^3	0.05954	0.05993	--
Exp_So	0.00266	0.00269	--

Model evaluation and validation

Evaluation of the model on Kuiu Island as a whole suggests that the model showed good agreement with observed patterns of long-term storm damage. The model explained 68% of known windthrow patterns found on Kuiu, using an equal classification error rate (FIG. 18b,c). However model performance varied considerably by landform type on Kuiu Island (FIG.19a-d) due to differences in geomorphology and forest pattern (FIGS. 2a-e). The 38 % percent improvement over a random model on the entire island (FIG. 18c), was considerably lower than the 58% improvement value in the glacial till landform type (FIG. 19b). This landform type was able to explain 79% of the actual storm damage patterns (FIG. 19b). Conversely, the Limestone Cliff area, and the Greywacke Lowlands could at best predict only 68% of actual storm damage patterns using an equal classification error rate (FIG. 19c,d).

Model validation was performed by comparing actual patterns of damage on nearby Zarembo Island to predictions of storm-prone areas using Kuiu coefficients. Fifteen percent of the forested landscape on Zarembo Island was identified as even-aged (stem-exclusion, understory-reinitiation forest) probable windthrow from photointerpretation (FIG. 20b). Model validation results from Zarembo Island did not consider landform type and was done for the island as whole (FIGS. 1b, 20a). Overall there was good agreement between predicted and observed patterns of long-term catastrophic storm damage - a 72% equal correct classification rate of both windthrown and non-windthrown forest (FIG. 21). Our predictions represented a 45% improvement a random model which is 7% higher than for Kuiu Island (38% improved over random) (FIGS. 18c, 21).

Stand structure

Stand age and structural characteristics were compared in storm-prone and storm-protected landscapes. Exploratory regression results between standard deviation of plot age and diameter and probability of windthrow suggested that the age and structural characteristics were increasingly homogenous as function of increasing storm susceptibility across the landscape (FIGS. 22a,b). Regression results between stand age and diameter in storm prone landscapes suggest a significant positive relationship between stand age and diameter (FIG. 23a). By contrast no relationship between age and diameter was found in storm protected landscapes (FIG. 23b).

Fixed radius stem plots were summarized and compared to provide more detailed comparison of age and structural characteristics. Five of the plots collected in areas least-prone to catastrophic wind exhibited age and structural characteristics indicative of stem-exclusion and early understory-reinitiation forests. These forests exhibit structural and age characteristics indicative of recent catastrophic disturbance events. The 6 plots collected in windthrow-prone areas on the landscape in areas where no even-aged patches were identified all showed evidence of at least one major catastrophic windthrow. All of these stands originated over 200 years ago. Poor site and older age characteristics of stands in those areas may have created a more heterogeneous canopy texture -however diameter and homogenous age characteristics suggest catastrophic windthrow affected all of them.

Clustering of stand structure (standing dead and alive) and population structure (age of trees cored) resulted in four distinct clusters. Each of these can be attributed to a range of age and structural categories ranging from even-aged young stands to all-aged older forests (FIG. 24). The majority of plots (36/39) exhibit age and structural characteristics indicative of late-seral stage forests (Clusters 2-5). Density of large trees (> 120 cm) is relatively constant in these forests (15 se 5) per hectare.

Cluster 1: Plots in this cluster are located primarily in storm prone locations. Plots in this range showed strong evidence of a catastrophic stand-replacement event. Ages were tightly grouped (FIG. 25a), and diameter distributions were normal (FIG. 25b), with a relatively tight range of diameter sizes found in the stand. The stand types ranged from stem-exclusion forests (not shown) to understory-reinitiation forests (FIGS. 25a,b), which was a function of time since last disturbance. The high number of small standing dead in these plots (FIG. 25b) suggest self thinning is still a dominant mechanism for mortality.

Cluster 2: Plots in this range showed evidence of a partial canopy disturbance, which resulted in some tight clustering of age groups (FIG. 25a), but stand characteristics (bimodal, negative exponential, or uniform) were indicative of late seral stage forests (not shown). These stands may have experienced one or more partial canopy disturbance events, and may reflect multiple distinct age groups (multi-aged stands).

Cluster 3: Plots in this cluster showed evidence of some partial canopy disturbance, and multiple small-scale disturbance events. Ages sampled did not reflect a distinct group of individuals (FIG. 25a), and diameter distributions were non-normal, with a wide range of diameter sizes, and standing dead. Smaller diameters in the stand

(FIG. 25b) do not reflect a single age group, but rather represent a wide range of ages (FIG. 25a).

Cluster 4: Plots in this cluster showed evidence of many small-scale disturbances that occurred at different times. Ages in these plots span a wide range (FIG. 25a), and no single identifiable group of ages can be found (FIG. 25a). Diameter distributions are uniform, with large and small trees well represented in the stand (FIG. 25b). Occurrence of cedar is higher in this cluster with an average of 20% which may explain the wider variation of age characteristics found in this site, due to the longer life span of cedar.

Evaluation of timber harvest on Kuiu Island

Most timber harvest on Kuiu Island has occurred at elevations below 200 m, primarily in valley bottoms (FIG. 26a). Probability values generated by extrapolating model coefficients to areas of known timber harvest show that more than 50% of known timber harvest has been located in least-susceptible to natural catastrophic blowdown (FIG. 26b). By contrast only 15% of the timber harvest patches are located in areas most-prone (probability of windthrow occurrence > .2) to natural catastrophic windthrow.

DISCUSSION

Past windthrow on Kuiu Island

Our results suggest many large catastrophic storms have affected Kuiu Island in the last 400 years. These storms may have blown down the same forested landscapes repeatedly, so our conclusions regarding the extent of damage caused by each storm are limited. Our evidence of wind damage caused from multiple storms is consistent with evidence of catastrophic wind damage found throughout the world in windy environments such as Ireland, New Zealand and Argentina (Gallagher 1974, Thomson 1976, Rebertus et al. 1997). A record of major gale-force damage in Ireland that dates as far back as 500 A.D suggests at least one major catastrophic storm event occurred each century in Ireland (Gallagher 1975). Gale-force storms in New Zealand, Ireland, and Chile are reported to travel in a characteristic prevailing storm direction which is consistent with prevailing storm movement patterns found in southeast Alaska (Harris 1989). Large-scale atmospheric circulation patterns are probably the cause for this (Harris 1989, McBean 1996). The extent of forest that was found to be windthrown (>20%) suggests catastrophic windthrow is an important disturbance agent on the forested landscape. These catastrophic storms are re-occurring in approximately 100-year intervals on Kuiu and occur well within the lifetime of dominant forest species. Prior to this study gap-phase disturbance processes were believed to be the predominant disturbance type in the coastal temperate rainforests of North America (Lertzman 1996, Alaback and Tappenier 1991).

