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Reconstructing the effects of hurricanes over 155 years on the structure and diversity of trees in two tropical montane rain forests in Jamaica

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Abstract

The effects of the spatiotemporal (> 100 years) range of hurricane disturbance intensity on tree diversity and density patterns are largely unknown, because data on past stand or landscape scale hurricane impacts are sometimes unavailable. We therefore reconstructed and mapped topographic exposure (a proxy to disturbance) to twelve category 2–4 hurricanes that affected the rain forests of the Blue Mountains (BM) and the John Crow Mountains (JCM) in Jamaica, over 155 years. Maps of average topographic exposure and the spatial outputs from a pixel-based polynomial regression of the cardinal directions of the tracks of past hurricanes (predictor) and past exposure (response) were then used to represent the aggregate spatiotemporal range of exposure. Next, we used data collected over the period 1974-2009 from 35, 10 x10 m nested subplots and 1991-2004 from 16, 200 m^2 circular plots for the BM and 2006-2012 from 45, 25 x 25 m plots for the JCM, and Bayesian spatiotemporal, Integrated Nested Laplace Approximation (INLA) models to determine whether stand-level (≈ 1 km^2) tree Shannon diversity and density patterns were primarily influenced by exposure to a single hurricane, the most severe hurricane or to multiple hurricanes and the duration of hurricane effects on Shannon diversity and tree density. In the BM, long-term diversity peaked at locations with intermediate values of average exposure for six hurricanes (five of which made landfall over the period 1903-1988). Short-term diversity peaked at locations that experienced significantly higher exposure situated to the south or north of the hurricane's track when the tracks were to the north or south of the island, respectively. Short-term density peaked at locations that were always highly exposed. Moreover, the influence of the most severe hurricane on diversity can last up to 101 years and the influence of the most recent hurricane (Gilbert) on diversity became evident after 16 - 21 years. The JCM was more susceptible to hurricanes and this diminished the influence of past hurricanes.

Consequently, density peaked at sites with the highest average exposure to the four most recent hurricanes (1988-2007), only one of which made landfall. If historical hurricane disturbance data are unavailable, reconstructed exposure maps can be used to provide valuable insights into the effects of past hurricanes on stand-level tree diversity and density patterns.

Keywords: Bayesian; Integrated Nested Laplace Approximation; intermediate disturbance hypothesis; topographic exposure; spatiotemporal models; cyclone; forest structure.

Introduction

Tropical forests on most islands worldwide are subject to repeated effects of tropical cyclones (also referred to regionally as hurricanes and typhoons) (Boose et al. 2004; Bellingham 2008). As a hurricane moves across a forested landscape, meteorological, biological and topographic factors interact to create complex patterns of damage at different spatial scales (Xi et al. 2008). At the ecosystem level (e.g. forest stands), hurricanes cause leaf stripping, branch breakage or loss, snapping of tree crowns and uprooting, and individual and multi-tree blow downs (Boose et al. 1994; Boose et al. 2004; Rossi et al. 2017). At landscape scales, hurricane impacts are generally heterogeneous and, as such, there are usually gradients of damage and mortality across the landscape (Gannon and Martin 2014). The heterogeneity of forest damage is determined by wind velocity gradients that result from the intensity, size and proximity of a hurricane, and their interaction with the abiotic and biotic attributes of a landscape (Zimmerman et al. 1994; Everham and Brokaw 1996; Boose et al. 2004). The abiotic attributes of a landscape that contribute to the heterogeneity of forest disturbance include soils and geomorphology, both of which affect windthrow vulnerability and landslide distribution and local topography which determines differences in site exposure (Bellingham, 1991; Scatena and Larsen, 1991; Zimmerman et al. 1994; Everham and Brokaw 1996; Boose et al. 1994; Gannon and Martin 2014). Biotic features such as forest type, species composition, structural attributes and the characteristics of tree species (stem size [height and diameter], architecture and wood density as examples) influence the susceptibility and response of trees and forest stands to wind damage, and contribute to the heterogeneity of forest disturbance (Boose et al. 1994; Zimmerman et al. 1994; Everham and Brokaw 1996; Tanner and Bellingham 2006; McGroddy et al. 2013; Gannon and Martin 2014).

The degree of structural change, species composition, and the method and rates of recovery within forested stands across landscapes are affected by the spatial patterns of hurricane disturbance (Runkle, 1985). Recovery of the forest canopy following a hurricane is quite rapid (< 10 years) and normally occurs through tree releafing, sprouting, or recruitment of fast-growing species (Boose et al. 2004). However, depending on the severity of hurricane disturbance, there may be major structural changes, such as a significant reduction in biomass (Weaver 2002; Heartsill Scalley 2017), wood volume, basal area, and canopy height (Luke et al. 2016a; Heartsill Scalley 2017), which may take much longer to recover (> 10 years) (Weaver 2002; Heartsill Scalley 2017). Additionally, over the long-term, trees may experience sudden or delayed mortality and variation in growth rates related to the severity of hurricane damage, alterations in regeneration pathways and successional trajectories, and increased species turnover (Weaver 2002; Boose et al. 2004; Tanner et al. 2014). Moreover, the heterogeneity of disturbance affects spatiotemporal variability in environmental conditions and resources (Roxburgh et al. 2004).

This facilitates the recruitment and establishment of species with diverse life history strategies in the community (Tanner and Bellingham 2006; Luke et al. 2016a). Over time, these effects can result in an increase in tree diversity and richness in forests (Denslow 1995; Vandermeer et al. 2000; Tanner and Bellingham 2006; Luke et al. 2016a; Heartsill Scalley 2017) and contribute significantly to tree species coexistence and the maintenance of forest diversity (*sensu*: the intermediate disturbance hypothesis [Connell 1978; Sheil 1999; Shea et al. 2004; Sheil and Burslem 2013]). In addition, there is an increase in stem density in disturbed areas following a hurricane (Tanner and Bellingham 2006) as a lower density of large trees is replaced by more small trees (Denslow 1995). This effect on stem density lasts for many years, even after the canopy has closed (Denslow 1995; Tanner and Bellingham 2006).

Forest susceptibility to wind damage is also influenced by previous hurricanes, as the impact of a single hurricane event is not independent of past hurricanes (Webb 1958; Boose et al. 2004; Hogan et al. 2018; Ibanez et al. 2019). A total of 152 hurricanes struck the islands of the Greater Antilles, located in the northern Caribbean, between 1851 and 2009 (Gannon and Martin 2014). The hurricane return interval for affected forest sites in the region is on average10 years, although the most that any one site (the far west of Cuba) was struck was 34 times (with a 4.6 year hurricane return interval) (Gannon and Martin 2014). As such, trees that live for over 100 years in these forests are likely to be affected by many hurricanes during their lifespan (Weaver 1986). Therefore, the long-term impact of hurricanes on forest stands can only be understood on a scale of decades to centuries (Boose et al. 1994). Yet, our understanding of hurricane damage, and the mechanisms of short- and long-term recovery at forest sites in the Caribbean, is largely based on stand-level assessments, conducted before and/or after a single hurricane event in decadal timescales. Meteorological models using data such as historical hurricane track, size, wind speed and wind direction have been used to reconstruct the spatial patterns of disturbance, over different periods (3–158 years) and at various scales (landscape and regional) (e.g. Boose et al. 1994, 2004; Gannon and Martin 2014; Batke et al. 2014; Luke et al. 2016a). However, these data are unavailable for most sites or they have been largely used to explain stand- or landscape-level disturbance patterns and are not often used to explain stand-level fluctuations in tree diversity and density. As a result, the cumulative effects of long-term (> 100 year) hurricane disturbance intensity on forest community responses, such as dynamics and diversity patterns, is less understood. Moreover, the number of high intensity cyhclones is predicted to increase due to the effects of global climate change (Elsner et al. 2008; Bender et al. 2010; Knutson et al. 2010). As a result, forest stands across the Caribbean and in other regions are beginning to become increasingly affected by multiple high-intensity hurricanes (Luke et al. 2016a; Lin et al. 2017, Uriarte et al. 2019). These hurricanes could accelerate structural and compositional changes, particularly at sites that are more exposed to recent and previous hurricane events (Luke et al. 2016a). There is a need to increase our understanding of the impacts of the historical and contemporary range of hurricane disturbance intensity, over space and time, on community dynamics and diversity patterns (Boose et al. 1994; Gannon and Martin 2014; Batke et al. 2014).

Elucidating the effects of past hurricanes on forest stands will require an integrative approach that combines stand-level (≈ 1 km^2) observations with past landscape level (≈ 10 km^2) hurricane disturbance intensity data (e.g. Xi et al. 2008; Luke et al. 2016a). However, there is usually little or no data available on past stand or landscape scale hurricane impacts. It is now possible to generate historical and contemporary landscape scale data on hurricane impacts, due to an increase in the processing power of personal computers and the advent and availability of Geographic Information System (GIS) software, spatial and geographic data and detailed weather data. In addition, the emergence of the interdisciplinary field of geomorphometry, which is concerned with the extraction or quantification of topographic parameters from digital elevation models (DEMs: a digital representation of the terrain or land surface) in a GIS software environment, has been instrumental (Pike et al. 2008; Batke et al. 2014). Topographic exposure is a geomorphometric feature that characterises a site based on the degree of protection it receives from the surrounding landscape and it is the main landscape feature that has been quantified, mapped and used as a proxy for past wind or hurricane disturbance intensity (Ruel et al. 2002; Mikita and Klimánek 2010; Batke et al. 2014; Luke et al. 2016a). Topographic exposure maps have been generated for single and multiple hurricanes (Boose et al. 1994, 2004; Luke et al. 2016a), and average exposure has been calculated based on multiple wind directions (Mikita and Klimánek 2010) and wind inflection angles (Batke et al. 2014), which are used to estimate the wind shadow (Boose et al. 1994). They have also been used to reconstruct > 100 years of hurricane disturbance regimes (Boose et al. 1994, 2004). Additionally, data from exposure maps have been extracted and used to determine the cumulative effects of disturbances from three hurricanes on structural changes and diversity at the stand-level (Luke et al. 2016a). However, reconstructed hurricane exposure maps representing > 100 years of hurricane disturbance have never previously been used to determine the cumulative effects of the spatiotemporal range of hurricane disturbances on forest structure and diversity at the stand-level.

In this study, we therefore sought to determine the cumulated effects of the spatiotemporal (> 100 years) range of hurricane disturbances on stand-level spatiotemporal patterns of tree diversity and density. To enable this, we reconstructed topographic exposure maps of hurricanes that affected two adjacent montane sites with a similar disturbance history, the Blue Mountains (BM) and the John Crow Mountains (JCM), in Jamaica, over 155 years (1852–2007). Two methods of aggregating or summarizing the spatiotemporal range or pattern of past hurricane exposure at the landscape scale (≈ 10 km^2) were then evaluated. Luke et al. (2016a) summarized the spatiotemporal range of exposure in the JCM by averaging exposure values extracted from exposure maps for three hurricanes. However, the spatial pattern of exposure or disturbance is also influenced by the distance and the angle/ cardinal direction of the hurricane's eye from and relative to an island or other landmass (Luke et al. 2016a; Boose et al. 1994, 2004). Therefore, we aggregated the spatial and temporal ranges of hurricane exposure by averaging the exposure maps and by modelling the relationship between exposure and the distance or cardinal direction of the tracks of the eye of each hurricanes from or relative to the study sites, and representing these relationships spatially. Data from these maps were then extracted and used to determine whether stand-level (≈ 1 km^2) tree diversity and density spatiotemporal patterns over the periods 1974–2009 and 1990–2004 for the BM and 2006–2012 for the JCM, were primarily influenced by exposure to a single hurricane, the most severe hurricane or multiple hurricanes and the duration of hurricane effects on tree diversity and density patterns. We hypothesized that past hurricanes will influence current patterns of diversity by maintaining the highest levels of tree diversity at sites that historically experienced intermediate levels of disturbance. Species coexistence and/or diversity are expected to peak under intermediate disturbance regimes because longer-lived species will not persist if there is too much disturbance and pioneers will be competitively excluded if there is too little disturbance (Connell 1978; Sheil 1999; Shea et al. 2004; Sheil and Burslem 2013). We also hypothesized that tree density will be highest at sites that historically experienced the highest levels of disturbance or exposure to hurricanes, on the basis that stands which are frequently exposed to hurricane winds will have continually high turnover rates and hence higher stem densities (Denslow 1995).

Study sites

The study sites are forests located on two mountain ranges in Jamaica, the Blue Mountains (BM) and John Crow Mountains (JCM)). Together these ranges comprise the Blue and John Crow Mountains National Park (Figure 1). Data used in this study were measured in plots that were established close to the Grand Ridge of the BM (18° 05′ - 18° 059′ N, 76° 38′ - 76° 40′W) at an elevation of 1320–1920 m in an upper montane tropical forest (Tanner 1977; Tanner and Bellingham, 2006). The data from the JCM were measured in plots established along an altitudinal gradient (400–800 m) at two different sites (18° 3′ N, 76° 21′ 39.6′′ W) (Figure 1). The JCM have a maximum elevation of 1143 m asl and the plots were established in both lower and upper montane tropical forests (Luke et al. 2016a). Both sites have been affected by hurricanes and the resulting effects on the forests have been documented: Hurricane Gilbert (1988) (Bellingham 1991; Bellingham et al. 1992; Bellingham and Tanner 2000; Tanner and Bellingham 2006; Tanner et al. 2014) and Hurricanes Ivan (2004), Dennis (2005) and Dean (2007) (Luke et al. 2016a,b).

Method and materials

Reconstructing hurricane topographic exposure vulnerability

Exposure vulnerability (EV) is a unitless measure that can be used to link the disparity in hurricane exposure to the responses of tree species and the forest ecosystem at sites where there is hurricane disturbance (Luke et al. 2016a). The calculation of EV requires hurricane tracks, a digital surface model (DSM), and information on wind direction and speed (Luke et al. 2016a). EV maps for three hurricanes (Ivan (2004), Dennis (2005) and Dean (2007)) were generated by Luke et al. (2016a) and were used in this present study. Wind speed and direction data that were used to construct the three EV maps were obtained from processed ultra-high-resolution images of circular hurricane wind bands. These were created from QuikSCAT scatterometer satellite data that were processed using a Scatterometer Image Reconstruction (SIR) technique (Early and Long 2001). The images included colour-coded information on wind speed (in knots) overlaid with wind flags, which point in the direction from which the wind is blowing (see: Luke et al. 2016a). However, QuikSCAT Scatterometer images (available at: http://www.scp.byu.edu/data/Quikscat/HRStorms.html) are only available for the period 1999–2009 for hurricanes that developed in the Atlantic Ocean and the Caribbean Sea. Therefore, in the present study, we used a method modified from Luke et al. (2016a) to reconstruct EV maps for hurricanes that preceded 1999 using information on wind speed and wind direction obtained from proxy or surrogate images.

To reconstruct the EV maps of pre-1999 hurricanes, we first downloaded an ESRI point .shp file of the tracks of all hurricanes recorded in the Caribbean from the National Oceanic and Atmospheric Administration (NOAA), National Climatic Data Center website (http://www.ncdc.noaa.gov/ibtracs/index.php?name=wmo-data) and the tracks were re-projected to the Jamaican datum, JAD 2001. Tracks of hurricanes categorized as category 2, 3 and 4 using the Saffir-Simpson Hurricane Wind Scale (maximum wind speed ≥ 154 km hr^{-1} at their eye as they passed at their closest points to the coastline of Jamaica) during the period 1852 to 1988 (Table 1), with centers that passed within 0–160 km of the northern or southern coastline of Jamaica, were then selected. A 160 km threshold was used because Hurricane Emily, which passed 160 km from the south coast (in 2005), had minimal effect on the JCM forest, as the outer bands that passed over the JCM had wind speeds < 65 km hr^{-1} (Luke et al. 2016a). Next, where possible, surrogate/proxy QuikSCAT images representing 'typical' category 2, 3 and 4 hurricanes over water in the Caribbean were selected and downloaded as a .gif file format and rectified to the Jamaican datum. These images included Hurricanes Michelle (November 3, 2001; wind speed: 167 km hr^{-1}; location: 18° N 84° W), Charley (August 12, 2004; wind speed: 148 km hr^{-1}; location: 20° N 81° W), Ivan (September 11, 2004; wind speed: 240 km hr^{-1}; location: 18° N 80° W), Jeanne (September 20, 2004; wind speed: 111 km hr^{-1}; location: 26° N 72° W), Emily (July 15, 2005; wind speed: 213 km hr^{-1}; location: 15° N 23° W), Dennis (July 7, 2005; wind speed: 167 km hr^{-1}; location: 18° N 75° W) and Dean (August 20, 2007; wind speed: 240 km hr^{-1}; location: 18° N 81° W). A list of hurricanes for which the EVs were reconstructed, and the proxy hurricane(s) used to model the EV of each hurricane are presented in Table 1. The best proxy image for Hurricane Gilbert was determined by comparing several proxy QuikSCAT images to a rectified satellite image of Gilbert as it passed over Jamaica. Hurricane Ivan closely matched the satellite image and was therefore used to model the final EV map of Hurricane Gilbert. The EV of Hurricane Gilbert was also modelled using proxy hurricanes from the same Saffir-Simpson Hurricane Wind Scale such as Hurricanes Emily and Dean, and the average of all three proxies (Ivan, Emily and Dean).

