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Assessing post-storm forest dynamics in the Pyrenees using high-resolution LIDAR data and aerial photographs

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Abstract: We evaluated how historical storm events have shaped the current forest landscape in three Pyrenean subalpine forests (NE Spain). For this purpose we related forest damage estimations obtained from multi-temporal aerial photographic comparisons to the current forest typology generated from airborne LiDAR data, and we examined the role of past natural disturbance on the current spatial distribution of forest structural types. We found six forest structural types in the landscape: early regeneration (T1 and T2), young even-aged stands (T3), uneven-aged stands (T4) and adult stands (T5 and T6). All of the types were related to the timing and severity of past storms, with early-regeneration structures being found in areas markedly affected in recent times, and adult stands predominating in those areas that had suffered lowest damage levels within the study period. In general, landscapes where high or medium levels of damage were common also presented higher levels of spatial heterogeneity, whereas the opposite pattern was found in the less markedly affected landscape, characterized by the presence of large regular patches. Our results show the critical role that storm regimes can play in shaping current forest structure and future dynamics in subalpine forests. The knowledge gained could be used to help define alternative forest management strategies oriented toward the enhancement of landscape heterogeneity as a measure to face future environmental uncertainty.

Keywords Storm regime, Forest succession, Forest structure, Airborne LiDAR, Spatial patterns

Introduction

Natural disturbances are a prevalent component of the functioning and dynamics of European forest (Schelhaas et al. 2003). In the last decades, their impact on forest has significantly increased (Doll 2000) and this trend is expected to continue in the future due to the combined effect of both land-use and climate changes (Seidl et al. 2011). Natural disturbances are often perceived as source of distress for forest managers and society. However, they are an integral part of forest ecosystems and a key factor driving forest dynamics and landscape heterogeneity (Oliver and Larson 1990; Vallecillo et al. 2009). Compared to other factors that modulate landscape configuration, such as physiographic or climatic conditions, disturbances are the one with a more sudden nature, i.e. they change drastically and in a short period of time the current shape and future spatial and temporal dynamics pathways (Forman 1995; Harcombe et al. 2004). In mountainous areas, where the occurrence of different types of natural disturbances is frequent, a better understanding of their regime, and their effects on forested ecosystems would improve the prediction of the future evolution of these ecosystems and their associated services (He and Mladenoff 1999; Mailly et al. 2000; Brotons et al. 2013), allowing the definition of adapted management regimes.

Wind and snow storms are among the most relevant and globally extended disturbances in mountainous areas. The effects of storms on forest structure and landscape configuration have been intensively studied worldwide, as for example in North America (Canham et al. 2001), New Zealand (Moore et al. 2013), Finland (Jalkanen and Mattila 2000), or in Switzerland (Dobbertin 2002). In contrast, in Southern Europe the role and consequences of storms in the dynamics of forest ecosystems have been widely overlooked. In these areas most attention has been paid on forest fires, which is the most common disturbance and main cause of tree mortality (Alexandrian et al., 2000). However, in mountainous areas important damages associated to storms have been pointed out (Martín-Alcón et al. 2010). In general, storm damage is highly dependent on fine-scale factors such as local climatic conditions (Quine 2000), the topographical position and soil properties of the stand (Ruel 2000; Mayer et al. 2005) and the stand structure and composition (Mason 2002; Jactel et al. 2009).

At larger scales, assessing the variability and spatial configuration of forest landscapes represents an important challenge, especially on areas where active disturbances regimes and abrupt topography. However, increasing the spatial extent of ground-based ecological studies, in which information is gathered in the field, is often limited by myriad practical considerations such as financial cost or the rigor of data collection (Rich et al. 2010). In this context, the use of remote sensing tools has been proved to be an affordable and rigorous means to characterize spatial heterogeneity in forest ecosystems, given that they allow the provision of spatially continuous information. In this regard, multispectral satellite images (Wang et al. 2010; Negrón-Juárez et al. 2014), aerial photographs (Pearson 2010; Boucher and Grondin 2012; Kane et al. 2013) and airborne LiDAR (Laser imaging Detection and Ranging) (Rich et al. 2010; Hayes and Robeson 2011) have shown their potential to identify the occurrence and impact of different types of disturbance. Moreover, the information generated from LiDAR can be also used to identify patterns and changes of the forest structure at landscape level (Vepakomma et al. 2010) and subsequently quantify the spatial characteristics of the forest landscape by selecting and estimating adequate landscape metrics (e.g. number and size of patches, diversity of fragments etc.) (McGarigal and Marks 1995). These indices have been found relevant to explain some of the ecological or physical processes influenced by the configuration of such landscape (Leitão et al. 2006), or to analyze the impact of past events on the resulting landscape spatial patterns. For example, heterogeneity and diversity at the landscape scale are recognized as desirable attributes to reduce damages associated to disturbances and long-term environmental change. On this regard, identifying the allocation, spatial arrangement and connectivity of the different forest structures and succession stages is a critical step for planning sustainable and adaptive forest management (O'Hara 1996; Puettmann et al. 2013). Therefore, advancing in the knowledge of how forest successional stages and its spatial distribution in the landscape are conditioned by the type, recurrence and intensity of disturbances may be of critical importance for defining adequate management objectives for heterogeneity at multiple scales as part of complex adaptive systems, and adapting forest management plans to future disturbances.