Abiotic controls on windthrow

Landscape patterns of windthrow that result from a single storm event are the consequence of complex and stochastic interactions between abiotic and biotic factors which can make prediction of storm damage patterns difficult (Foster 1988b). At large spatial and temporal scale, topographic, edaphic conditions and prevailing storm direction appear to constrain disturbance intensity on some portions of the landscape resulting in a gradient of long-term storm effects across the landscape. This gradient can be made spatially-explicit and predicted on a broad-scale using multiple logistic regression. The good agreement between predicted and actual patterns of windthrow on Zarembo Island suggests our model is generalizable to nearby islands, and that landscape-scale long-term catastrophic windthrow patterns are similar on both of these islands. Our conclusion that disturbance rate, scale and severity are constrained by relatively few abiotic factors may be applicable to other widespread disturbances such as forest fire. Numerous studies on fire have found variation in return interval, intensity and extent of fire over relatively large landscapes (Morrison and Swanson 1990, Bergeron and Brisson 1990). These differences may also be the result of relatively few abiotic factors such as susceptibility to lightening strike and soil moisture (Foster 1988b), which could be used to make spatially-explicit predictions that quantify the long-term disturbance regime across the landscape.

Variation in model performance over different landform types on Kuiu suggest that broad-scale vegetation patterns and geomorphic characteristics play an important role in determining long-term storm damage patterns on Kuiu. The pronounced ridge and valley formations, and contiguous forest cover in the Sedimentary Hills landform, for example, appeared to strengthen or accentuate this long-term storm damage gradient. Many ridges ran perpendicular to prevailing storm directions (E-W) with well defined valley and ridge formations that adequately protected some portions of the landscape from catastrophic windthrow. By contrast, the topographically smoother, glacially striated, less contiguous forested region of the Greywacke Lowlands weakened the long-term storm damage gradient. Leeward blowdowns were observed possibly due to relatively mild ridge and valley formations unable to protect lee ridge and valley formations. In a review of windthrow studies around the world, Everham (1996) concluded blowdown on leeward ridges can occur if relative ridge height is not too high and hillslopes are not steep enough. Windward sides were not always blowndown, possibly due to less prominence of ridge formations on the landscape.

Limitations

The simple assumptions made regarding wind dynamics over complex terrain, prevailing storm direction, and storm movement over forested regions may underestimate portions of the landscape subject to long-term catastrophic storm damage. Unusual storm directions, eddy effects, channeling of wind through valleys, and other effects created from complex wind-topography interactions may result in catastrophic storm damage to forests in unpredictable locations using a simple linear windflow model.

Windthrow patterns in the Limestone Cliff region were least predictable (60%) of all landform types examined. Wind sheer and eddy effects due to cliffs may be more pronounced in this region and our model had no way to account for storm exposure above cliffs. Windthrow patterns in the Plutonic Mountains regions on Kuiu were also less predictable (62%), probably due to complex interactions between wind and pronounced topographic features that our simple linear model could not account for. Evidence of eddy effects was most pronounced in this region. Unusual blowdown patterns may have been the result of channeling and obstruction of windflow at higher elevations.

Complex interactions between wind and topography can sometimes lead to greater lee and valley damage from a storm (Everham 1996). Long-term windthrow evidence may be greatest along ridges that run parallel to prevailing storm direction, and in valleys on some portions of Kuiu. On the north portion of the island blowdown was observed (based on our fixed-radius plots based on photointerpretation) on both windthrow-protected and windthrow-prone portions of the Rowan ridge formation (south of Rowan Bay) (FIG. 1a). This ridge system ran approximately parallel to prevailing storm direction (SW-NE). Both valleys Rowan Bay to Saginaw Bay, and Rowan Bay to Camden Bay showed evidence of a valley effect where blowdown may have been the consequence of bending and channeling of wind in areas that our linear exposure model could identified as low exposure (FIG. 1a). Robertus et al. (1997) concluded that valleys and ridges that ran parallel to direction of storms showed greatest susceptibility to a 1972 catastrophic storm that struck Tierra Del Fuego- however the study area was 1/10 the size of Kuiu Island. The good agreement with predicted storm-prone locations and actual catastrophic storm-damage patterns found both on Kuiu and Zarembo Islands (FIGS. 18c, 21) suggests that while windthrow on ridges that run parallel to direction of prevailing storm direction, and in valley bottoms occur, other portions of the landscape have greater windthrow susceptibility.

On a regional scale, long-term storm damage patterns could vary considerably from those found on Kuiu and Zarembo Islands. For example nearby Prince of Wales and Kupreanoff islands are both over 500,000 ha in size, and have a more concentric shape. Storms may weaken before they pass over inland portions of these islands (Foster 1988b). In addition, complex deflection through narrow island waterways, may result in unpredictable storm damage patterns. Evidence of extensive catastrophic wind damage has been found north and south of Kuiu Island on Prince of Wales (Harris 1989), and Chichagoff islands (Garvey unpublished data). These islands are on the outermost portion of the archipelago, and may be more exposed to catastrophic winds as a consequence. However, they comprise a substantial portion of total area in the archipelago (35%). Further inland, topographic protection, and weakening storm patterns may result in a considerably weaker, less extensive long-term pattern of storm damage. Future work should include an analysis of regional meteorological data, and actual observations of wind damage and wind speeds during a catastrophic storm, as well as an exploration of weakening storm patterns further inland.

Our best-candidate model includes second order and interaction terms, as well as all first order variables (FIG. 18a, Table 3). The relative role of these abiotic factors and their interactions are complex and in many ways inseparable due to spatial autocorrelation inherent in the data. Nonetheless the inclusion of second order and interaction terms suggests the relationship between the 4 abiotic factors and the occurrence of windthrow is highly non-linear, and our linear model is at best an approximation of this relationship. A non-linear predictive model may improve predictive capabilities, however spatial dependence in the data will still present difficulties in any interpretation of model coefficients. While univariate relationships suggest EXPOSE is the most important explanatory variable, SOIL, SLOPE and ELEVATION are important as well. Generally in forests with high EXPOSE values with flatter surfaces occurring at lower elevations on low-hazard soil types are less susceptible to long-term storm damage, whereas steeper, higher elevation forests occurring on unstable soils are more susceptible to storm damage.

Stand structure

The negative relationship between range of stand age and storm susceptibility (FIG. 22a) suggests that as storm susceptibility decreases, the population attains an all-aged structure. Conversely, the population shows tighter homogenous structure as storm susceptibility increases (FIG. 22a). This same trend was observed for tree diameters (FIG. 22b). Although largely exploratory, these results suggest dramatic differences in the competitive interactions, and population dynamics in these two landscape settings which can be attributed to continuum of disturbance that is manifest in both space and time.

Forests most susceptible to long-term damage from prevailing storms may never reach a late-seral stage. The return interval of catastrophic storms appears to be sufficiently high to cycle these forests back to a stand initiation stage before turnover from the last catastrophic event is complete (approx. 350-950 years) (Lertzman 1996). It is possible that forests in these storm prone landscapes may experience a stand-replacement much sooner than that (50-100 years), based on the high representation of these stand ages in our windthrown age plots.