For each hurricane, the ‘Georeferencing’ function in ArcGIS was used to center the surrogate or proxy hurricane images on the approximate location of the hurricane’s eye, specifically on track points found close to or over Jamaica. Wind flags found close to the JCM and BM were digitized as polylines in ArcGIS. For wind speeds ≥64 km hr^{-1}, the upper value/range of the wind bands that were likely to affect the BM and the JCM were used as estimates of wind speed. There were no wind speed values for the wind bands closer to the track points (that is, for wind speeds > 93 km hr^{-1}). Average wind speed was estimated for these wind bands by averaging the wind speed at the track point over which the image was centered and 93 km hr^{-1}, which was the maximum wind speed of the wind category below the > 93 km hr^{-1}category. The ‘hillshade’ feature in ArcGIS was used with a digital surface model (DSM; 6.5 m resolution) of the eastern section of Jamaica, to generate maps of topographic exposure to wind from various directions (following Mikita and Klimánek 2010 and Batke et al. 2014). The hillshade feature requires the input of an azimuth angle (wind direction) and an altitudinal angle (range 0‾90°) (wind inflection angle). A fixed wind inflection angle of 20° that was used by Luke et al. (2016a), was used to create the EV maps. Hillshade maps of exposure for each hurricane were generated by inputting the following formula from Luke et al. (2016a) into the raster calculator in ArcGIS:

$$\mathrm{EV} = \left(\sum_{i=1}^{n}(\text{wind speed}_i \ * \ \text{hillshade map of exposure}_i)\right)/n,$$

where *i* is one of several locations where the surrogate/proxy hurricane image(s) was (were) centered and evaluated (e.g., location (*i*) = 1, 2, 3, 4…) and *n* is the total number of locations evaluated/hillshade maps created.

Permanent sample plot data from the Blue and John Crow Mountains

Data from the upper montane rain forest of the BM are from the "Tanner's plots" established in 1974 in four sites, within which are contiguous 10 × 10 m plots (Col [0.09 ha], Mor [0.06 ha], Mull [0.10 ha], and Slope [0.10 ha]; Tanner 1977). The plots were established within 300 m of each other, at elevations 1580–1600 m (Figures 1 and 6) and covered a total area of 0.35 ha. Although the plots are small in size and number, they sampled a representative area due to the low tree species diversity in the BM. Specifically, 33 species that were sampled in the plots in 2009 accounted for 93% and 95% of all the stems (≥ 3 cm DBH) and basal area, respectively (Chai et al. 2012). For a full description of the sites see Tanner (1977) and Tanner et al. (2014). All stems ≥ 3 cm diameter at breast height (DBH, measured at 1.3 m aboveground) were identified to species, scored as live or dead, and measured (DBH) in 1974, 1984, 1989, 1991, 1994, 2004, and 2009 (Tanner et al. 2014). When the plots were re-enumerated after Hurricane Gilbert in 1989 and 1991, visible signs of hurricane damage and modes of recovery were documented (i.e., percentage of all stems in the plots scored as defoliated, dead and resprouting; Bellingham et al. 1995) and these data were used in this study.

More extensive data from the BM were derived from the "Bellingham's plots", specifically, 16 permanent 200 m^2 circular plots covering a total area of 0.32 ha that were established in 1990, 20-23 months after Hurricane Gilbert, along five, 500-m transects, 1 km apart (Bellingham 1991) (Figures 1 and 7). The plots were established at elevations 1320–1920 m, and were located orthogonal to the Grand Ridge of the BM at distances of 0, 250 and 500 m along each transect, at the northernmost point, the top of the Ridge and the southernmost point, respectively (Bellingham 1991) (Figures 1 and 7). All stems, living and dead, that were ≥ 3 cm DBH were measured and identified and the plots were re-enumerated in 1994 and 2004. Types of damage caused by Hurricane Gilbert and modes of recovery that were recorded included mortality, uprooting, breakage, crown defoliation and resprouting (Bellingham 1991). Damage and recovery (resprouting) were expressed as a percentage of all stems in the plots.

Table 1. Information on the hurricanes reconstructed in this study, including the date the first exposure vulnerability map for each hurricane was reconstructed, average wind speed or range of wind speeds at the eye, distance from the eye of the hurricanes to the closest point along the coastline of Jamaica, average cardinal direction (or angle) of the track of the eye of the hurricanes relative to the study sites (used in the Curve Fit and the *calc* polynomial regressions) and the proxy hurricanes used to reconstruct their exposure vulnerability.

Hurricane	Date	Wind speed (km hr^{-1})	Distance (km)	Angle (degrees)	Proxy hurricane(s)
1852 (unnamed)	06/10/1852	167	73.5	199.08	Jeanne
1880 (unnamed)	06/08/1880	148	71	195.81	Jeanne
1903 (unnamed)	11/08/1903	195	0	279.17	Jeanne
1912 (unnamed)	17/11/1912	93 - 185	0	336.14	Jeanne
1915 Galveston	13/08/1915	176	13.2	333.19	Jeanne
1951 Charlie	17/08/1951	139 - 176	0	202.08	Michelle, Charley and Dennis
1964 Cleo	25/08/1964	232	113.7	40.71	Michelle and Dennis
1980 Allen	06/08/1980	213	49	300.39	Ivan, Emily and Dean
1988 Gilbert	12/09/1988	204 - 213	0	215.75	Ivan, Emily and Dean
2004 Ivan	11/09/2004	241 - 250	40.3	203.44	Ivan
2005 Dennis	07/07/2005	185	45.9	40.82	Dennis
2007 Dean	20/08/2007	231	40.9	167.69	Dean

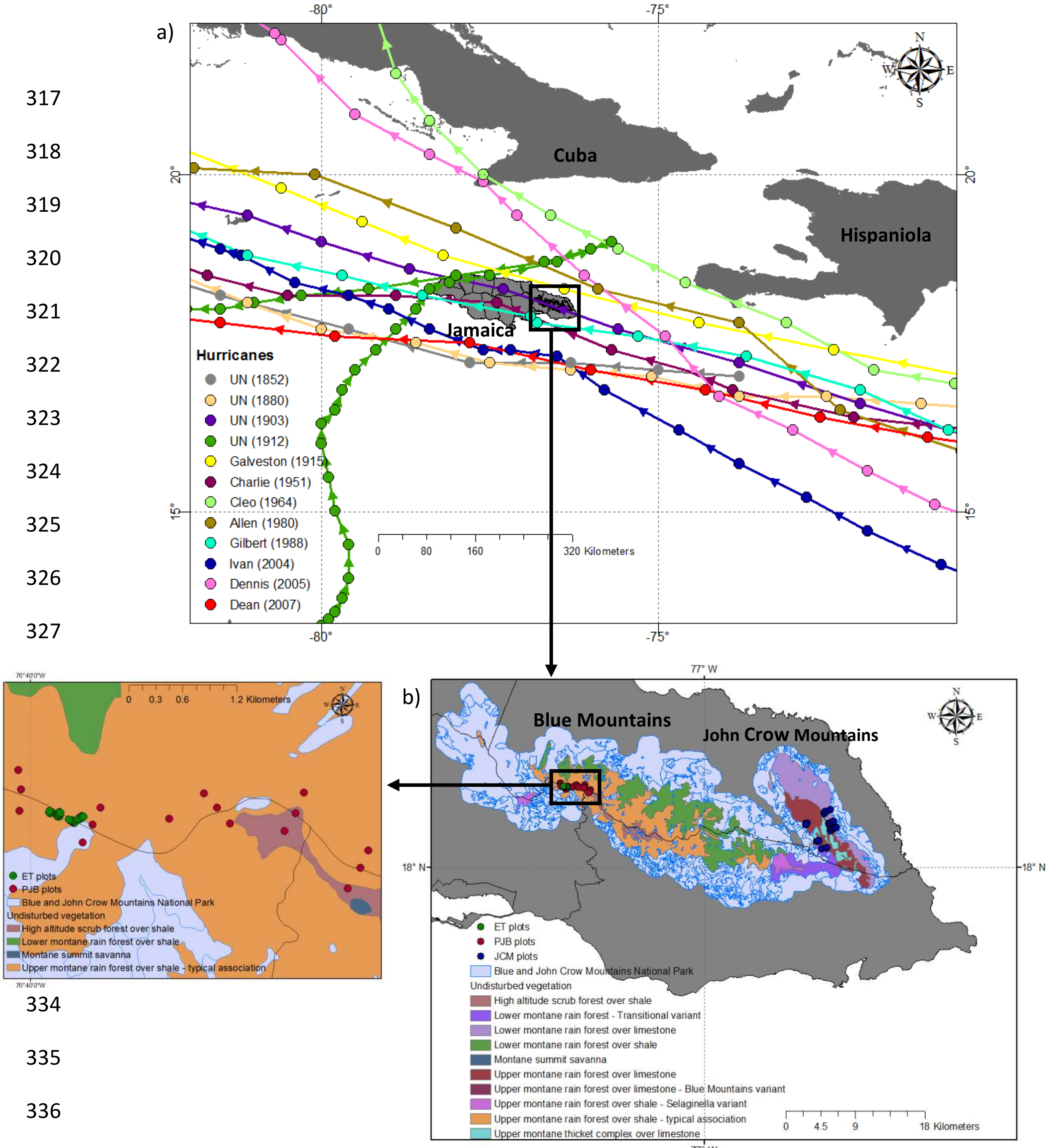

Figure 1. a) Tracks of hurricanes categorized as category 2, 3 or 4 using the Saffir-Simpson Hurricane Wind Scale, with centers that passed within 0–113 km of the northern or southern coastline of Jamaica during 1852–2007. Exposure vulnerability of these hurricanes was reconstructed. Also included are b) maps of the study site, the Blue and John Crow Mountains National Park (source: Muchoney et al. 1994), showing the extent of several old growth vegetation classes, and overlaid with the location of permanent sample plots (ET: Tanner (1977); PJB: Bellingham (1991) and JCM: Luke et al. (2016a)) established in the Blue and John Crow Mountains, Jamaica. The colour coded arrows show the direction of the hurricanes.

EV model evaluation data

Luke et al. (2016a) used global site factor (GSF) (calculated from hemispheric photographs) data collected six months after Hurricane Dean (in 2008) in PSPs located in the JCM to test how well their EV model performed. Specifically, they used a spatially explicit generalized additive mixed model (GAMM) to showed that the EV values, which were extracted from the EV maps using the GSF plot location, explained the highest deviance in the GSF data and that GSF increased significantly with Hurricane Dean EV (Luke et al. 2016a). In the present study, we used a similar approach. In particular, we used a spatially explicit generalized linear mixed model (GLMM) and damage and recovery data from Bellingham's and Tanner's plots to determine if the reconstruction method accurately modelled sites that were exposed to Hurricane Gilbert. Dependent variables used in the GLMM included percentage of stems in the plots that died, had crown defoliation, and had resprouted in 1990 from Bellingham's plots. From Tanner's plots, the dependent variables included percentage of stems with crown defoliation and resprouting in 1989 and 1991.

Based on previous stand-level assessments (Bellingham 1991), it was expected that plots with the highest exposure would suffer greater hurricane damage and show evidence of a higher percentage of recovering stems. Nevertheless, we evaluated the influence of several independent variables on the damage and recovery data to determine if EV was the most important predictor. As such, the independent variables included elevation, aspect, topographic position index (TPI) and EV values for Hurricane Gilbert, which were extracted at each plot location. Elevation values were obtained from the DSM, whereas aspect and TPI values were extracted from maps that were generated from the DSM. The TPI map was generated using the Land Facet Corridor Designer Tools for ArcGIS 10 (Jenness et al. 2013). TPI values are continuous and as they change from negative to positive this is indicative of a transition from valleys to slopes to ridge tops. Specifically, negative TPI values represent valleys and gullies, TPI values near zero represent mid-slopes, and positive and comparatively large TPI values represent ridges and ridge tops (Jenness et al. 2013). To determine the effects of hurricane proxy choice (Hurricane Dean QuikSCAT Scatterometer image) on EV map accuracy, the model evaluation was repeated for Gilbert EV maps reconstructed using other proxies such as Hurricanes Dean and Emily and average EV of the three proxy hurricanes. The accuracy of EV maps generated using the best single proxy, which was Hurricane Ivan, a proxy from the same Saffir-Simpson Hurricane Wind Scale category, which is Hurricanes Dean and Emily, and the average of the three proxies, was then compared. The statistical method used to evaluate the EV model is described below.

Aggregating the spatial patterns of hurricane disturbance: modelling the influence of hurricane direction and distance on exposure vulnerability

Unless stated otherwise, statistical tests were performed using the R programming language (R Development- Core-Team, 2017). The path of the hurricane is determined by the storm forward speed and direction. Both influence the angle of approach of the hurricane to an island or a landmass and the cardinal direction of the track of the hurricane. Bivariate plots of EV and aspect were therefore generated and inspected, and were used to determine the directional patterns of exposure based on the cardinal direction/angle of the track of a hurricane's eye. Before the data were plotted, a raster image of undisturbed upper montane forest in the BM (Figure 1) was converted to a point .shp file. This was used to extract EV and aspect values from the respective maps. The *polarPlot* function from the 'openair' package (Carslaw and Ropkins, 2012) was then used to construct a bivariate plot of the relationship between EV and aspect for each hurricane. This process involves creating a smooth surface by fitting a generalized additive model (GAM) to the data. The level of smoothness is controlled by the smoothing parameter *k* and we used the default value (100). The *polarPlot* function and the resultant bivariate plot are suitable for a graphical analysis but not for quantitative purposes. As such, directional information on EV was discerned graphically when the smooth surface was plotted in polar coordinates. Plots for the JCM were very similar to those of the BM, and therefore, they are not presented. The relationships between the cardinal direction of the tracks of the eyes of the hurricanes relative to the study sites and EV and distance from the eyes of the hurricanes to the study sites and EVwere then explored (Figures 5-8). A polynomial (2nd-degree) model was found to be the most suitable model for representing this relationship. As such, a pixel-level (2nd-degree) polynomial regression analysis was conducted using the USGS Curve Fit extension for ArcMap (De Jager and Fox, 2013). This was used to map the spatial patterns of exposure based on the angle or cardinal direction of the track the hurricane’s eye and distance to the hurricane’s eye, over the period 1852–2007. Curve Fit uses a linear or nonlinear regression to calculate a unique mathematical model at each pixel of the input raster data sets (De Jager and Fox, 2013). The input for the Curve Fit function included a time series of EV maps for the BM and JCM (dependent variable), and the average angle or cardinal direction (in degrees) of the track of the eye of each hurricane relative to the study sites or the distance to the eye of each hurricane from the study sites, as an independent variable (Table 1).