By contrast, the wide range of ages, and lack of a single identifiable cohort in storm protected plots such as those found in cluster 4 (FIG. 25a), suggests one turnover period or more may have occurred in at least 7 of our forest plots since the last stand-replacement event. Wind dynamics including unusual storm direction, valley effects, bending and complex associations with mountainous terrain are the likely cause for the limited catastrophic blowdown that was found in storm protected areas (FIGS. 24, 25a,b). Evidence of larger more intense events, which led to a distinct pulse of new recruitment in some clusters 2 and 3 suggest that late seral stage forests experienced a range of disturbance intensities and frequencies (FIGS. 24, 25a,b), but overall wind disturbance was characteristically less intense than in forested landscapes most-prone to catastrophic storms.

Stand development patterns

Characteristic stand development stages from plots collected in wind-prone landscapes include stand initiation, stem-exclusion and understory-reinitiation forests. Oliver (1981) suggests that as forests develop after a catastrophic disturbance event, mortality is largely a consequence of self thinning until an old-growth stage is reached. Mean plot diameter to age relationships suggest that forests in these landscape settings are still undergoing this early stage of stand development where self thinning is the dominant mechanism for tree mortality, and that late-seral, climax structure and competitive interactions have not been attained (FIG. 23a).

Forest plot data collected in areas least-prone to prevailing catastrophic storms suggest that complex lower intensity wind disturbances (partial canopy disturbance and small-scale gaps) serves to maintain a late-seral stage age and structure in these forests. The lack of relationship between mean tree diameter and age suggest that competition is not equal among individuals in these forests. As gaps open up, shade tolerant individuals compete with over-story neighbors to fill the available light niche (FIG. 23b). This pattern of stand development has been studied extensively elsewhere and is consistent with a gap-phase or late seral stage model of forest development.

Long-term windthrow patterns and ecosystem function

The predominance of high or low intensity disturbance events in regulating long-term forest dynamics on the landscape could have important consequences for ecosystem function and process (Shulze and Mooney 1994). Numerous authors have suggested catastrophic wind events may serve to maintain long-term productivity (Bormann and Sidle 1990). Root throw may serve to disrupt soil development processes, which could in turn increase mineral weathering processes, and increase nutrient availability (Bormann et al. 1995). If this is true, forests located in areas prone to catastrophic storm effects may maintain a higher rate of nutrient availability and forest productivity than those least susceptible to catastrophic storm damage in similar edaphic and elevation conditions. If disturbance frequency and intensity is sufficiently low, which may be the case in landscapes least-prone to catastrophic storm effects, a decline in forest productivity, possibly leading to bogification may occur (Zach 1954). Landscapes prone to stand-replacement events may also experience an increase in decomposition of organic matter, through increased temperature (Bormann and Likens 1979b).

Differences in light (due to stand structure differences) and soil nutrient conditions (due to soil disturbance differences) may also lead to a difference species richness and composition in each of these landscape settings. Storm protected landscapes may have high plant and animal diversity due to heterogeneity in light and structural conditions (Alaback 1982). Conversely understory plant diversity and abundance may be considerably lower in areas most-prone to windthrow, due to the characteristic light limited, homogenous canopy conditions associated with second growth forests (Alaback 1982). This in turn may have long-term consequence for species viability planning efforts for species dependent on late seral stage forests such as the pine martine, Sitka black-tailed deer (Boyle 1996, Kirchhoff and Shoen 1987).

Management implications of long-term windthrow patterns

To understand the impact of forest management, a good knowledge of disturbance history is essential (Peart et al. 1992). This is especially true in southeast Alaska, where late seral stage forests in particular are valued for high structural and species diversity (Kiester and Eckhardt 1994, Boyle 1996). Our results suggest there is less naturally-occurring old-growth then previously believed. Yet a central goal in the Tongass Land Management Plan is to maintain late-seral stage characteristics over much of the forested landscape (USFS 1991). Past management activities have further reduced the amount of forest that are in a late-seral stage condition or on a late-seral stage successional trajectory. On Kuiu Island, more than 50% of the timber harvest units have occurred in areas where forests are most protected from long-term catastrophic storm damage (FIG. 26b). Timber harvest in these areas has an additive effect; that is, old-growth forests are converted to second-growth stands that will not develop beyond the stem-exclusion stage due to planned 100-year cutting rotations. These early developmental stages are historically infrequent on such landscapes (FIG. 18b). Only 20% (1,000 hectares) of timber harvest units occurred in landscapes where stand-replacement processes predominate. The removal of standing biomass (by clearcutting) is a substantial departure from small-scale turnover in the forest that may serve to maintain long-term forest productivity (via root throw) (Bormann and Sidle 1991).

The amount of forests in later stages of development will be noticeably reduced if current harvest trends continue. An alternative approach may be to tailor management so that they are more compatible with prevailing natural disturbance processes (Hansen et al. 1991, Swanson and Franklin 1992). For example, greater emphasis could be placed on single-tree or small-group selection harvesting in areas where late seral stage forests occur to maintain natural processes such as root throw and coarse woody debris in the understory. One tradeoff, however, is that more frequent entries over large areas would be needed to maintain the current harvest volume. In areas most-prone to long-term catastrophic storm damage, two-aged management may be more appropriate to maintain disturbance function (via root throw of standing residual), and similar historical stand attributes (stem-exclusion, understory-reinitiation forests). Consideration of long-term windthrow patterns should be a requisite to devising management alternatives to ensure management practices can be tailored to better maintain ecosystem process, function, and habitat conditions that will assure species viability common to those areas.

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APPENDIX

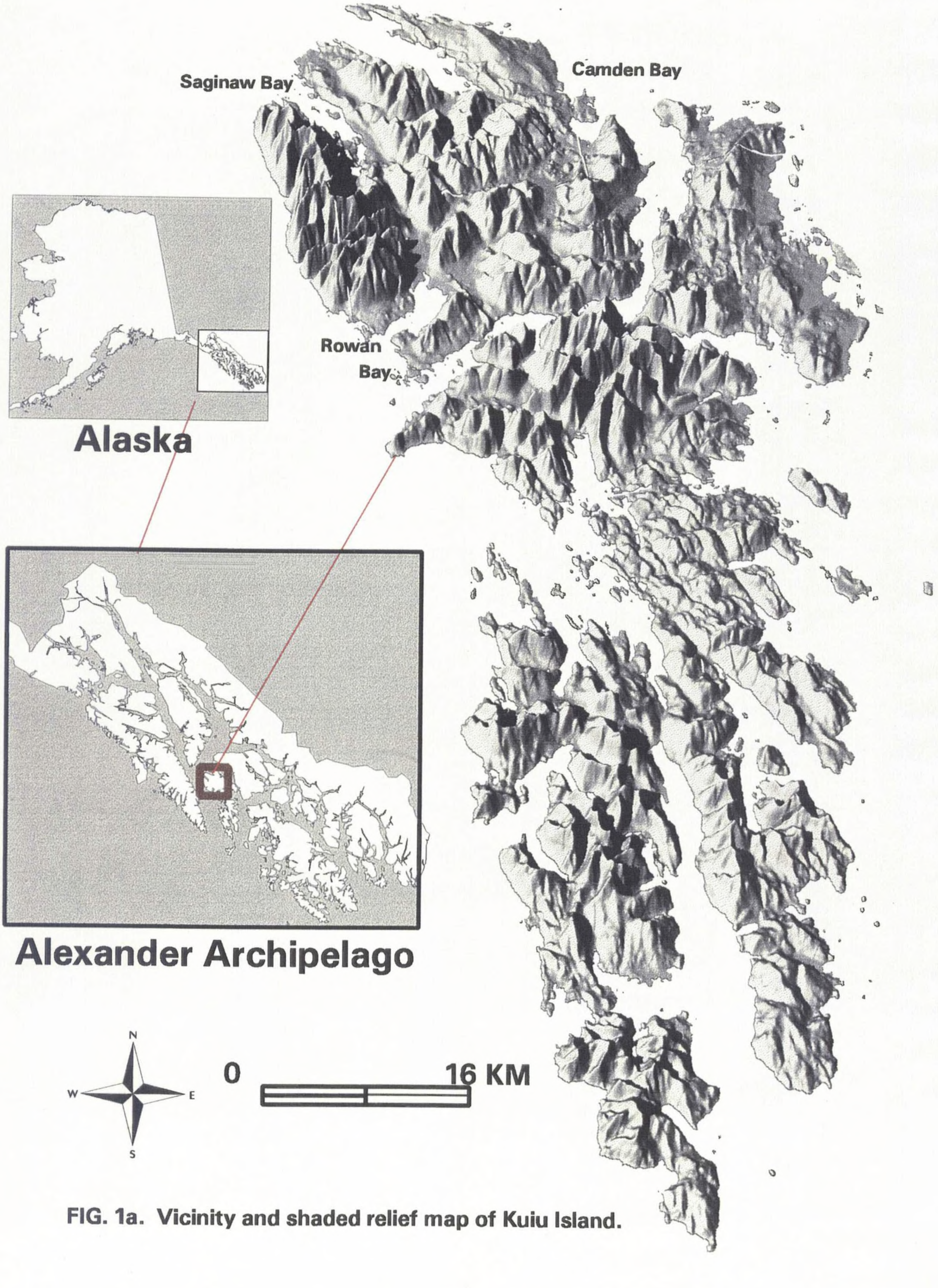

FIG. 1a. Vicinity and shaded relief map of Kuiu Island.

FIG 1b. Vicinity and shaded relief map of Zarembo Island.

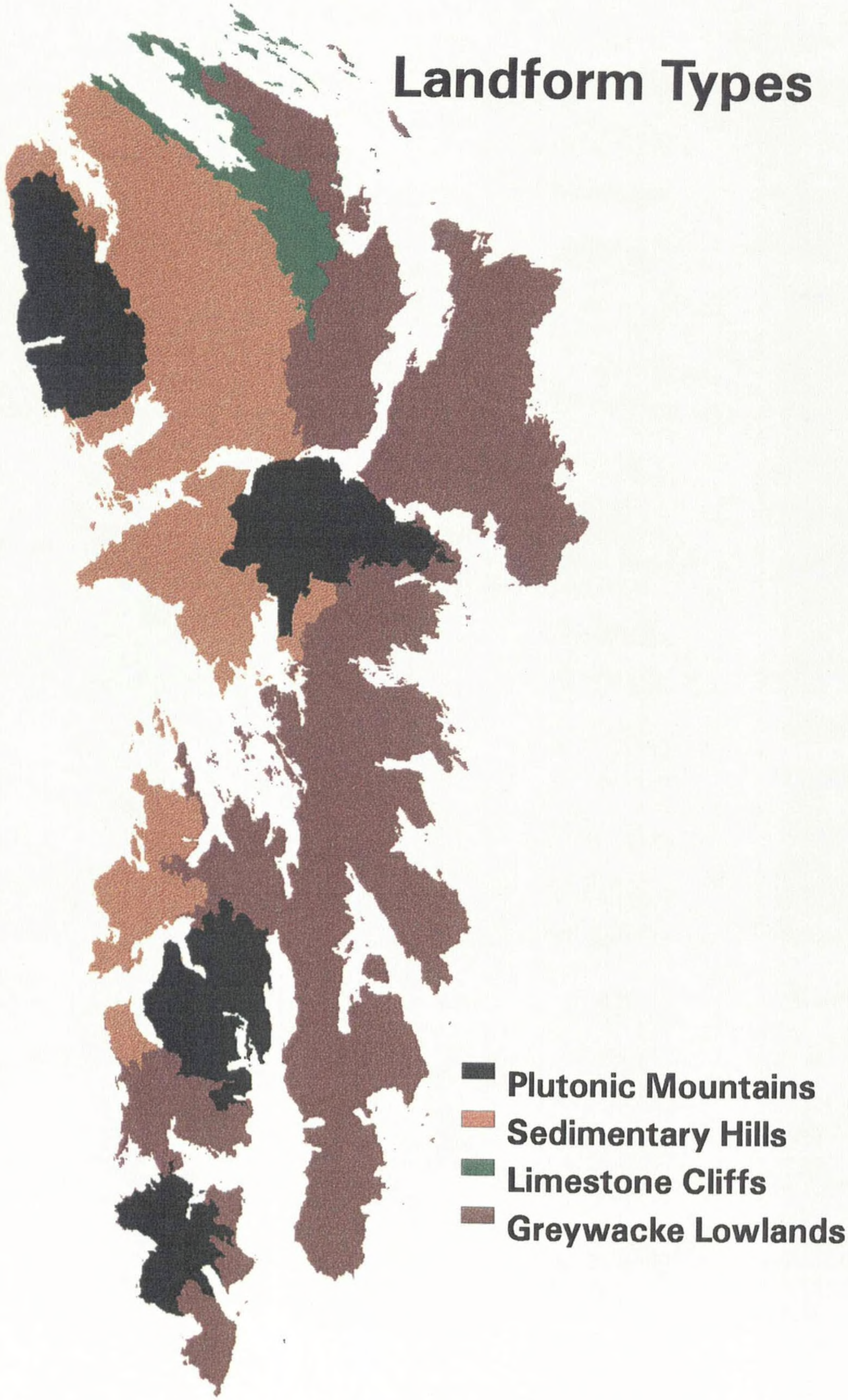

Fig 2a. Major landform types on Kuiu island.