Before the exposure maps were added to the Curve Fit function, they were first clipped to an area of interest that included only natural old growth (including old secondary) forest of the predominant forest type found at both sites where the plots were established (Figure 1). This helped to reduce processing time. The Curve Fit output products generated for this study included the P-value, adjusted R^2 and parameter a2 of the fitted polynomial regression, as image files. The a2 parameter is the regression coefficient for the squared term. If $a2 > 0$, then the relationship with the response is convex or concave upward, whereas if $a2 < 0$, then the relationship is concave downward. The *calc* function in R can be used to generate similar outputs and this was used to generate maps from a fitted pixel-level polynomial regression for the period 1852-1988. At each plot location, these values (from the Curve Fit image files) were extracted and used in subsequent analyses. Bellingham's plots were likely to be influenced by hurricanes that struck the island before the final census was conducted in 2004; therefore, only values from the *calc* image files were extracted and used. Although adjacent pixels would likely influence the EV value of a pixel, the pixel-level regression only considers a single pixel at a time and generates a model for each pixel. Consequently, there was no spatial autocorrelation, but the data were likely to be temporally autocorrelated. We therefore used the partial autocorrelation function (PACF) and the autocorrelation function (ACF) to assess the residuals from polynomial models developed using EV data extracted using the plot data to confirm that there was no temporal autocorrelation, that is, they followed a white noise (random) process.

Bayesian hierarchical spatiotemporal/spatial model structure: EV model evaluation and the effects of EV and/or topographic features on tree diversity and density

Tanner’s plots were established according to a nested design, which included several contiguous subplots nested within four plots or ‘sites’. Also, the layout of Bellingham’s plots followed a fully systematic design and Luke et al.’s (2016a) plots followed a structured or a stratified randomized block design. Consequently, Tanner’s subplots were spatially pseudo-replicated and auto-correlated because they were adjacent to each other in space. Additionally, the plots within each transect of Bellingham (1991) and within each block of Luke et al. (2016a) were also close enough to each other to potentially be spatially auto-correlated. Nested, systematic and structured data can be fitted in a standard linear model with nested, systematic, that is, using each transect as a block, and structured fixed effects. However, the degrees of freedom must be adapted to the design of the study, because the errors will likely be spatially correlated and thus violating the assumption of independent observations or errors. This must be accounted for by a model to obtain accurate mean sum of squares (Gelman 2005; Schielzeth and Nakagawa 2013). As such, data from the nested subplots, the transects and structured plots can only be appropriately modelled using mixed effects models, which cluster the data in groups as a random effect (Schielzeth and Nakagawa 2013; Zuur et al. 2017) and estimate the standard errors correctly (Gelman 2005), because the latter will be biased if they are not corrected for clustering. A better approach is to use a mixed-model with a spatial autocorrelation structure (using the coordinates of the center of the subplots and plots), as the errors are allowed to be correlated and/or to have unequal variances (Crawley 2012). However, some of the data were also likely to be temporally auto-correlated; as a result, the most appropriate models should include spatial and temporal autocorrelation structures. Nonetheless, the choice of frequentist methods that can cope with these structures is limited, and the most appropriate methods require Bayesian statistics (Zuur et al. 2017). Consequently, the models that were developed in this study were fitted using a

Bayesian approach based on the Integrated Nested Laplace Approximation (INLA), implemented using the 'INLA' package (Rue et al. 2009; Lindgren et al. 2011; Martins et al. 2013; Lindgren and Rue 2015; Rue et al. 2017). The method was used due to its flexibility (see below) and because the posterior marginal probabilities are approximated more efficiently and faster, when compared with traditional MCMC approaches (Rue and Martino 2007; Rue et al. 2009).

Two types of model were developed: models with either a spatiotemporal random effect for overall assessments, regardless of time, and models with a spatial random effect for each individual census. Models were developed for EV model evaluation and to determine whether average EV from several hurricanes, topographic parameters or data from the Curve Fit and the *calc* function output products could be used to explain spatial and/or spatiotemporal patterns of tree diversity and density in the BM and JCM. For the JCM, Luke et al. (2016a) reported the results of assessments of the Shannon–Wiener (H') diversity index versus EV and topographic parameters for individual censuses. As such, in the present study, only the influence of the Curve Fit output products was checked for the individual census periods. The models were developed following a spatially explicit generalized linear mixed model (GLMM) framework. The response variable at a given plot location and census interval was assumed to have a distribution that belonged to the exponential family. As such, suitable distributions and link functions were chosen for the response variables. For the EV model evaluation exercise, the response variables were expressed as a percentage of the stems found in each plot (percentage defoliated, resprouted and dead stems) and as such, either a binomial (BIN), or a zero-inflated binomial Type 0 (ZIB.0) with a logistic link function was used. The ZIB.0 was chosen if the data had four or more zero values and it was deemed a better fit. The dependent variables in the other models were either H' values or density values for each plot that was sampled during the periods 1974-2009 (Tanner's plots), and 1991-2004 (Bellingham's plots) in the BM, and 2006-2012 (Luke et al.'s (2016a) plots) in the JCM. For H' values derived from Tanner's plots, a Gaussian distribution was used. A Gamma distribution and log-link function were used for H' and density values derived from Bellingham's and Luke et al.'s (2016a) plot data. A value of 0.00001 was added to the density values, because a Gamma distribution does not include zeros.

The parameters of the chosen exponential family (ϕ) were linked to a structured additive predictor η through their canonical link function $g(\cdot)$, such that $g(\phi) = \eta$. The linear predictor was defined as:

$$\eta = \beta_0 + \beta_1 * Var.1 + \beta_2 * Var.2 + f\,(Var.3) + f(s,t)$$

where η was the linear predictor for any one of the response variables, β_0 was the intercept, β_1 and β_2 were the regression coefficients for the predictors *Var.1* and *Var.2*, and *Var.3* was also a covariate/predictor. In general, the semiparametric function $f(\cdot)$ can be used either to relax the linearity of the covariates/predictors, that is smooth effects similar to a GAM, or it can be used to define either the spatial or spatiotemporal random effect (Rue et al., 2009). In this study, $f(\cdot)$ was used to model the smooth, non-linear effects of some covariates/predictors using either a first-order or second-order random walk process (RW1 or RW2) given by $f(Var.3)$. A polynomial INLA spatiotemporal model was used to confirm that there was a non-linear relationship between the response and the predictor before smoothing was applied, i.e. that all the degrees or the orders of the polynomial were important. The $f(\cdot)$ was also used to represent the effects of the spatial position of each plot location (using the coordinates taken at the center of each plot) by allowing for the inclusion of a spatially structured random effect $f(s)$, and for the spatiotemporal models this followed an autoregressive process $f(s,t)$. The latter represented a Matérn correlation structure but with a different realization every year (Cosandey-Godin et al. 2014).

The spatially-structured random effect was modeled by a Gaussian random field (GRF) using the stochastic partial differential equation (SPDE) approach of Lindgren et al. (2011). A GRF with a Matérn covariance function can be represented as a Gaussian Markov Random Field (GMRF) (Lindgren et al. 2011). A GMRF is a spatial process that models the spatial dependence of data observed on a regular grid, lattice or geographic region (Cameletti et al. 2013). The SPDE approach is used to find a GMRF with local neighbourhood and sparse precision matrix **Q** (i.e., the inverse of the covariance matrix) that best represents the Matérn field (Lindgren et al. 2011), to avoid the "big n problem" that occurs with large spatiotemporal datasets (Banerjee et al 2004). The SPDE method achieves this by allowing for the evaluation of the continuous GRF as a discretely-indexed random process (i.e. a Gaussian Markov Random Field; Lindgren and Rue 2015). In particular, the SPDE method subdivides the domain, in this case the area of interest where the plots were established (the forests of the BM and JCM), into non-intersecting triangles creating an index mesh, instead of a regular grid (Lindgren et al. 2011). Linear combinations of basis functions, defined on the locations of the set of vertices, are used in the triangulation to represent the field (Lindgren et al. 2011). The meshes that were used to approximate the spatial fields for the BM and JCM are shown in Appendix S1. The meshes were confined to the area of interest for both sites. Different mesh sizes were used for both sites, including a mesh that only encompassed the plot locations. This was gradually extended to include the entire study area for each site. Also, the mesh should typically be extended beyond the study area to reduce boundary effects where the variance is twice as large as inside the domain. For this study, the final mesh used for either site yielded very similar results as the mesh size increased. As such, the final mesh that was bounded by the area of interest was used. For a more detailed explanation of the SPDE approach see Lindgren et al. (2011).

The sampling times for Tanner's and Bellingham's plot censuses were unequally spaced, so for the models they were treated as data collected over a continuous time domain and were discretized over a set of knots, with equal spacing over the sample period. When applying models with spatial correlation, a 2-D mesh is defined (Zuur et al. 2017). When knots are used, a 1-D mesh that is dependent on knot values is constructed (Zuur et al. 2017) and, similar to the spatial model, piecewise linear basis functions are used, but at a set of time knots (Krainski et al. 2017). The knot values are used to calculate weighting factors that are inversely proportional to the distance between the sampling year and the knots (Zuur et al. 2017). To fit the space-time continuous model, the time knots and the temporal mesh need to be determined. Specifically, the seven and three sample times for Tanner's and Bellingham's plot data were discretized over four and three knots, respectively (Appendix 1). For Tanner's plots, the knots represented the years 1974, 1985.7, 1997.3 and 2009, whereas for Bellingham's plots, the knots represented the years 1990, 1997 and 2004. The final model was specified as a SPDE model for the spatial domain and an AR(1) model for the time dimension. This model allowed for the simulation of the conditional marginal distribution at each time, that is, it simulated a realization of the spatial random field for each time. Two space-time models were used: one for discrete time domain (two years for the JCM) and for the second model, time was discretized over a set of knots (for the BM).

Before the statistical tests were performed, significantly correlated independent variables (with a correlation > 0.5) were identified using Spearman's rho statistic and test. The Deviance Information Criterion (DIC), which was computed by R-INLA, was used to compare the goodness-of-fit of the models. The DIC is comparable to the Akaike Information Criterion (AIC), but it is more suitable for hierarchical Bayesian models (Spiegelhalter et al. 2002). Models with the lowest DIC values were generally considered as the best models. In addition, the marginal R-squared (following Zheng (2000)) was calculated as follows:

$$100*(1 - (\sum_{t=1}^{t}\sum_{n=1}^{n}(depend - fitted)2 \;/\; \sum_{t=1}^{t}\sum_{n=1}^{n}(depend - \text{mean}\ (depend))2)),$$

where *t* is time when *n* subjects were considered, *depend* is the response variable, and *fitted* is the values predicted by the model. The most parsimonious final models that included independent variables, which were not significantly correlated, were identified and reported. Model fit was also evaluated using scatter plots of the observed and predicted data and quantile-quantile residual plots. In addition, INLA performs a 'leave out one' cross-validation from which two indices that can be used to evaluate model predictive performance are computed (Blangiardo and Cameletti 2015): the probability integrity transform (PIT) (Dawid 1984) and the conditional predictive ordinate (CPO) (Pettit 1990). The empirical distribution of the PIT can be used to evaluate model predictive performance (Gneiting et al. 2007). If a histogram of the PIT values follows a uniform distribution, this means that model predications are coherent with the observed data (Blangiardo and Cameletti 2015). In addition, when the PIT and CPO indexes are computed, numerical problems can occur (Held et al. 2010). The 'failure' vector automatically provided by INLA contains a value of 0 or 1 for individual observations (Blangiardo and Cameletti 2015). A value of 1 indicates that for a particular observation, the predictive measures are not reliable due to some problems with the calculation (Blangiardo and Cameletti 2015). If the vector is summed, a value of 0 indicates that no failures were detected. Final models were not selected unless the sum of the CPO was equal to 0 and a histogram of the PIT values showed a uniform distribution.

In most cases, the default and recommended priors were used; specifically, vague priors or estimations of non-informative priors (Cosandey-Godin et al. 2014). However, to avoid overfitting, the penalized complexity prior (PC-prior) framework was adopted. A PC-prior derived by Fuglstad et al. (2019) was used to define the model parameters of the SPDE model as the practical range and the marginal standard deviation. It is weakly informative, and complexity is penalised by shrinking the range to infinity and the marginal variance to zero (Fuglstad et al. 2019). For the SPDE, the PC-prior ensured that the spatially structured effect operated at a similar but not smaller spatial scale as the model covariates/predictors. Otherwise, the spatial effect would explain the data better than the covariates, rendering the model meaningless while inflating model accuracy and the marginal R-squared and deflating the DIC, rendering them useless for model selection. Several values for the range were used (starting with half the distance between the farthest points), until there was no overfitting. A PC-prior, developed by Simspon et al. (2017), was also considered for the random walk processes (RW1 and RW2). It requires defining a reference standard deviation σ_0 and the right-tail probability u, as $P(\sigma_0 > \sigma) = u$ (Simspon et al. 2017). The PC-prior controlled the level of smoothness and a value of 1 for σ_0 is the suggested starting point. Using lower values will result in a smoother fit and progressively lower values will give a straight line.

Before the models were accepted, several ways in which EV could be used to explain spatiotemporal trends were first explored. Average 'legacy' EV calculated from multiple hurricanes that affected a site before a census, with no adjustment for time (since each hurricane affected the sites/plots), was found to be the best predictor of diversity in the JCM (Luke et al. 2016a). In the present study, we found that average 'legacy' EV was more suitable for assessing the overall effects of EV when multiple re-numeration times were used in the models (Figure 9). However, we used a manual stepwise forward selection approach to identify the best or most suitable hurricanes and the number of hurricanes for averaging. Specifically, EV values for each hurricane were first included in a regression model with a response variable (diversity or density), and important EVs were identified. The two most important EVs (based on DIC and the marginal R-squared values) were then averaged and model fit, that is the DIC and the marginal R-squared values, was assessed. If model fit was improved by averaging the two most important hurricane EVs, that is if the DIC decreased and the marginal R-squared increased, additional EVs were then included in the average. If model fit did not improve when the EV of a hurricane was included in the average, it was dropped. This was repeated until an average 'legacy' EV that yielded the lowest DIC and the highest marginal R-squared values was identified. This was then used to identify the most parsimonious model.

The most parsimonious final models were identified using a manual stepwise backward selection approach and were reported. Specifically, important predictors with the highest marginal R-squared and the lowest DIC were identified, and other predictors that were correlated with these predictors but had a lower marginal R-squared and higher DIC were dropped. If there were > 1 uncorrelated predictors, they were all included in a model and the final model was accepted if they were all important. If one or more of the predictors were not important when they were added to the model, they were dropped until the most parsimonious model was identified. These models yielded the lowest DIC, the highest marginal R-squared and included independent variables that were not significantly correlated.

Results

The nominal range, which is the minimum distance at which data from two plot locations are uncorrelated (or correlation between the two plots is ≤ 0.1), varied for the models that were used to analyze plot data from the two study sites. For all the models that included Tanner's plot data, the nominal range was 5.1–8.2 km, for Bellingham's plot data 4.7–8.4 km and for Luke et al.'s (2016a) plot data 5.9–8.4 km (Tables 2–8). For the assessments (e.g. EV versus tree diversity or density) that included all the censures (i.e. assessing the overall effects regardless of time), the data used were not found to be temporally auto-correlated; but in all cases model fit improved with the inclusion of spatiotemporal random effects. In addition, for all models, the variance of the spatial effect was lower than that of the model variance (Tables 2–8).

EV model evaluation

For the BM, damage and recovery data from Bellingham's plots, in particular completely defoliated and reprouting stems, were found to increase significantly with Hurricane Gilbert EV (Figure 2a,b; Table 2), with marginal R-squared (mR^2) values of 37.5% and 47.1%, respectively (Table 2). This indicated that the method used to reconstruct the EV of past hurricanes generated maps of EV that can be considered as a proxy to damage caused by these hurricanes. In addition, the best proxy for Hurricane Gilbert, that is an EV map created using metrological data from a processed QuikSCAT Scatterometer image of Hurricane Ivan, could be used to explain the damage and recovery data from Bellingham's plots. Average EV from three proxies (Hurricanes

Emily, Ivan and Dean; $mR^2 = 36.2\%$), and the other proxies ($mR^2 = 30.1\%$ (Dean) and $mR^2 = 27.2\%$ (Emily)) could only be used to explain the recovery data (Figures 2c–e; Table 2). Therefore, in the absence of a single 'best' proxy, proxy images of other hurricanes from the same Saffir-Simpson Hurricane Wind Scale category or the average of three proxies from the same wind scale category, could, at the very least, be used to represent forest recovery from hurricanes. The percentage of dead stems was better explained by elevation, that is dead stems increased with elevation ($mR^2 = 44.6\%$) (Figure 2f; Table 2). If data from Tanner's plots were used, defoliated stems showed an S-shaped non-linear relationship with TPI ($mR^2 = 66.1\%$), indicating that the topographic location of the plots had a greater influence on hurricane damage than was the case for Bellingham's plots, and in this case, damage was highest at or near ridge crests (Figure 2g; Table 3). A similar pattern was reported by Bellingham et al. (1992) and Tanner et al. (2014). Similarly, resprouting in 1989 and 1991 was explained by TPI being highest at or near ridge crests ($mR^2 = 40.3$ and 60.8%, respectively) (Figure 2h & j; Table 3).