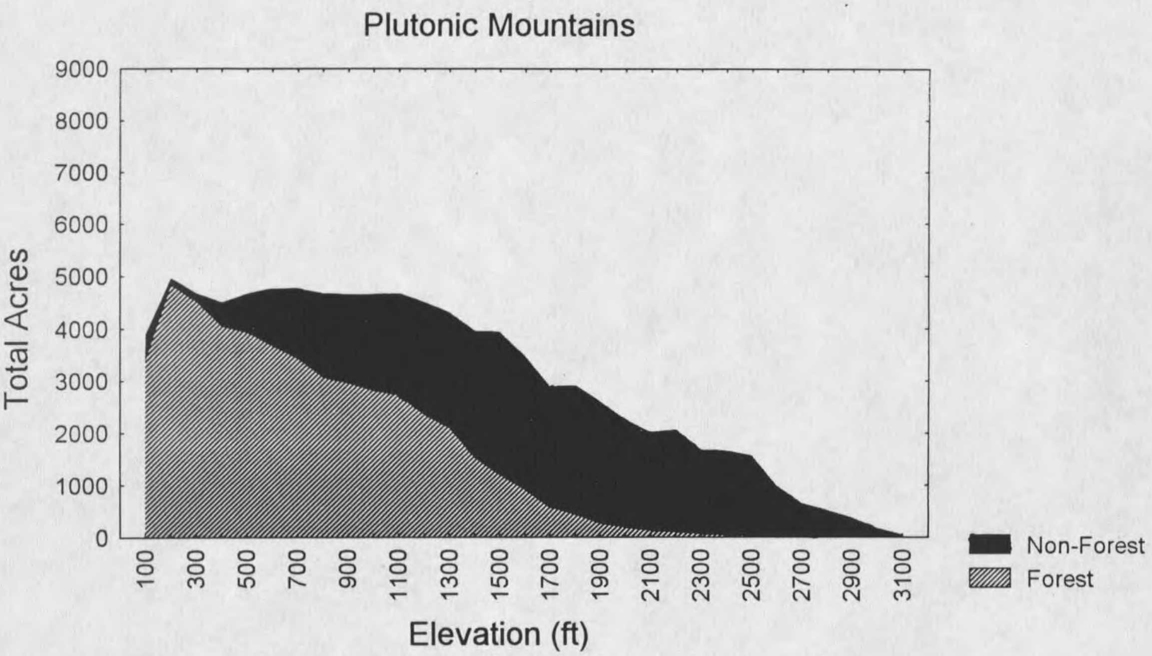

FIG 2b. Forested and non-forested area by elevation in the Plutonic Mountains landform type.

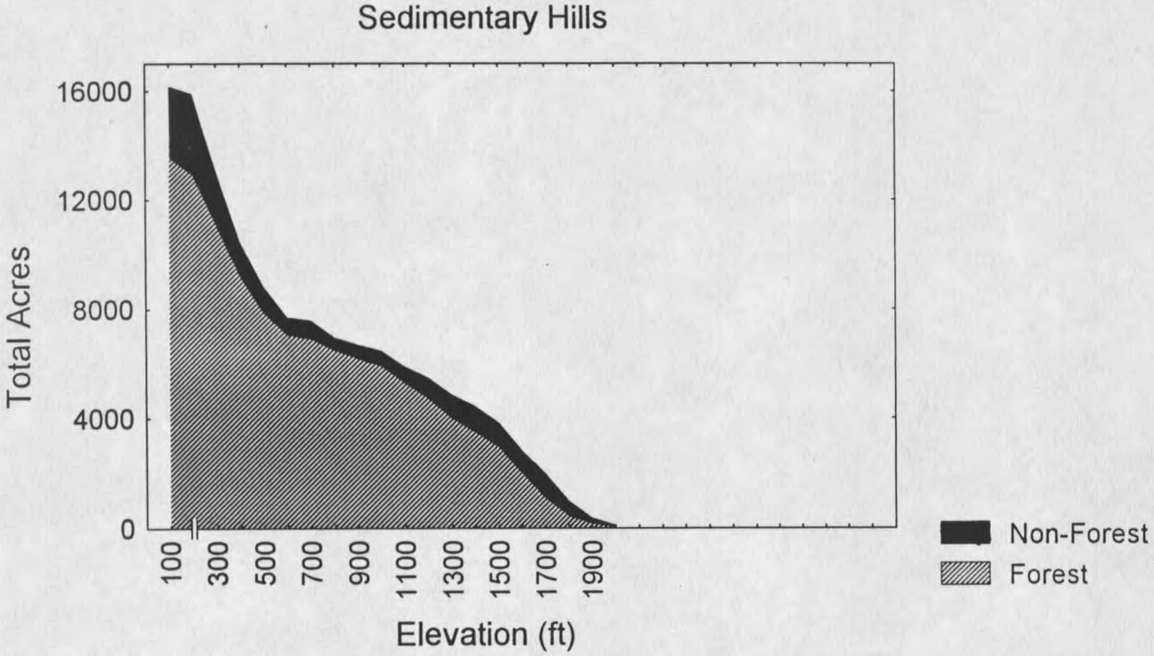

FIG 2c. Forested and non-forested area by elevation in the Sedimentary Hills landform type.

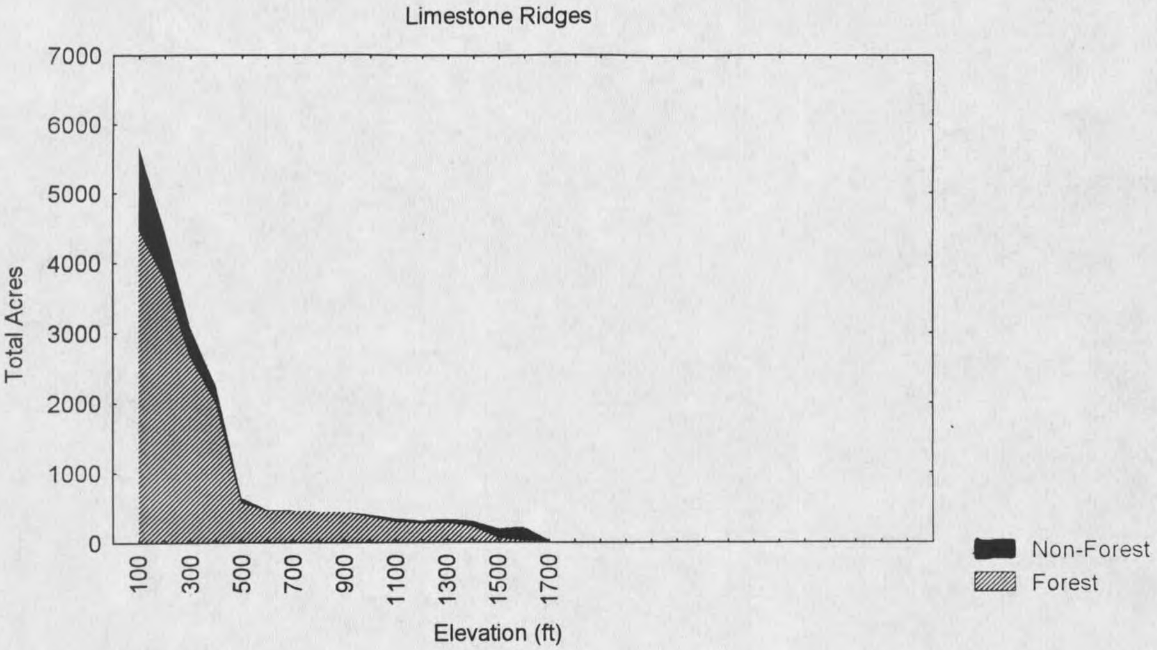

FIG 2d. Forested and non-forested area by elevation in the Limestone Cliffs landform type.