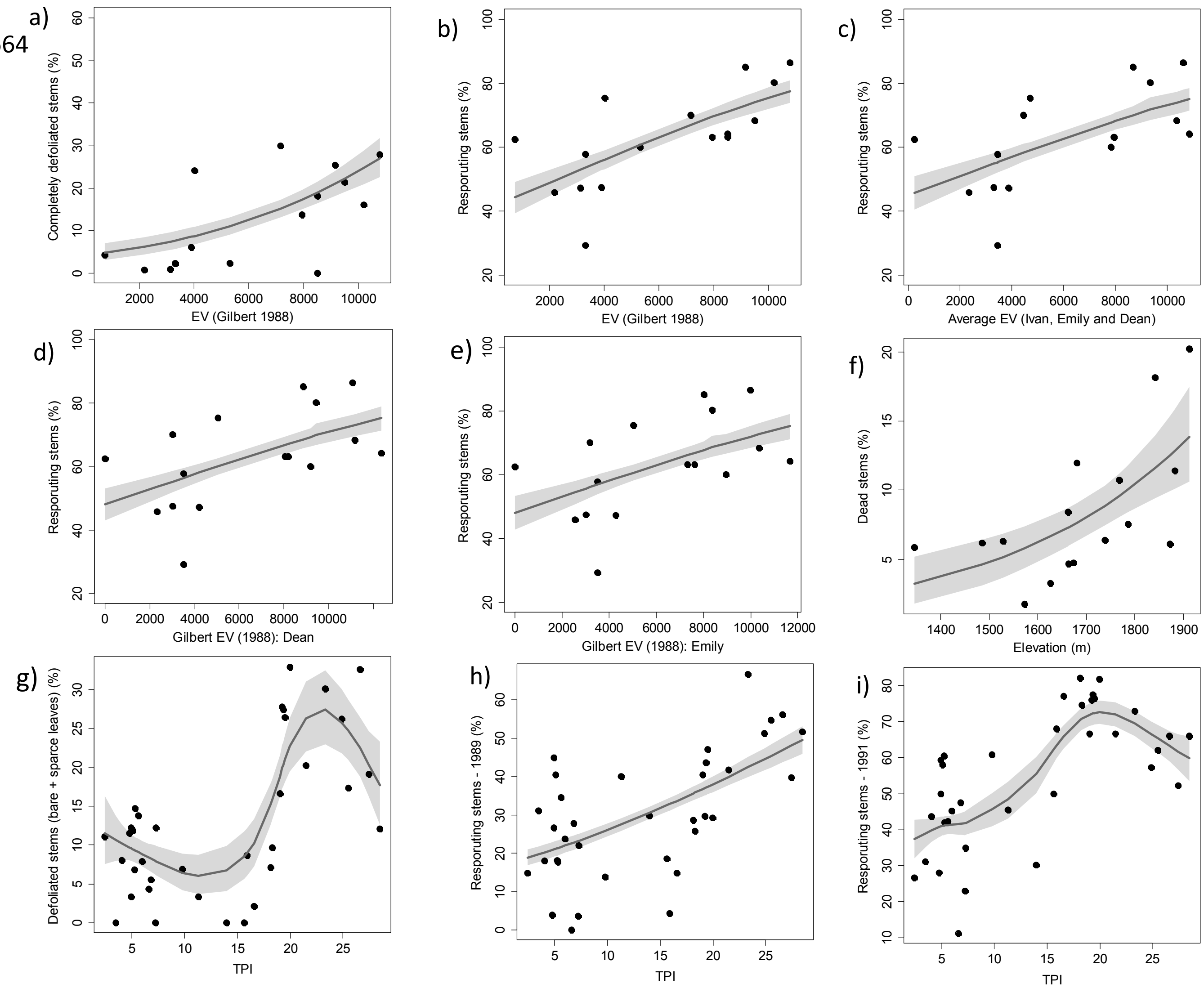

Figure 2. Observed (closed circles) and posterior mean predicted values (solid lines) and the 95% credible intervals (shade) obtained from hierarchal Bayesian spatial models used to assess the relationship between damage and recovery data obtained from Bellingham's (a–f) and Tanner's (g–i) plots several months after the passage of Hurricane Gilbert in 1988, and the reconstructed Hurricane Gilbert exposure vulnerability (EV) based on three proxy hurricanes (in the order of model fit: Ivan, the average of all three hurricanes, Dean and Emily) and other topographic parameters (elevation and topographic position index (TPI)).

Table 2. Summary of the marginal posterior distribution for model parameters obtained from hierarchical INLA Bayesian models used to assess the relationship between damage and recovery data from Bellingham's plots and Hurricane Gilbert exposure vulnerability (EV), reconstructed using several proxy hurricanes including Hurricanes Ivan (2004), Dean (2007), Emily (2005) and average (mean) EV from all three proxies that were found to be the most important predictors (95% credible intervals did not contain zero) of damage and recovery in the montane forest of the Blue Mountains, Jamaica, after the passage of Hurricane Gilbert in 1988.

Year	Variable	Parameters	Mean	$Q_{0.025}$	$Q_{0.975}$	mR^2	DIC	Priors
1989	Completely defoliated stems (%) ZIB.0	Intercept	-3.2	-3.6	-2.7	37.5	155.7	
		Glibert (Ivan)	0.0002	0.0001	0.0003			
		obs.var	6.7	2.5	17.5			
		spde.var.nom	0.0000295	-0.0000004	0.0002002			0.0023, 0.5
		spde.range.nom	6.5	0.7	30.8			3.9, 0.5
1989	Resprouting stems (%) BIN	Intercept	-0.3	-0.6	-0.1	47.1	159.2	
		Glibert (Ivan)	0.0001	0.0001	0.0002			
		spde.var.nom	0.0000196	-0.0000004	0.0001245			0.0023, 0.5
		spde.range.nom	8.1	0.7	41.3			3.9, 0.5
1989	Resprouting stems (%) BIN	Intercept	-0.19	-0.42	0.06	36.2	178.1	
		Glibert (Mean)	0.0001	0.0001	0.0002			
		spde.var.nom	0.0000197	-0.0000005	0.0001238			0.0023, 0.5
		spde.range.nom	8.2	0.8	42.0			3.9, 0.5
1989	Resprouting stems (%) BIN	Intercept	-0.07	-0.28	0.19	30.1	187.8	
		Glibert (Dean)	0.0001	0.0001	0.0001			
		spde.var.nom	0.0000251	-0.0000004	0.0001666			0.0023, 0.5
		spde.range.nom	7.4	0.7	36.6			3.9, 0.5
1989	Resprouting stems (%) BIN	Intercept	-0.06	-0.29	0.30	27.2	192.5	
		Glibert (Emily)	0.0001	0.0001	0.0001			
		spde.var.nom	0.0000277	-0.0000004	0.0001863			0.0023, 0.5
		spde.range.nom	7.1	0.7	34.3			3.9, 0.5
1989	Dead stems (%) BIN	Intercept	-7.2	-9.6	-5.0	44.6		
		Elevation	0.0028	0.0015	0.0042			
		spde.var.nom	0.0000194	-0.0000004	0.0001235			0.0023, 0.5
		spde.range.nom	7.3	0.7	35.7			3.9, 0.5

$Q_{0.025}$, and $Q_{0.975}$ = quantiles of the credible interval; DIC = Deviance Information Criterion; mR^2 = marginal R-squared; ZIB.0 = zero inflated binomial Type 0 likelihood; BIN = Binomial likelihood; obs.var = model variance; spde.var.nom = nominal spatial variance (priors = prior marginal standard deviation and right tail probability); spde.range.nom = nominal spatial range (km) (priors = practical range and right tail probability).

Table 3. Summary of the marginal posterior distribution for model parameters obtained from hierarchical INLA Bayesian models used to assess the relationship between damage and recovery data from Tanner's plots and topographic parameters (topographic position index (TPI)) that were found to be the most important predictors (95% credible intervals did not contain zero) of damage and recovery in the montane forest of the Blue Mountains, Jamaica, after the passage of Hurricane Gilbert in 1988.

Year	Variable	Parameters	Mean	$Q_{0.025}$	$Q_{0.975}$	mR^2	Priors
1989	Defoliated stems (%)	Intercept	-1.94	-2.06	-1.82	66.1	
	ZIB.0	obs.var	183.4	7.5	964.5		
	RW2	TPI.var	0.13	0.04	0.30		0.1, 0.05
		spde.var.nom	0.0000183	-0.0000004	0.0001149		0.0023, 0.5
		spde.range.nom	8.2	0.8	42.0		3.9, 0.5
1989	Resporuting stems (%)	Intercept	-1.60	-1.76	-1.44	40.3	
	ZIB.0	TPI	0.06	0.05	0.06		
		obs.var	44.1	8.1	166.3		
		spde.var.nom	0.0000406	-0.0000007	0.0002875		0.0023, 0.5
		spde.range.nom	5.3	0.5	23.4		3.9, 0.5
1991	Resporuting stems (%)	Intercept	0.20	0.13	0.28	60.8	
	ZIB.0	obs.var	183.4	7.5	964.5		
	RW2	TPI.var	0.027	0.009	0.061		0.03, 0.05
		spde.var.nom	0.0000379	-0.0000005	0.0002664		0.0023, 0.5
		spde.range.nom	5.1	0.5	22.3		3.9, 0.5

$Q_{0.025}$ and $Q_{0.975}$ = quantiles of the credible interval; mR^2 = marginal R-squared (%); RW2 = second-order random walk process (predictor variance is followed by .var, e.g., TPI.var for RW2 and Prior = reference standard deviation and the right tail probability); ZIB.0 = zero inflated binomial Type 0 likelihood; obs.var = model variance; spde.var.nom = nominal spatial variance (Priors = prior marginal standard deviation and right tail probability); spde.range.nom = nominal spatial range (km) (Priors = practical range and right tail probability).

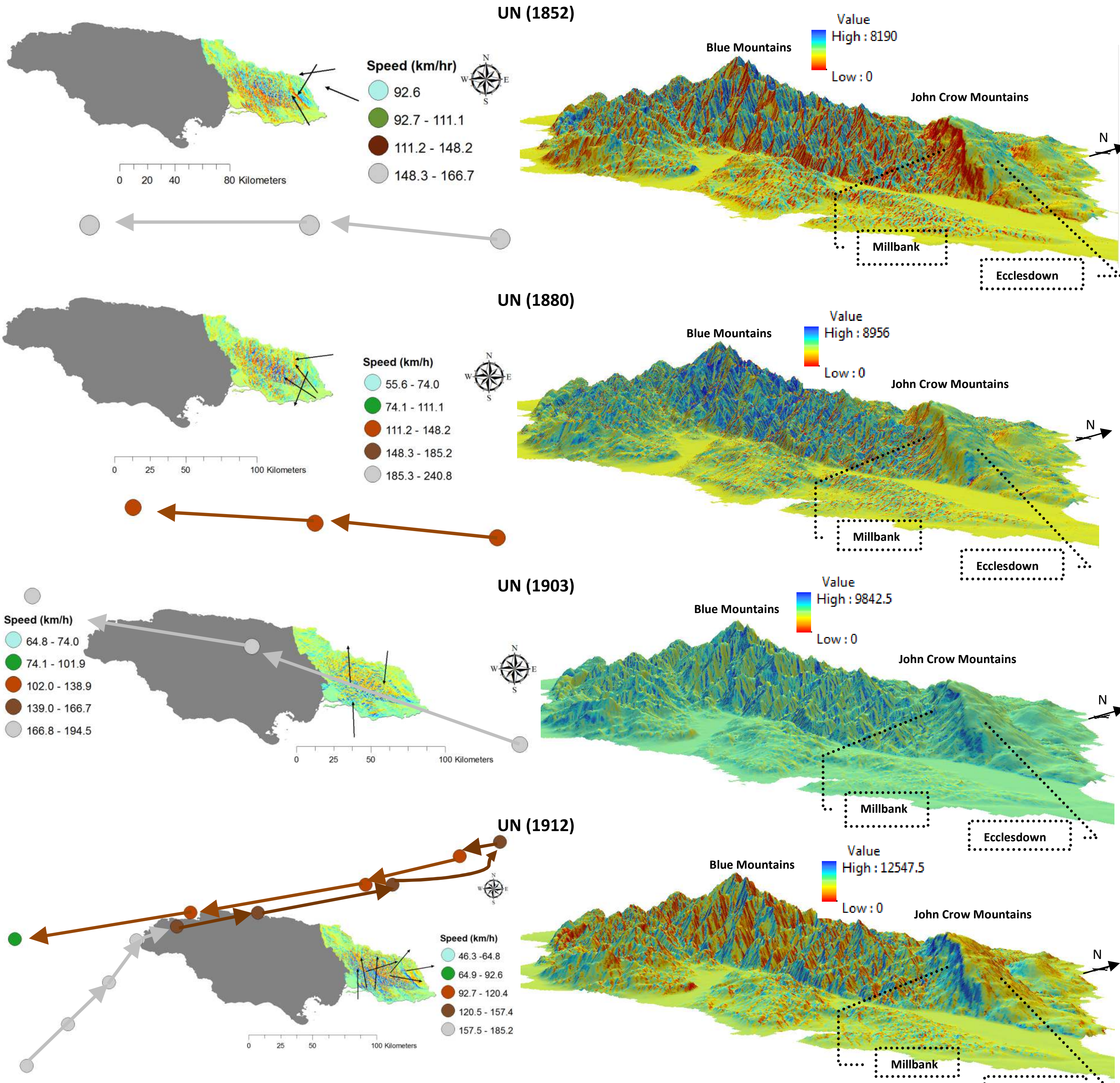

Figure 3. Exposure vulnerability (EV) maps (three-dimensional view) for category 2, 3 or 4 hurricanes, with centers that passed within 0–113 km of the northern or southern coastline of Jamaica, during the period 1852–1988. The two-dimensional inserts include hurricane tracks and direction (closed circles with arrows) with information on wind speed at each track location and wind direction (black arrows). Value = highest and lowest EV values. UN = unnamed hurricane.

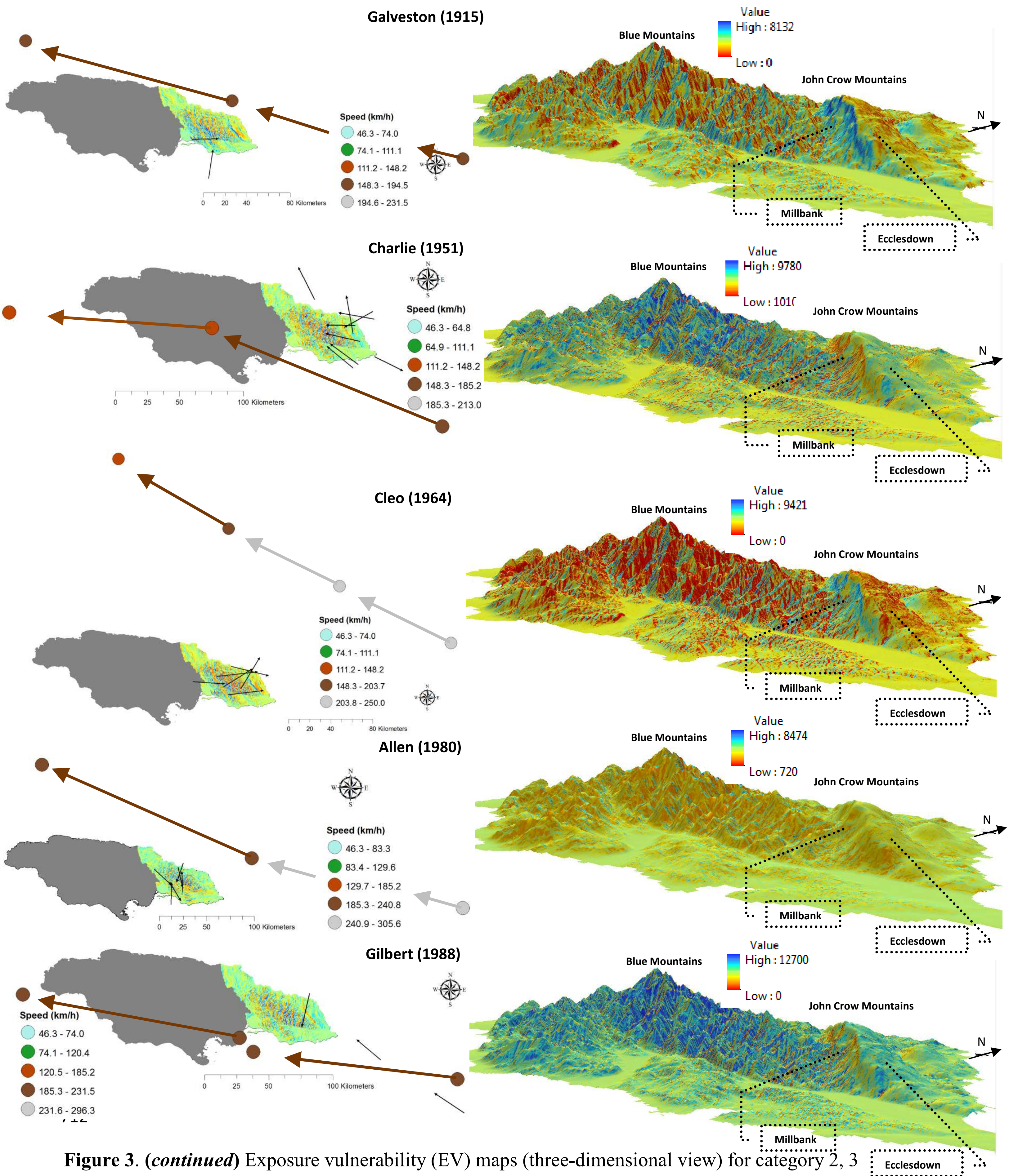

Figure 3. (***continued***) Exposure vulnerability (EV) maps (three-dimensional view) for category 2, 3 or 4 hurricanes, with centers that passed within 0–113 km of the northern or southern coastline of Jamaica, during the period 1852–1988. The two-dimensional inserts include hurricane tracks and direction (closed circles with arrows) with information on wind speed at each track location and wind direction (black arrows). Value = highest and lowest EV values. UN = unnamed hurricane.

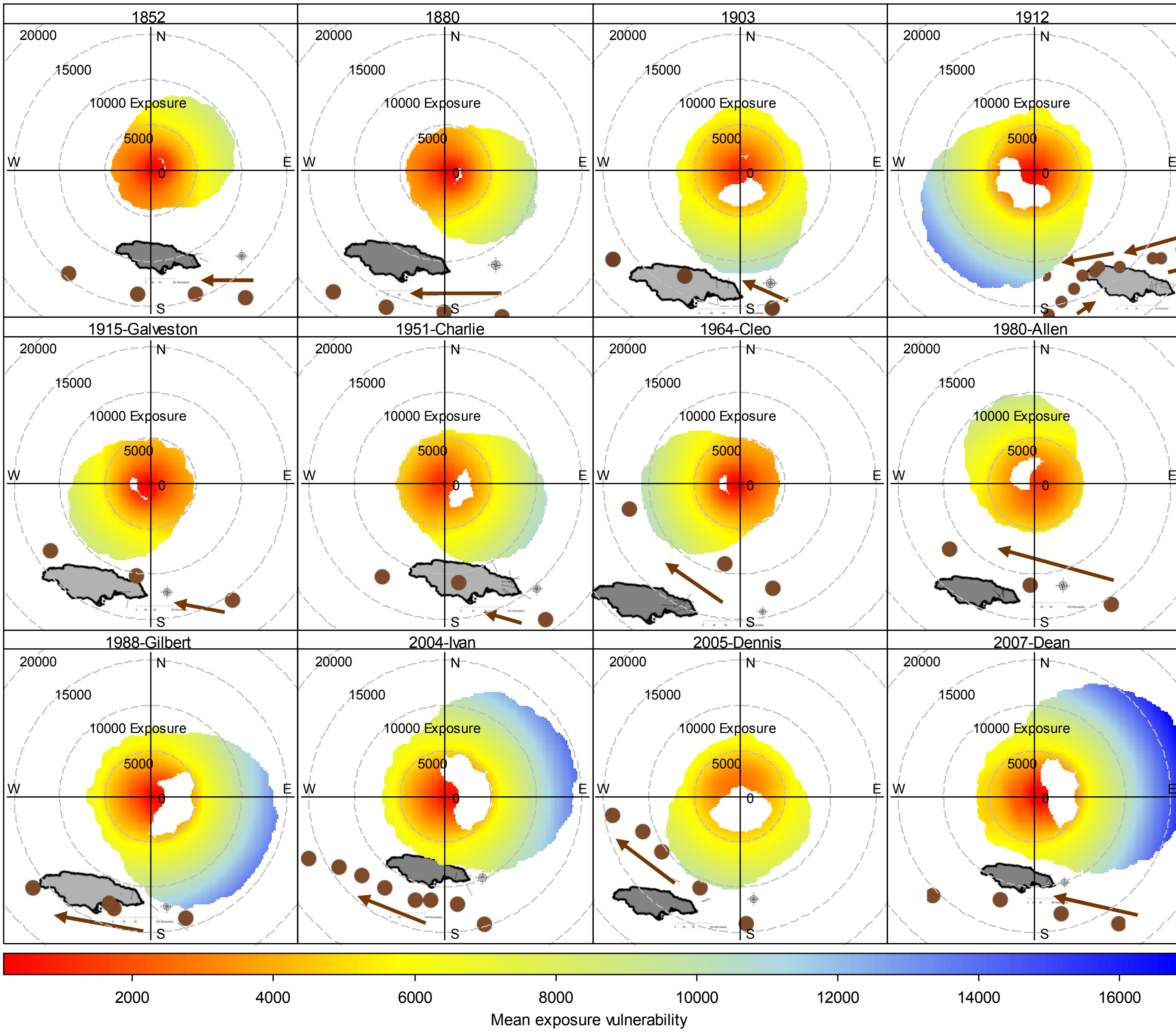

Figure 4. Bivariate polar plots (in polar coordinates) of aspect and exposure vulnerability (EV or Exposure) for each hurricane with insert maps showing hurricane tracks (brown closed circles) relative to the island of Jamaica. The polar plots show the aspect (or direction) with the highest and lowest EV values when each hurricane affected the Blue Mountains. Arrows show the direction of the hurricane tracks. The map inserts were placed where they can be viewed.

Long-term exposure in the Blue and John Crow Mountains

EV was found to be directional depending on the angle or cardinal direction of the track of the eye of each hurricane as it passed relative to the two study sites (Figures 3 and 4). If the track of a hurricane's eye passed the sites at angles or cardinal directions ranging from 279° to 41°, it passed along a trajectory from north-east to north-west of the study sites if it made landfall, or if it passed along the northern coastline (Figures 1, 3 and 4; Table 1). Due to the counter-clockwise rotation of hurricane winds, this resulted in southern to western aspects being more exposed (Figure 4). If the track of a hurricane's eye passed the sites at angles or cardinal directions ranging from 167° to 216°, it passed along a south-eastern to a south-western direction relative to the study sites if it made landfall, or it passed along the southern coastline (Figures 1, 3 and 4; Table 1). This resulted in north-eastern to south-eastern aspects being more exposed (Figure 4). Maximum EV was lower for reconstructed hurricanes that made landfall when compared with the three most recent hurricanes that did not make landfall. The reason for this discrepancy was that maps for the three most recent hurricanes were created using actual images of each hurricane and the EV maps were therefore more accurate. If the maximum EV values from the reconstructed hurricanes were compared, the hurricanes that made landfall all had a higher maximum EV value, unless wind speed at the eye was lower than that of the eye or outer bands of other hurricanes.

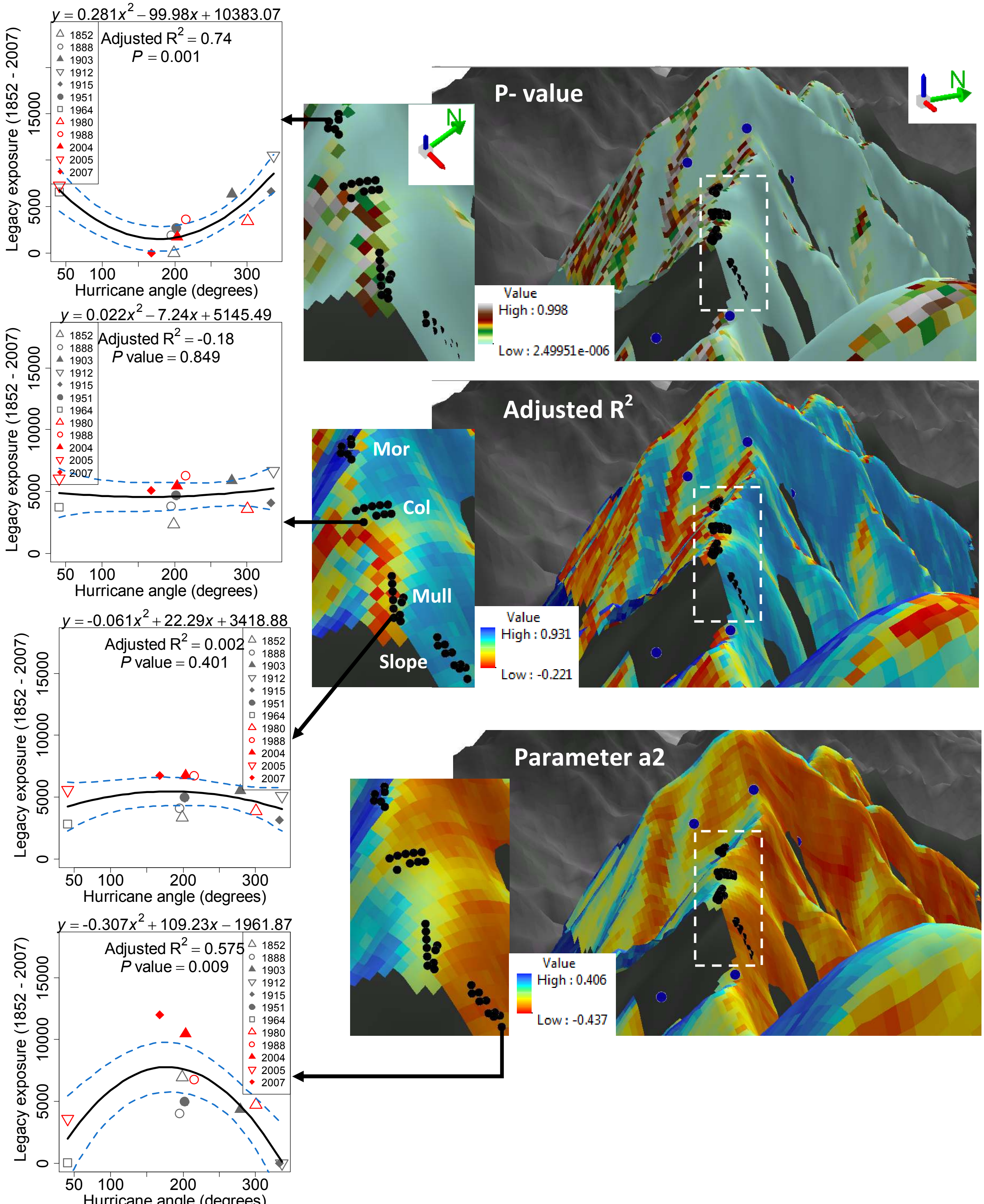

Figure 5. Observed and predicted values (solid lines) obtained from polynomial regression models of the relationship between hurricane direction and a time series of exposure vulnerability (for 12 hurricanes during 1852–2007 or Legacy exposure), at several of Tanner's (1977) plot locations (black dots) in the Blue Mountains, Jamaica. Dashed blue lines = standard error. Blue dots in the larger maps = Bellingham et al.'s (1991) plot locations.

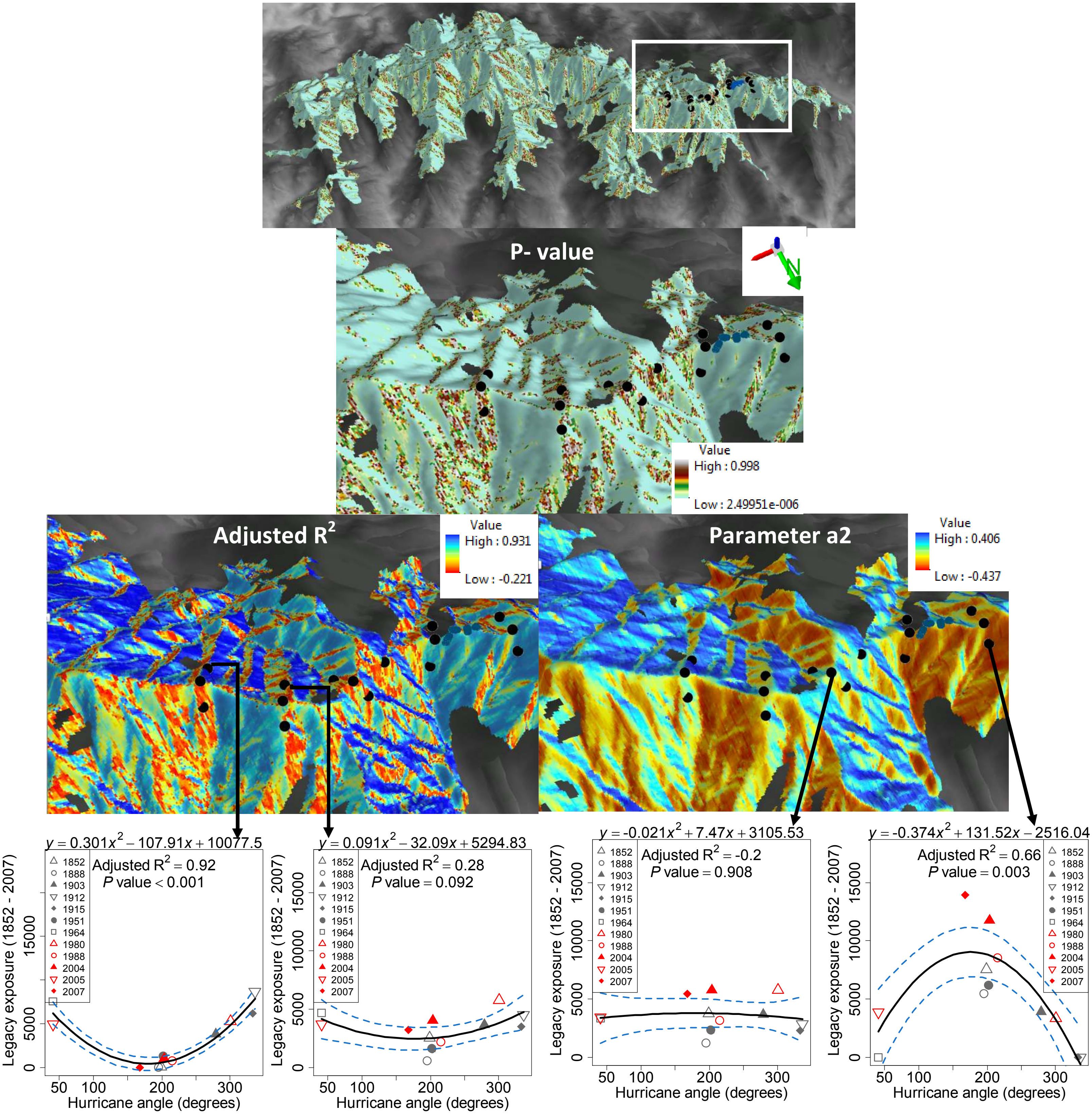

Figure 6. Observed and predicted values (solid lines) obtained from polynomial regression models of the relationship between hurricane dir ection and a time series of exposure vulnerability (for 12 hurricanes during 1852–2007 or Legacy exposure), at several of Bellingham et al.'s (1991) plot locations (black dots) in the Blue Mountains, Jamaica. Dashed blue lines = standard error.