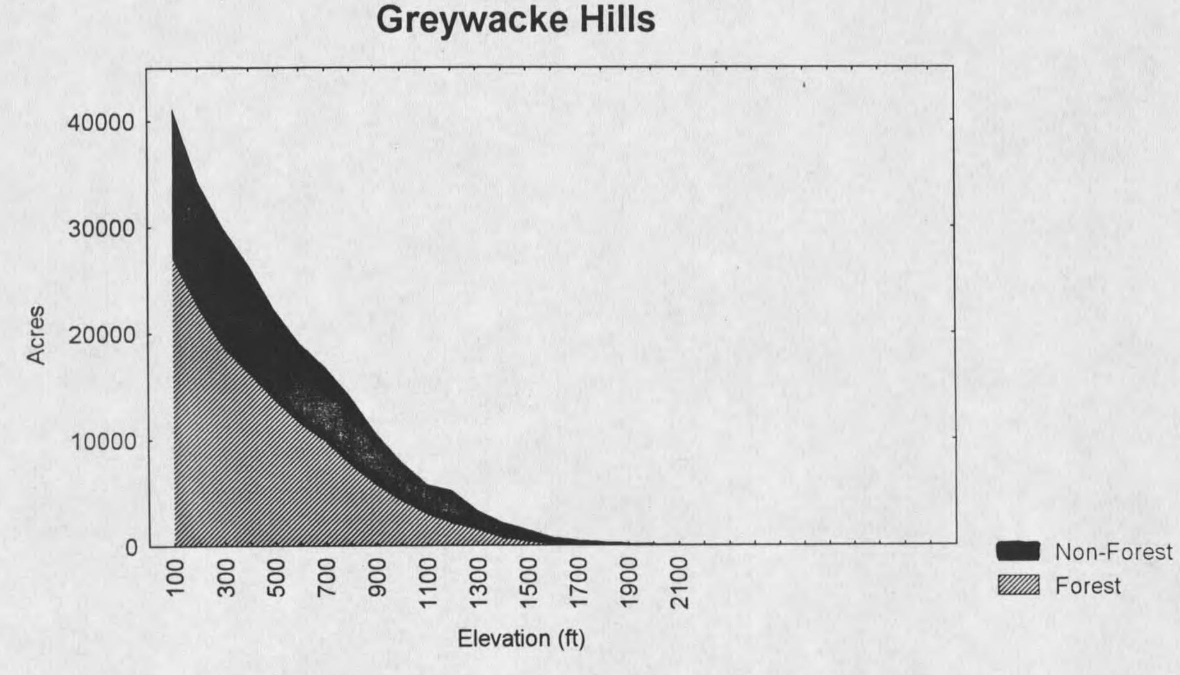

FIG 2e. Forested and non-forested area by elevation in the Greywacke Lowlands landform type.

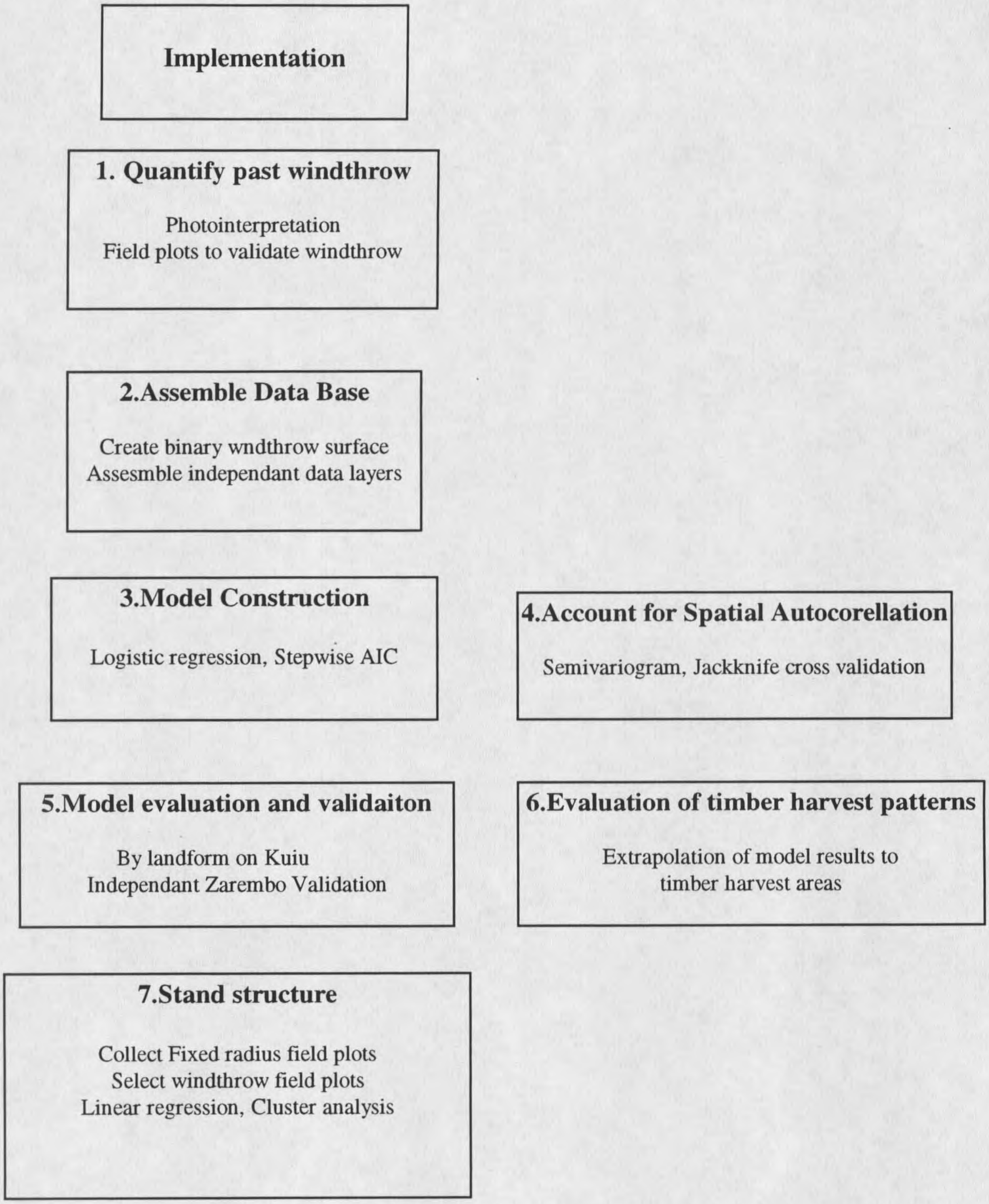

FIG 3. Seven steps used in the study design.