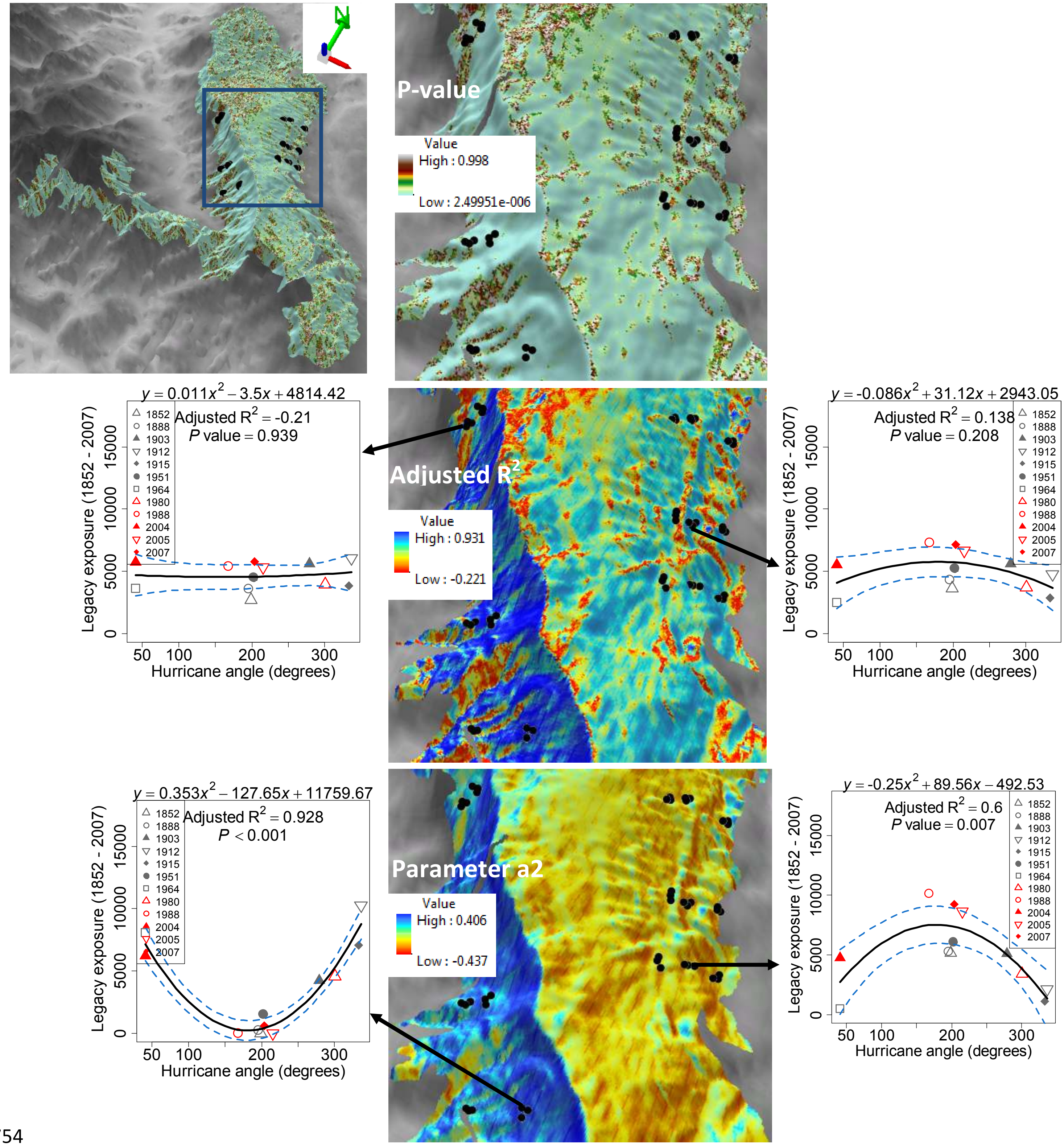

Figure 7. Observed and predicted values (solid lines) obtained from polynomial regression models of the relationship between hurricane direction and a time series of exposure vulnerability (for 12 hurricanes during 1852–2007 or Legacy exposure), at several of Luke et al.'s (2016a) plot locations (black dots) in the John Crow Mountains, Jamaica. Dashed blue lines = standard error.

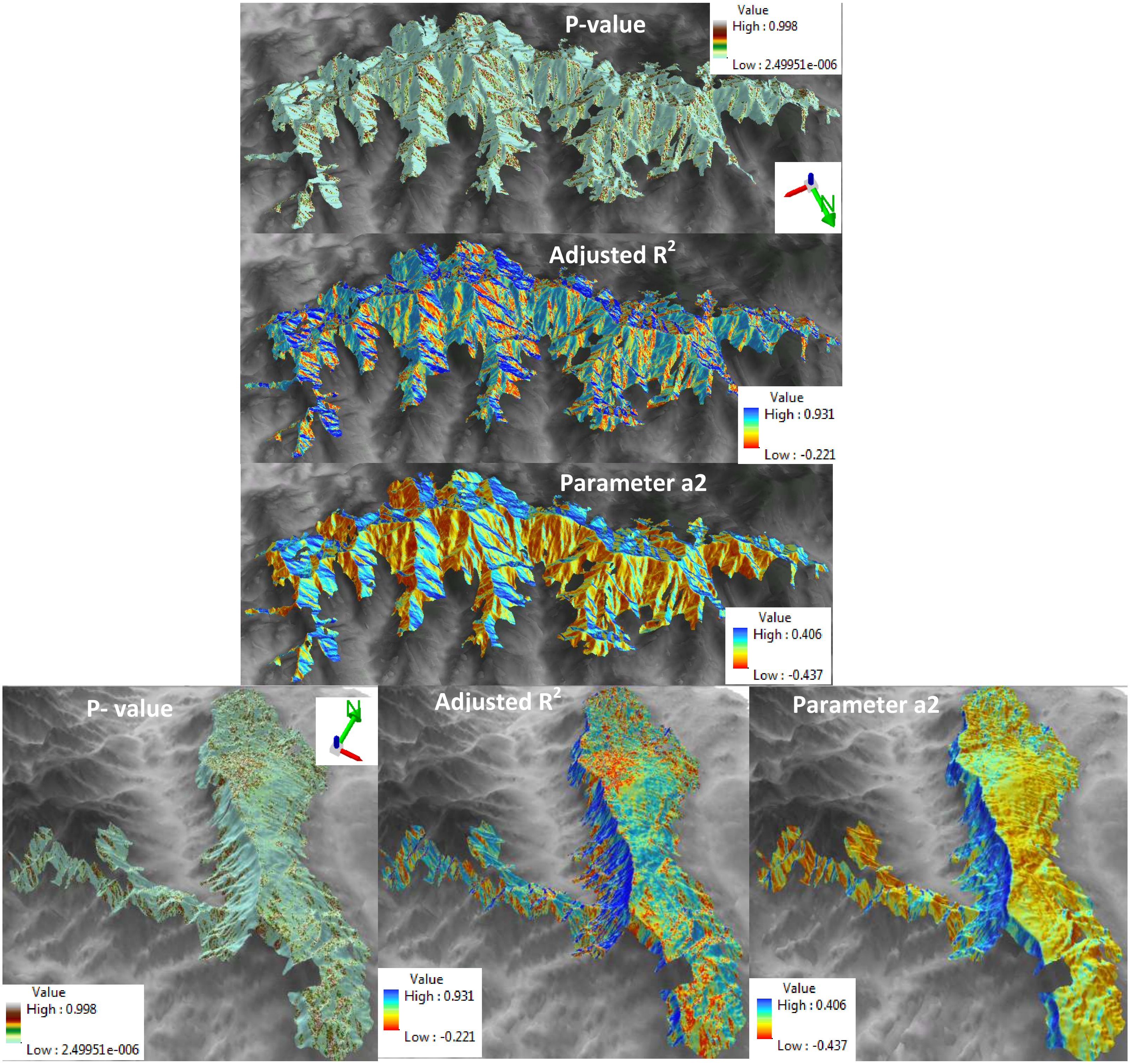

Figure 8. Three dimensional views of the outputs from the Curve Fit pixel-level polynomial regression (clipped to the undisturbed forest types in the Blue [top three] and the John Crow [bottom three] Mountains) that was used to assess the influence of average direction (in degrees) of each hurricane at its closest point (independent variable) to the coastline of Jamaica, relative to the center of the Blue and John Crow Mountains, and a time series of exposure vulnerability maps (for 12 hurricanes during 1852–2007 or Legacy exposure) for the Blue Mountains (dependent variable). Value = highest and lowest values for Curve Fit maps.

When the influences of the distance from the eye and the cardinal direction of the track of the eye on the spatial pattern of EV were considered for all hurricanes, the angle or cardinal direction of the track of the eye had a much greater influence on the spatial pattern of EV. In particular, for the Curve Fit P-value cardinal direction map, 78.5% of the pixels had a value of $P < 0.05$, whereas for the Curve Fit P-value hurricane distance map, only 7.8% of the pixels had a value of $P < 0.05$. Therefore, the distance results were not presented. Angle or cardinal direction of the tracks of the eyes of hurricanes were more important because most of the hurricanes considered in this study either made landfall or passed extremely close to the coast of Jamaica (Figure 1; Table 1). Distance affected the severity of damage caused by the winds, and hence the magnitude of the EV values, but this was dependent on the strength of the winds at the eye and at the outer bands of the hurricanes (Figures 3 and 4; Table 1). If wind speed was very high at the eye and/or at the outer bands, the EV values were usually higher (Figures 3 and 4; Table 1).

Several outputs from the Curve Fit extension can be used to explain the spatial pattern of long-term EV across the landscape and at the stand-level (Figures 5–8). For example, data extracted from the parameter a2 map can be used to separate EV based on aspect (Figures 5–8). Negative and positive parameter a2 values indicate whether the relationship between EV and the cardinal direction of the hurricane was concave or convex, respectively. This indicated that there was higher EV when the hurricanes passed to the north or south of a site, respectively (Figures 5–8). Negative (concave) and positive (convex) parameter a2 values were almost exclusively found on the northern- and southern- facing slopes, respectively, or on aspects that were more likely to be exposed when a hurricane passed to the north or south of the site, respectively (Figures 5–8). Depending on plot location and the cardinal direction of the tracks of the eyes of hurricanes, three main patterns of EV can be identified at the stand-level: (1) plots that were highly exposed to all hurricanes irrespective of the cardinal direction of the tracks of the eyes ($R^2 < 0.3$, and *P*-value ≥ 0.05), (2) plots with an inverted U-shaped (convex) relationship that had significantly higher EVs when the tracks of the eyes of the hurricanes had a southerly cardinal direction (a2 > 0), and significantly lower EVs when the of the tracks of the eyes of the hurricanes had more northerly cardinal directions, or (3) plots with a U-shaped (concave) relationship that had significantly lower EVs when the tracks of the eyes of the hurricanes had more southerly cardinal directions (a2 < 0), and significantly higher EVs when the hurricanes had more northerly cardinal directions (Figures 5–7).

Modelling stand-level tree diversity and density spatiotemporal patterns

Tree Shannon diversity for the period 1974–2009, calculated from Tanner's plot data, was best explained (the most parsimonious model) by average 'legacy' EV for the period 1903–1988 (hurricanes in 1903, 1913, 1915, 1951, 1964 and 1988) (Figure 9a; Tables 4 and 5). Hurricane Allen (1980) and hurricanes that affected the site before 1903 and after 1988 were not included in the calculation of legacy EV because they did not improve model fit. Shannon diversity was highest at the lowest and intermediate (where it peaked) legacy EV values, but Shannon diversity was much lower at the highest legacy EV values (Figure 9a). Using data from Bellingham's plots, the best predictor of overall Shannon diversity patterns was the P-value output from the *calc* function that encompassed 1852–1988 (Figure 9b; Tables 4 and 5). Locations with the lowest P-values, particularly locations with the strongest relationship between EV and the cardinal direction of the track of a hurricane's eye (which were highly exposed when the track passed either to the north or the south of the sites), had the highest Shannon diversity overall;

values decreased as P-values increased and became non-significant (sites that are always exposed to hurricanes, regardless of the angle of the track of eye) (Figure 9b). There were no significant overall relationships between Shannon diversity values and the parameters that were assessed for the JCM using data from Luke et al. (2016a). However, Luke et al. (2016a) found that Shannon diversity values for the 2012 plot data increased as average EV for the three most recent hurricanes (Ivan, Dennis and Dean) increased.

Tree (stem) density, calculated using data from Tanner's plots, was overall best explained by topographic position index (result not presented here), whereas for Bellingham's plot data, the most important predictor of tree density was the adjusted R^2 values (Figures 9c; Tables 4 and 5). For the latter, tree density peaked at sites that were always exposed to hurricanes that affected the site during 1852–1988, regardless of the cardinal direction of their tracks (adjusted $R^2 = 0.2 – 0.4$). Tree density in the JCM was highest at more exposed aspects (Luke et al. 2016a). Therefore, the most important predictor of tree density was average legacy EV (1988–2007), with higher tree (stem) densities at higher EVs (Figures 9d; Tables 4 and 5). For the individual censuses of Tanner's plots, the best predictor of Shannon diversity for the census years 1974, 1984, 1989, 1991 and 1994 was average (legacy) EV for hurricanes that affected the site over the period 1903–1964 (Figures 9e–i; Table 6). For the year 2009, legacy EV for hurricanes in the period 1915–1988, was the best predictor (Figures 9j; Table 6). The individual censuses reflected the overall diversity pattern, with Shannon diversity being highest at lower and intermediate legacy EV values and lower at the highest values (Figures 9e–j). The marginal R^2 increased from 33% in 1974 to 43% in 1984, then subsequently decreased in 1989 (40.5%) until 1994 (25.6 %) (Table 6). It increased again in 2009 (31.8%). There were no important predictors of Shannon diversity in 2004. Similarly, for Bellingham's plots, Shannon diversity in 2004 was best explained by legacy EV (hurricanes in the period 1903–1988), with the highest diversity values occurring at intermediate EV values (Figure 9k; Table 6).

Table 4. The best predictors of overall (regardless of census) tree diversity calculated as Shannon-Wiener H' and stem density calculated using data from Tanner's (ET) and Bellingham's (PJB) plots in the Blue Mountains (BM), Jamaica, and stem density from Luke et al.'s plots in the John Crow Mountain (JCM), Jamaica. Important variables included 'legacy' (average) exposure vulnerability to hurricanes during the period 1903–1988 (Exposure), Curve Fit (ET and JCM) and *calc* (PJB) outputs (P-value, Parameter a2, Adjusted R^2) and topographic parameters (Aspect).

Site	**Smoother and/or distribution**	**Variable**	**Parameters**	**DIC**	**mR^2**
BM (ET)	RW1	H'	Exposure	23.19	25.3
BM (ET)	RW1	H'	Parameter a2	29.36	23.2
BM (ET)	RW1	H'	Adjusted R^2	31.87	22.9
BM (ET)	RW1	H'	Aspect	34.54	22.0
BM (PJB)	Gamma	H'	P-value	22.51	32.9
BM (PJB)	RW2 Gamma	H'	Adjusted R^2 + (Adjusted $R^2)^2$	23.57	34.7
BM (PJB)	RW2 Gamma	H'	Exposure	31.87	30.62
BM (PJB)	RW2 Gamma	Density	Adjusted R^2	-69.2	85.1
BM (PJB)	RW2 Gamma	Density	P-value	-54.1	79.0
BM (PJB)	Gamma	Density	Exposure	-17	40.5
BM (PJB)	RW2 Gamma	Density	Aspect	-10.7	37.7
JCM	RW1 Gamma	Density	Exposure	-156.2	27.1
JCM	RW1 Gamma	Density	Parameter a2	-154.7	26.6
JCM	Gamma	Density	Aspect	-154.8	24.2
JCM	Gamma	Density	Adjusted R^2	-142.7	17.6

DIC = Deviance Information Criterion; mR^2 = marginal R-squared (%); Gamma = Gamma likelihood; RW1/RW2 = first or second-order random walk process (smoother).