FIG 4. Location of windthrow validation plots on Kuiu Island.

VEGETATION

FIG 5. Each forested cell was classified in a binary state Windthrown (1) and Non-windthrown (0).

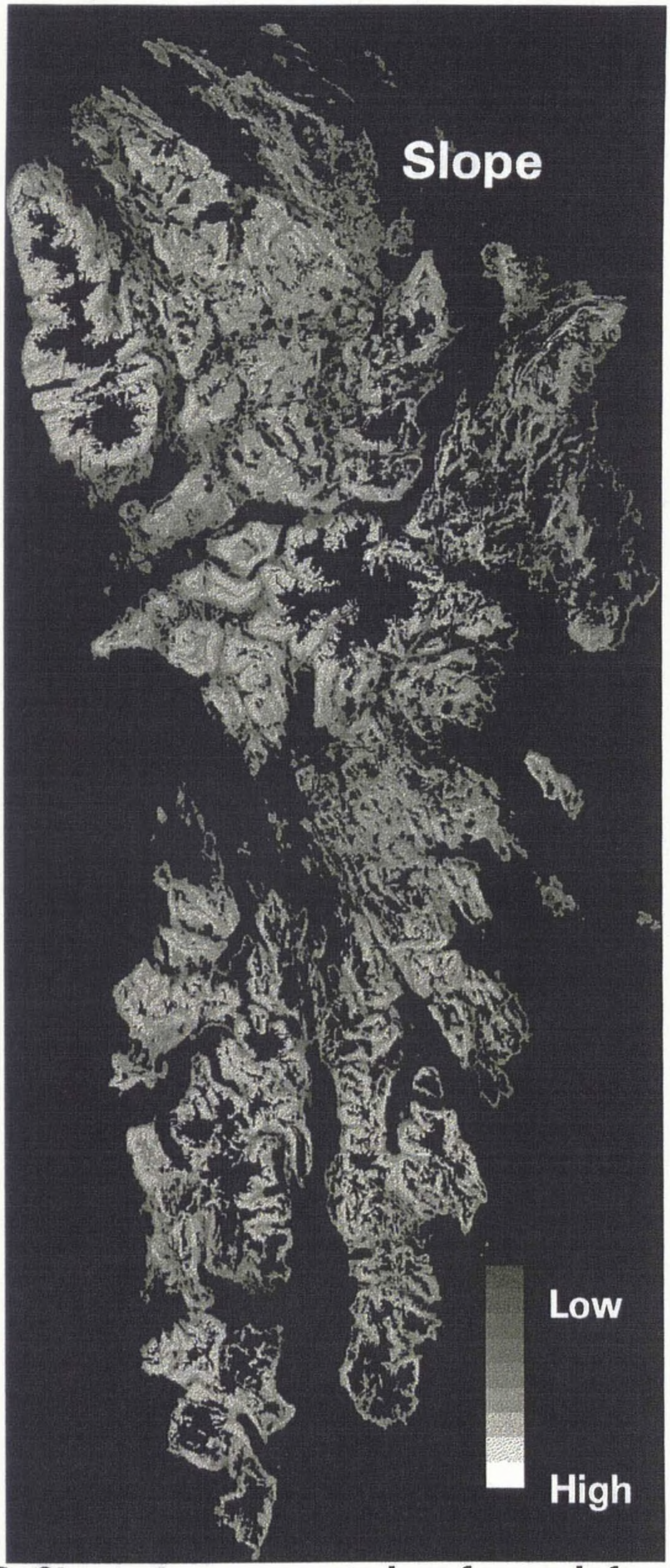

FIG 6. Slope classes created on for each forested cell. Slope catagories range from 1 (flat) to 9 (steep).

FIG 7. Soil stability classes created on for each forested cell. Soil hazard catagories range from 1 (stable) to 4 (unstable).

FIG 8. Elevation classes created for each forested cell. Elevation catagories range from 1 (< 62 m) to 9 (> 1112 m).

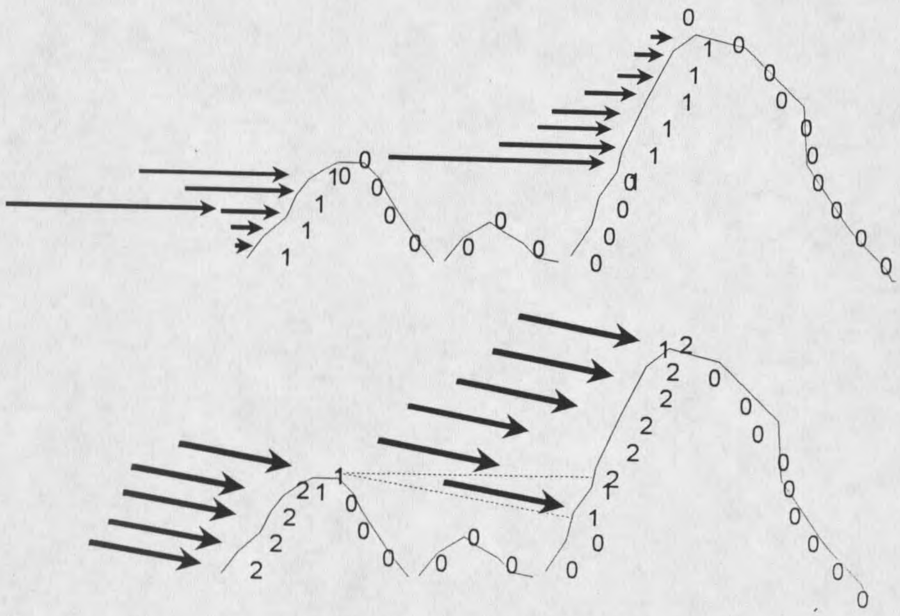

FIG. 9. Modification of EXPOSE model (Boose et al. 1994) to a continuous exposure gradient. Using 0 Degrees to 14 inflection angle, exposure ranges from 1 to 9. Wind direction is from SE to SW (Harris 1989)