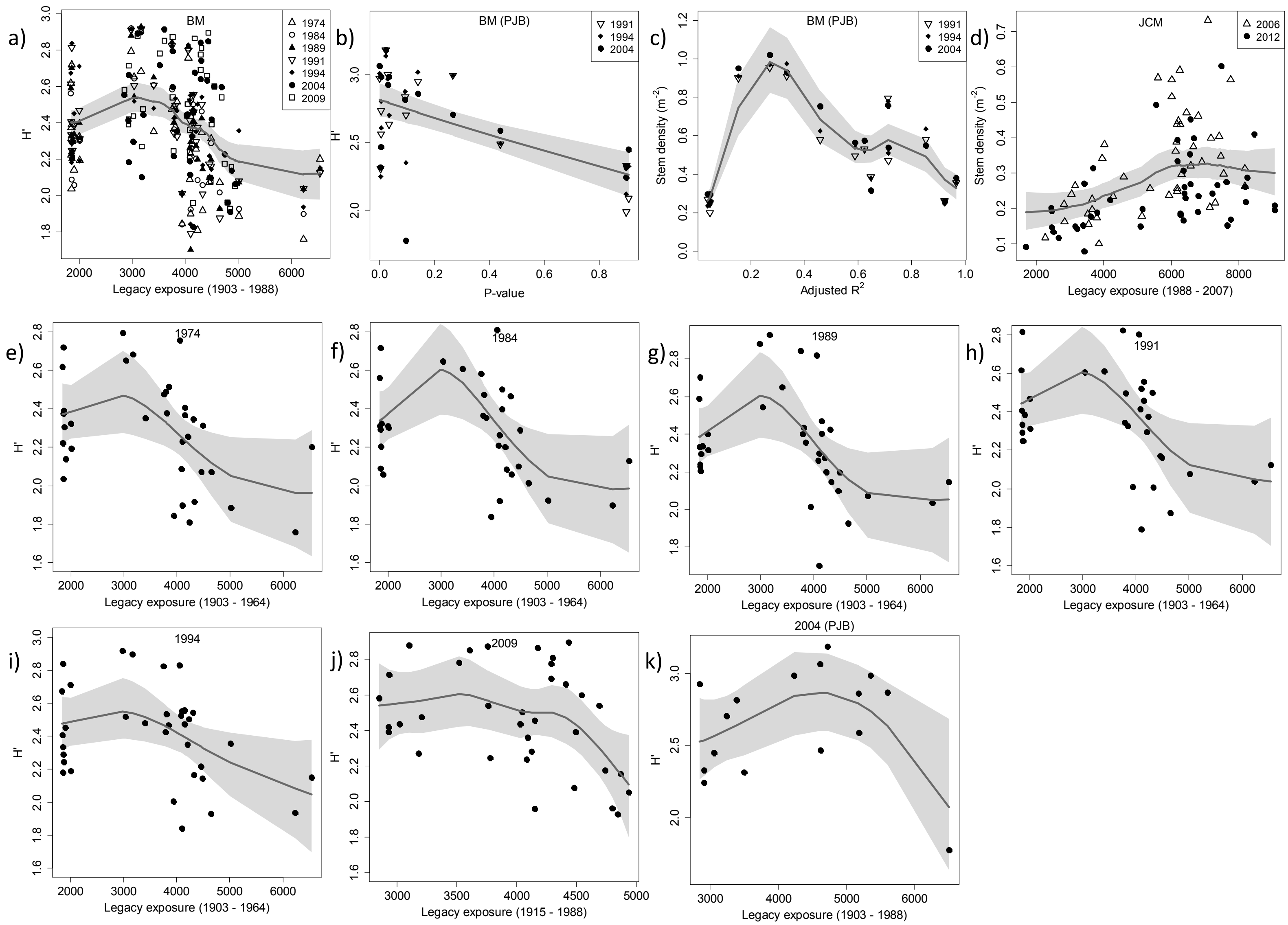

Figure 9. Observed and predicted mean values (solid lines) and the 95% Bayesian credible intervals for the posterior distribution (shade) obtained from hierarchal Bayesian space-time models for the best predictor of overall (regardless of time) a) diversity calculated as Shannon–Wiener diversity index (H') for the Blue Mountains (BM), Jamaica, using data from Tanner's plots, b) H'and c) stem density values for the BM, calculated using data from Bellingham's plots, and d) stem density values for the John Crow Mountains (JCM), Jamaica, calculated using data from Luke et al.'s plots and best predictor of H' values for each census, calculated using data from e–j) Tanner's and k) Bellingham's plots in the BM. Important variables included 'legacy' (average) exposure vulnerability for different periods/years and the *calc* output (P-Value and Adjusted R^2).

Table 5. Summary of the marginal posterior distribution for model parameters obtained from hierarchical INLA Bayesian space-time models for the best predictors of overall (regardless of census) diversity calculated as Shannon-Wiener H' and stem density calculated using data from Tanner's (ET) and Bellingham's (PJB) plots in the Blue Mountains (BM), Jamaica and stem density calculated from Luke et al.'s plots in the John Crow Mountain (JCM), Jamaica. Important variables (95% credible intervals did not contain zero) included 'legacy' average exposure vulnerability to hurricanes during the periods 1903–1988 for the ET plots and 1988–2007 for the JCM plots (Exposure) and *calc* outputs (P-value).

Site	**Variable**	**Parameters**	**Mean**	**$Q_{0.025}$**	**$Q_{0.975}$**	**mR^2**	**Priors**
BM	H'	Intercept	2.38	2.34	2.41	25.3	
(ET)		obs.var	0.062	0.051	0.076		
	RW1	Exposure.var	0.003	0.001	0.006		0.009, 0.05
		spde.var.nom	0.000102	-0.000015	0.000683		0.0023, 0.5
		spde.range.nom	6.0	0.5	27.9		3.9, 0.5
		AR.rho	-0.02	-0.99	0.98		
BM	H'	Intercept	1.0	0.99	1.1	32.9	
(PJB)	Gamma	P-value	-0.2	-0.3	-0.1		
		obs.var	0.01	0.009	0.02		
		spde.var.nom	0.00003	-0.0000004	0.0002		0.0023, 0.5
		spde.range.nom	4.8	0.5	19.9		3.9, 0.5
		AR.rho	0.004	-1.0	1.0		
BM	Density	Intercept	-0.7	-0.7	-0.6	85.1	
(PJB)	Gamma	obs.var	0.04	0.03	0.07		
	RW2	Adjusted R^2.var	0.09	0.04	0.17		0.065, 0.05
		spde.var.nom	0.00002	-0.0000003	0.0001		0.0023, 0.5
		spde.range.nom	7.9	0.7	40.1		3.9, 0.5
		AR.rho	0.002	-1.0	1.0		
JCM	Density	Intercept	-1.30	-1.37	-1.22	27.1	
	Gamma	obs.var	0.14	0.10	0.19		
	RW1	Exposure.var	0.009	0.003	0.021		0.03, 0.05
		spde.var.nom	0.0000232	-0.0000009	0.0001545		0.002, 0.5
		spde.range.nom	6.4	0.7	29.9		4, 0.5
		AR.rho	-0.002	-0.988	0.988		

$Q_{0.025}$ and $Q_{0.975}$ = quantiles of the credible interval; DIC = Deviance Information Criterion; mR^2 = marginal R-squared (%);Gamma = Gamma likelihood; RW1/RW2 = first or second-order random walk process (predictor variance is followed by .var, e.g., Exposure.var for RW1 and Prior = reference standard deviation and the right tail probability); obs.var = model variance; spde.var.nom = nominal spatial variance (Priors = prior marginal standard deviation and right tail probability); spde.range.nom = nominal spatial range (km) (Priors = practical range and right tail probability); AR.rho = autoregressive parameter, temporal correlation coefficient.

Table 6. Summary of the marginal posterior distribution for model parameters obtained from hierarchical INLA Bayesian space-time models for the best predictors of diversity calculated as Shannon-Wiener H-Index from Tanner's (ET) and Bellingham's (PB) plots in the Blue Mountains, Jamaica, for each census. Average exposure vulnerability (Expos) to hurricanes during the period 1903–1988 was the most important variable (95% credible intervals did not contain zero).

Site	Variable	Parameters	Mean	$Q_{0.025}$	$Q_{0.975}$	mR^2	Priors
BM	H’	Intercept	2.28	2.20	2.37	33	
ET	1974	obs.var	0.06	0.03	0.10		
	RW2	Expos (1903 -1964).var	0.0732	0.0005	0.3326		0.3, 0.05
		spde.var.nom	0.0000234	-0.0000003	0.0001544		0.0023, 0.5
		spde.range.nom	7.3	0.7	35.6		3.9, 0.5
BM	H’	Intercept	2.32	2.24	2.40	43	
ET	1984	obs.var	0.05	0.03	0.08		
	RW2	Expos (1903 -1964).var	0.114	0.010	0.380		0.3, 0.05
		spde.var.nom	0.0000194	-0.0000004	0.0001249		0.0023, 0.5
		spde.range.nom	8.1	0.7	40.8		3.9, 0.5
BM	H’	Intercept	2.35	2.27	2.43	40.5	
ET	1989	obs.var	0.05	0.03	0.08		
	RW2	Expos (1903 -1964).var	0.101	0.007	0.345		0.3, 0.05
		spde.var.nom	0.0000183	-0.0000004	0.0001159		0.0023, 0.5
		spde.range.nom	7.9	0.7	39.7		3.9, 0.5
BM	H’	Intercept	2.38	2.30	2.46	37.9	
ET	1991	obs.var	0.05	0.03	0.09		
	RW2	Expos (1903 -1964).var	0.0749	0.0023	0.2896		0.3, 0.05
		spde.var.nom	0.0000181	-0.0000004	0.0001139		0.0023, 0.5
		spde.range.nom	8.2	0.8	41.8		3.9, 0.5
BM	H’	Intercept	2.41	2.33	2.50	25.6	
ET	1994	obs.var	0.06	0.04	0.10		
	RW2	Expos (1903 -1964).var	0.0479	0.0003	0.4525		0.3, 0.05
		spde.var.nom	0.0000192	-0.0000004	0.0001230		0.0023, 0.5
		spde.range.nom	8.1	0.7	41.0		3.9, 0.5
BM	H’	Intercept	2.46	2.38	2.55	31.8	
ET	2009	obs.var	0.06	0.04	0.10		
	RW2	Expos (1915 -1988).var	0.0414	0.0002	0.4477		0.3, 0.05
		spde.var.nom	0.0000300	-0.0000005	0.0002044		0.0023, 0.5
		spde.range.nom	5.1	0.6	21.9		3.9, 0.5
BM	H’	Intercept	0.98	0.92	1.04	51.1	
PB	2009	obs.var	0.013	0.006	0.027		
	RW2	Expos (1903 -1988).var	0.0024	0.0003	0.0083		0.05, 0.05
		spde.var.nom	0.0000185	-0.0000004	0.0001167		0.0023, 0.5
		spde.range.nom	8.2	0.8	41.3		3.9, 0.5

$Q_{0.025}$ and $Q_{0.975}$ = quantiles of the credible interval; mR^2 = marginal R-squared (%); RW2 = random second-order random walk process (predictor variance is followed by .var, e.g., Expos.var for RW2 and Prior = reference standard deviation and the right tail probability); Gamma = Gamma likelihood; obs.var = model variance; spde.var.nom = nominal spatial variance (Priors = prior marginal standard deviation and right tail probability); spde.range.nom = nominal spatial range (km) (Priors = practical range and right tail probability); AR.rho = autoregressive parameter, temporal correlation coefficient.

Discussion

Topographic exposure in the Blue and John Crow Mountains

Topographic exposure models are generally used to identify points on a landscape-scale topographic surface that are protected from (wind shadow) or exposed to specific wind directions (Boose et al. 1994). The wind shadow is estimated by assuming that the wind bends downwards at a fixed inflection angle from the horizontal as it passes over an elevated surface (Boose et al. 1994). It does not however, estimate changes in wind speed or direction caused by local topography (Boose et al. 1994). In addition, exposure models do not consider the movement of wind over complex terrain and meteorological conditions usually found near the center of a hurricane such as steep gradients of pressure velocity, local convective cells and curved wind paths and rain bands (Boose et al. 1994). Also, exposure models do not consider changes or alterations in these gradients at fixed locations due to a storm's forward movement, intensification or weakening (Boose et al. 1994). These complexities are difficult and problematic to model (Boose et al. 1994).

The simple topographic exposure model used in our study therefore lacks complexity, nevertheless, exposure models work at landscape scales (≈ 10 km) and provide useful predictions of areas protected from or exposed to damaging winds (Boose et al.1994). Also, reconstructed landscape-level exposure maps are generally tested by comparing predicted exposure to actual landscape-level (Boose et al. 1994) or stand-level damage (e.g. Batke et al. 2014; Negrón-Juárez et al. 2014a and 2014b; Luke et al. 2016a) to determine if they can be used as proxies for hurricane damage. Stand-level damage data are generally collected within 2 years within after a disturbance event, although stand-level damage data have been collected up to 12 years after a hurricane stuck (Gannon and Martin 2014). In our study, the reconstructed exposure maps for Hurricane Gilbert were tested or evaluated using stand-level damage and recovery data from Bellingham's plots, which were collected 20–23 months after that hurricane struck the BM. Bellingham's plots included locations with a wider range of topographic positions (Bellingham and Tanner 2000) (Figure 7) and were more suitable for the EV model evaluation than those of Tanner. Tanner's plots varied more in topographic position than in EV due to the location of the plots in nearby blocks located in strongly contrasting topographic positions (Figure 7). As such, Bellingham's plot data showed a stronger relationship of damage and recovery to EV and have greater general validity/power for this analysis than do Tanner's plot data (Figure 2; Tables 2 and 3). The method presented in this study can therefore be used to reconstruct past hurricane (legacy) EV, which can be used as a proxy for landscape-scale hurricane disturbance/damage at un-sampled locations and for hurricanes for which no disturbance data are available. We found that if less ideal proxies were used, at the very least they could be used to produce landscape-level maps that summarize the extent of forest recovery.

At the landscape scale, the spatial pattern of hurricane exposure that was reported in this study was consistent other published observations. In the southern hemisphere, disturbance severity is usually greater on the left side of a cyclone's path due to clockwise rotation of cyclone winds. For example, large areas of undisturbed forest were found on the right side of the track of tropical cyclone Yasi after it struck the northeastern rainforests of Queensland, Australia (Negrón-Juárez et al. 2014a and 2014b). In contrast, in the northern hemisphere (US Gulf Coast forest ecosystems), forest disturbance severity was observed to be greater on the right side of the tracks of four hurricanes (Negrón-Juárez et al. 2014a) due to counter-clockwise rotation of cyclone winds. Additionally, in central new England, USA, the most destructive winds of a 1938 hurricane occurred to the east (right) of the eye where the highest wind speeds were produced from the anticlockwise rotary velocity and forward movement (Foster, 1988). In addition, damage was lower to the west (left) of the eye where wind speeds were lower (Foster, 1988). These observations were consistent with those of Boose et al. (1994), who found that as Hurricane Hugo approached the Luquillo Experiment Forest (LEF), Puerto Rico, from the east, with a track that was initially oriented to the south of the site, the strongest winds associated with the leading eye wall were to the northeast (to the right). At the same site, after ≈ 2 hrs, the trailing eyewall winds were weaker and were from the SSW (Boose et al. 1994). As a result, the north-facing slopes of the LEF were more exposed and the southern slopes, facing the weaker trailing eyewall winds from the SW and SSW, were less exposed (Boose et al. 1994) and showed little damage (Scatena and Larsen 1991). Similarly, after tropical cyclone Yasi struck the northeastern rainforests of Queensland, forest disturbance was found to be higher at aspects that were facing away from the dominant surface winds (Negrón-Juárez et al. 2014b).

In our study, the orientation of the tracks of the eye or center of the hurricanes, even if they made landfall, passed either to the north or south of the study sites and this influenced the pattern of exposure (Figures 4–8). We found that when the eye of a hurricane followed a path or track with a southern orientation, the pattern of exposure was similar to other reported observations; that is, the right side of the track (the north-eastern to south-eastern aspects) were more exposed (Figures 4–8). However, when the eye followed a northern orientation, wind bands from the leading eye wall were mostly offshore, and it was the wind bands from the trailing eye wall that passed over the sites, resulting in greater exposure on the left side of the track (the southern to south-western aspects) (Figures 4–8). Furthermore, there were equal numbers of hurricanes (six each) that followed a path north or south of the sites, and multiple hurricanes followed a similar path in relatively quick succession (Figures 1, 3 and 4). For example, two hurricanes, in 1852 and 1889, had tracks to the south of Jamaica and three hurricanes that made landfall over a period of 12 years (1903, 1912 and 1915) had northerly tracks (Figures 1, 3 and 4). Also, four hurricanes made landfall over a period of 48 years (1903–1951) or followed a track to the north of the island in 61 years (1903–1964) (Figures 1, 3 and 4). Since 1988, most hurricanes followed a track to the south (four in 19 years), although only one made landfall (Gilbert) (Figures 1, 3 and 4). Therefore, since 1852, most aspects at the two sites have been exposed to multiple hurricanes, with only locations with a north-western aspect being severely exposed to only a single hurricane (Allen in 1980) (Figure 4). At the two study sites (both on steeply-sloped mountain ranges), exposure, hence disturbance history at the stand- level, was a function of angle or cardinal direction of both hurricane tracks and local topography (Figures 5–8). As a result, the stand-level assessments of hurricane impacts in the BM and JCM were strongly influenced by plot location. Some plots, despite being located close to each other, had a different disturbance history or degree of exposure (Bellingham et al. 1991), while the disturbance history and exposure was similar for some plots that were located far away from each other (Figures 5–7).

The impact of legacy hurricanes on stand-level spatiotemporal diversity and density patterns

Advances in historical hurricane damage modelling create opportunities for improving estimates of hurricane impacts (Logan and Xu 2015). Models can now account for temporal correlation and spatial dependence simultaneously (Logan and Xu 2015). Therefore, these models can be used (and were used in this study to evaluate 1) whether individual hurricanes had effects, 2) whether it was only the most severe hurricanes that made a difference, 3) whether it was the cumulative effect of several hurricanes over many years that was more important and 4) whether the hurricane effects were temporary or prolonged (Logan and Xu 2015). For the BM, there was an increase in tree diversity at the stand-level in the decades following the passage of Hurricane Gilbert (Tanner and Bellingham 2006). However, diversity also increased during the pre-Gilbert census period and there were mostly light-demanding species present in the canopy in 1974 (Tanner and Bellingham 2006), possibly due to the effects of previous disturbances, including hurricanes. Also, five hurricanes struck in 61 years (1903–1964), four of which made landfall over a period of 48 years (1903–1951), and the eyes or centers of four hurricanes followed a more northerly track (Figures 1, 3 and 4). The BM were therefore exposed to frequent high-intensity hurricanes and, as such, the heterogeneity of disturbance caused by, for example, the 1903 hurricane may have been maintained for an extended period (85 years) by successive hurricanes (Figure 4). This may have permitted greater species co-existence at sites with intermediate exposure and an increase in diversity to occur over time, even after Hurricane Gilbert affected the BM. As a result, the influence of legacy EV on the pattern of diversity, that is peak diversity at intermediate exposures, was similar overall (regardless of time) (Figure 9a) and for the individual censuses of both Tanner's and Bellingham's plots (Figures 9e–k). This is despite the two sets of plots differing in the number, size, shape and layout or design. However, for Bellingham's plots, the effects of past disturbance were manifest in a different way. In particular, the magnitude of exposure resulting from the cardinal direction or orientation of the hurricane's eye or center (P-value from the *calc* function) was the most important predictor of tree Shannon diversity and density in Bellingham's plots (Figure 9b). That is, tree diversity was highest at plot locations that were more likely to be exposed when a hurricane's eye followed a track that was either to the north or to the south of the sites, and lowest at sites that were highly exposed to all hurricanes . In contrast, tree density peaked at sites that were always exposed, regardless of the cardinal direction of the center of the hurricanes (Figure 9c). Both patterns, with that for diversity also being found for the clustered Tanner plots, agree with the two hypotheses, i.e. tree diversity was highest at sites subject to intermediate levels of disturbance but tree density was greatest at sites subject to the highest levels of disturbance. Differences between the two data sets in terms of the importance of predictors of exposure may be due to plot location. Tanner's plots were purposefully located in four clusters each placed in a contrasting forest type that occurred in close proximity (Tanner 1977), whereas Bellingham's plots were located in a more dispersed sampling design stratified between three topographic positions (Bellingham 1991) (Figures 5 and 6).

The results from the individual census assessments can be used to determine when the effects of a hurricane on tree diversity and density became important or for how long their effects lasted. Average legacy exposure of five hurricanes occurring during 1903–1964 was the most important predictor of diversity in Tanner's plots in 1974, and this effect lasted until 1994 or 91 years (Figures 9e–i). Exposure vulnerability to Hurricane Gilbert was not important in these plots (because it did not improve model fit) until 21 years after the hurricane affected the plots (Figure 9j). For Bellingham's plots, average 1903–1988 legacy exposure, which included the EV for Hurricane Gilbert, was important in 2004, 16 years after Gilbert struck, and the 1903 hurricane was still important 101 years after it struck (Figure 9k). In comparison, the effects of three successive hurricanes that made landfall (in 1928, 1931 and 1932) on forest structure and composition in the Luquillo Experimental Forest, Puerto Rico, lasted for nearly 50 years after the last hurricane (Weaver 2002). Moreover, stand-level spatiotemporal patterns in tree diversity in the BM plots are likely to have been most influenced by the hurricanes that made landfall, with their highest wind speeds closest to the study sites. With the exception of Hurricane Cleo in 1964, all other hurricanes that passed Jamaica at some distance off the coast had little or no influence.

Although the BM and JCM had a similar disturbance history, the effects of hurricane disturbance were manifest in different ways. In particular, we found that forest type influenced the heterogeneity of forest damage across a landscape (Zimmerman et al. 1994; Everham and Brokaw 1996; Boose et al. 2004).The ridge-top forest of the BM was found to be the least damaged (the least crown breakage and little tree uprooting) of four Jamaican forests that were assessed 3–8 months following the passage of Hurricane Gilbert (Bellingham et al. 1992). This was attributed to greater resistance of the ridge-top forest to winds, due to a more streamlined, aerodynamic and even canopy, because of its exposed topographic position (Bellingham et al. 1992). Also, there had presumably been a strong selection for tree species and/or structural characteristics (shorter canopy and greater ratio of stem width to height (Lawton 1982)) with greater resistance to strong winds (Bellingham et al. 1992). In contrast, trees in the lower montane forest of the JCM were found to be more susceptible to uprooting than at the other sites due to the greater impact of Hurricane Gilbert on this site, the greater average height of trees, and poor anchoring of trees due to the limestone substrate (Bellingham et al. 1992). The JCM may have also been more affected than the BM by the outer bands of the last three hurricanes that passed 40–45 km from the island (Figures 3 and 4). There were obvious signs of hurricane damage in the JCM after Hurricanes Ivan and Dennis struck (pers. obs.), and eight months after Hurricane Dean, in 2004, 2005 and 2007, respectively (Luke et al. 2016a), but no obvious evidence of damage or disturbance was found in the BM plots during the 2009 census (Tanner et al. 2014). As a result, EV from these hurricanes was not an important predictor of spatial variation in tree density and/or diversity in the BM (or the effects take longer to become manifest). Individual hurricane EV, or the average EV for the last three hurricanes, was however an important predictor of stand-level data from the JCM, in particular individual tree and community structural changes in 2012, diversity patterns in 2012, and density patterns in 2006 and 2016 (Luke et al. 2016a), and across both censuses of the plots (2006 and 2012). However, individual hurricane EV or the average over past hurricanes could not be used to explain the 2006 stand-level diversity patterns. Species composition of the JCM plots may have either recovered by 2006, after the JCM was struck by Hurricane Gilbert in 1988, or the impact of Hurricanes Ivan and Dennis may have masked the effects of Gilbert and other past hurricanes.

The rate of turnover of tree stems and species is another potential explanation for the differences between the BM and JCM. Low turnover rates can be equated to greater resistance to hurricane damage (Tanner and Bellingham 2006). After Hurricane Gilbert, turnover of tree stems for the period 1990–1994 was 2.6% yr^{-1} for Bellingham's plot data (Bellingham and Tanner 2000), and 4.06% yr^{-1} for the period 1989–1994 and 1.6% yr^{-1} for the period 2004–2009 for Tanner's plot data (Tanner and Bellingham 2006). In comparison, over the period 2006–2012, turnover was 2.9% yr^{-1}, for trees in the JCM following Hurricanes Ivan, Dennis and Dean (Luke et al. 2016a,b). As such, turnover at the stand-level for the JCM was within the range of values for the

BM after Gilbert made landfall, but higher than the BM during a period that overlapped, when three hurricanes passed closed to the island. Additionally, 25–50% of trees 2–10 cm in DBH died during the period 2006–2012 in the JCM (Luke et al. 2016b), likely removing some of the trees recruited since Hurricane Gilbert (and before). Moreover, in the BM, the mortality of damaged trees was 2–8 times higher than undamaged stems 19 years after Gilbert (Tanner et al. 2014). Therefore, the greater resistance and recovery of trees in the BM may have resulted in a delayed response that was manifest over a longer time. As such, the influence of Gilbert was not evident until 2004 and 2009 for tree diversity in Bellingham's and Tanner's plots, respectively, and the influence of several hurricanes was evident for long periods. In contrast, rapid changes in the JCM due to the impacts of the rapid succession of hurricanes during 2004–2007 may have removed any signs of the influence of past hurricanes. The rate of turnover of tree stems and species at the two sites were different and therefore, the effects of hurricane disturbance were manifest in different ways.

Conclusion

We developed and validated a method to reconstruct and map landscape scale ($\approx 10\ km^2$) exposure to 12 high-intensity hurricanes (category 2–4), which affected the forests of the BM and JCM in Jamaica, over the past 155 years. The maps were then aggregated and used to identify the spatial patterns of hurricane exposure and to determine if exposure could be used to explain current stand-level ($\approx 1\ km^2$) tree diversity and density patterns. Exposure variability at the landscape and local scales was best explained by the orientation or angle of the eye or center of the hurricane relative to the coastline of Jamaica. This was used to identify three patterns of historical exposure: exposure was significantly higher to the south or north of a hurricane's track when the track was to the north or south of the island/sites, respectively. In the BM, the pattern of exposure determined by the cardinal direction of all hurricane tracks or exposure to six hurricanes (over the period 1903–1988), five of which made landfall, was the best predictor of stand-level spatiotemporal patterns of diversity and density. In particular, there was co-existence of a greater number of species at sites with intermediate exposure (sensu the intermediate disturbance hypothesis) and the highest densities were found at sites that were always highly exposed. In the JCM, stand-level spatiotemporal variation in overall tree density (highest where exposure was highest) was explained by four of the most recent hurricanes, three of which did not make landfall. The difference in predictors between the two sites can be explained by forest type. The ridge top forest in the BM had a greater resistance to hurricane effects, as tree diversity and density were only influenced by the hurricanes that made landfall. The forest of the JCM had a lower resistance and, as such, the influence of past hurricanes was reduced by the impact of three or four of the most recent hurricanes, due to a high turnover of stems and species in the JCM over a short period of time. The reconstructed landscape-scale maps can therefore be used to provide valuable insights into the effects of past hurricanes on contemporary patterns of tree diversity and density at the stand-level ($\approx 1\ km^2$) in different forest types.

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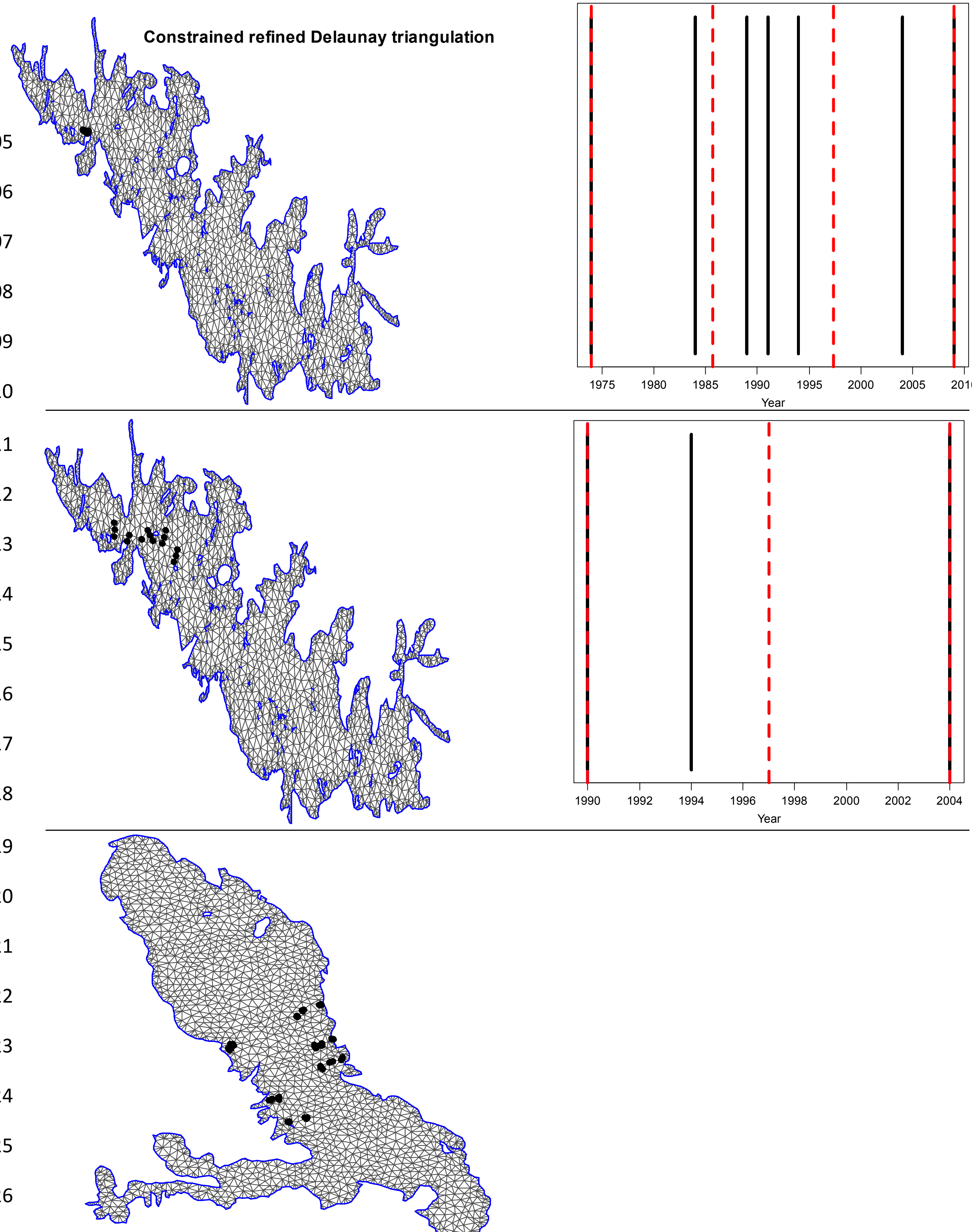

Appendix S1. Two-dimensional mesh/constrained refined Delaunay triangulation used to calculate the Gaussian (Markov) random field in the SPDE approach (left) and the knots (dashed red lines) used for a one-dimensional mesh for the temporal component of the models (right) for the Blue Mountains (top: Tanner's plots; middle: Bellingham's plots). The bottom mesh is for the John Crow Mountains (Luke et al.'s (2016)) plots. The plots are shown as black closed circles. The solid black lines are the censuses.