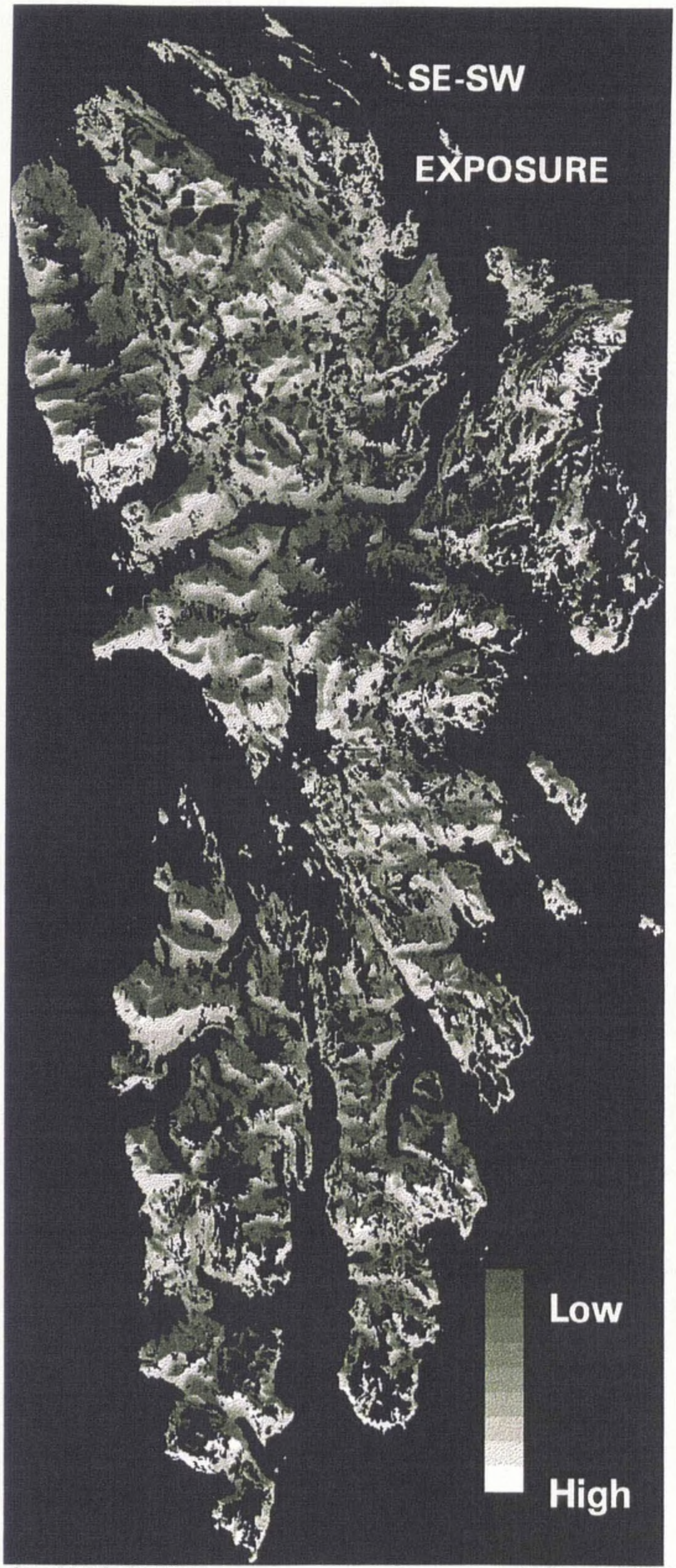

FIG 10. SW-SW Exposure using modified EXPOSE model (Boose et al. 1994). Exposure values range from 1 (least exposed) to 9 (most exposed).

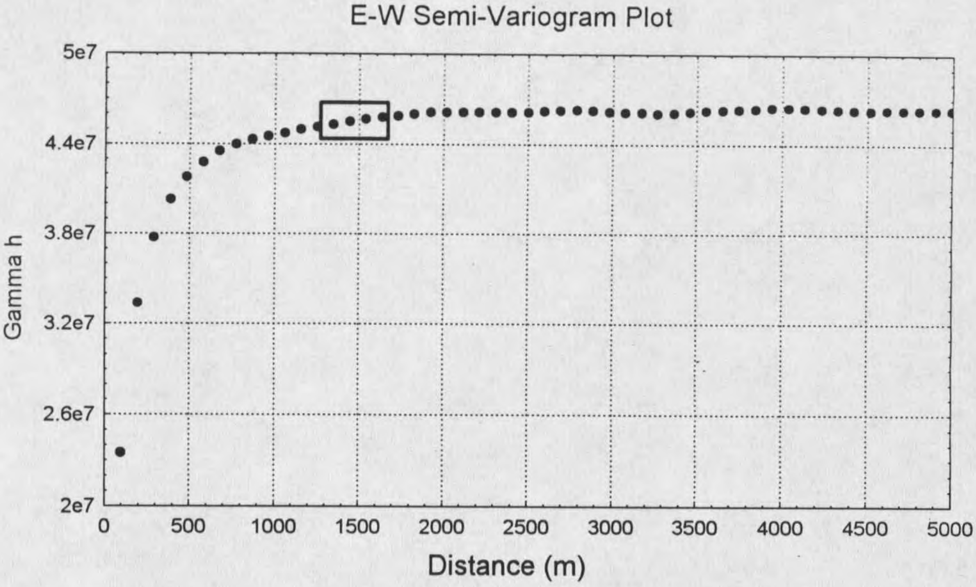

FIG. 11a. E-W directional semivarience results.The lag (distance) at which Gamma h (semivarience) achieves a maximum and constant value is approx. 1500 meters.

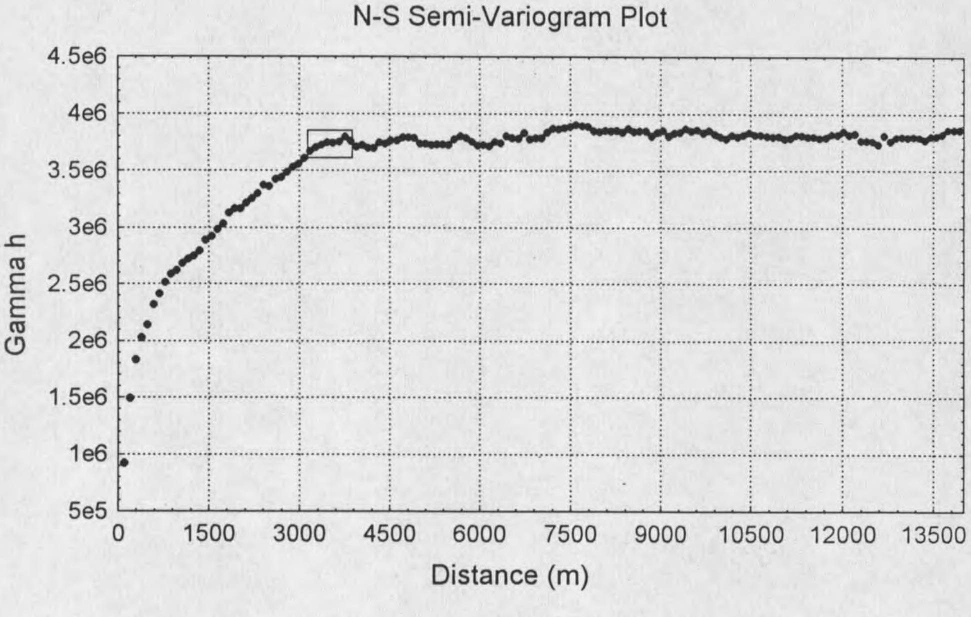

FIG 11b. N-S directional semivarience results. The lag (distance) at which Gamma h (semivarience) achieves a maximum and constant value is approx. 3000 meters.

Jackknife cross-validation

FIG 12a.For each cell selected, a block of data with high spatial autocorrelation to that cell, was removed.

FIG 12b. 95% prediction and coefficient confidence intervals were obtained by jackknifing all non-overlapping blocks.