With this ultimate objective, we have studied the structural response of Pyrenean subalpine forests dominated by *Pinus uncinata* to different degrees of damage associated to recurrent storm events. For this purpose, we have: (1) determined stand-level forest typologies from LiDAR derived data (2) identified how the timing and damage of storms influence the actual state of the forest, regarding the abundance of

the previously defined forest typologies across the landscapes; and (3) examined how the current spatial configuration of the studied landscapes relates to the effects of past natural disturbances.

1 Methods

The procedure used to obtain landscape-level information on forest structural attributes and their evolution over time based on LiDAR data and damage estimations is outlined in Fig 1. It comprises (i) acquisition of LiDAR data and transformation of the raw data into individual tree metrics, (ii) conversion of the tree-level data into stand-level dasometric variables, (iii) definition of forest types, (iv) identification of historical storm damage by comparison of aerial photographs, (v) combination of forest types and storm damage to study the relationship between historical damage and current forest structure, and (vi) assessment of the spatial patterns for the three landscapes.

#Figure 1 approximately here#

1.1 Study area

The study area was located in the north-eastern part of the Iberian Peninsula (Fig. 2), in the eastern Pyrenees (mean altitude 1800 m.a.s.l, precipitation above 900 mm and mean annual temperature below 9 °C). Three different forest landscapes, dominated by mountain pine (*Pinus uncinata* Ram.), were selected for the study: L1 (54 ha), L2 (69 ha), and L3 (85 ha). The selection of these landscapes was based on a previous survey of forest areas affected by storms in 1973 and 1982 (Martín-Alcón and Coll 2008) and was motivated by the importance of mountain pine in the region (dominating approximately 64,000 ha), and the challenge that storm damage entails for the management of these forests (Martín-Alcón et al. 2010).

#Figure 2 approximately here#

1.2 Converting LiDAR data into tree-level attributes

LiDAR data were provided by the Cartographic and Geological Institute of Catalonia (ICGC). Data were acquired from a specific flight conducted for this study in October 2011, using an ALS50 II laser scanner. The LiDAR flight plan provided a minimum first return point density of 6 pulses per square metre, generating a point cloud of returned laser pulses. The processing of the raw LiDAR data consisted of an initial calibration and adjustment of the point cloud, obtaining a georeferenced cloud in terms of the x, y and z coordinates, followed by an automatic classification to differentiate ground from non-ground points. Then a manual edition of the classified cloud was done with the purpose to refine the automatic classification and extract wires and towers from power line infrastructures. After manual edition, a new automatic classification was done in order to extract building roofs, leaving only vegetation points in the non-ground returns. Finally, non-ground returns were classified in different vegetation strata, and were then height-normalized by replacing the elevation with its vertical distance to a triangular irregular model (TIN) generated from ground returns, obtaining a canopy height model. A predefined height of 0.15 m was used as a threshold to separate woody and shrubby vegetation from herbaceous vegetation and soil. Once the canopy height model defined, tree detection has been done with ICGC tools based in standard hydraulic modelling which detects local minimums that are linked to the position of the trees and basins which are similar to canopy areas. In fact this segmentation founds aggregation of trees around a dominant tree, not individual trees. Tree height was obtained by computing the maximum height value of the canopy height model within each small aggregation of trees. Additionally, the relationship between the crown area obtained from LiDAR data and the expected crown area according to Ameztegui et al (2012) was used to identify and split groups of single trees that were wrongly classified from LiDAR. Finally, based on the tree height and crown area of the trees, allometric relations for mountain pine (Gracia et al. 2004; Ameztegui et al. 2012) were used to estimate the diameter at breast height (DBH) of each single tree.

1.3 Estimating stand structural attributes

Based on the size of the trees, stand-level variables were estimated across all the landscapes studied. These stand variables were calculated by creating a regular grid of 3325 squares measuring 25 by 25 meters (0.0625 ha), and aggregating the tree-level information for each square. A first group of variables described the main stand characteristics in terms of tree canopy cover (TCC, %), tree density (N,

stems·ha⁻¹ with DBH greater than 7.5 cm), tree recruitment (N_m , stems·ha⁻¹ with DBH between 2.5 and 7.5 cm), basal area (G , m²·ha⁻¹), mean tree height (H_M , cm), dominant tree height (H_0 , cm), and dominant diameter (D_0 , cm), which were estimated with the mean of the 20% largest trees, and mean diameter (D_M , cm). A second group of variables described the distribution of basal area and stocking density according to tree size: fine wood (FW: with DBH between 7.5 and 22.4 cm), medium wood (MW: with DBH between 22.5 and 32.4 cm), and thick wood (TW: with DBH greater than 32.5 cm). A variable reflecting the stand's structural irregularity was also defined by estimating the relative difference between dominant height and mean height (RD_H).

1.4 Forest structural typology

Based on the previously estimated attributes, a subset of seven stand-level variables was chosen as the basis for defining a structural typology for our mountain pine-dominated forest landscapes. The variables were chosen according to previous studies (Reque and Bravo 2008; Martín-Alcón et al. 2012), as meaningful and non-redundant in terms of information: tree canopy cover, basal area, mean diameter, tree recruitment, and the percentages of fine wood and thick wood, and the relative difference between dominant height and mean height. The different structural types were determined using Ward's hierarchical clustering method with squared Euclidean distance as the similarity metric (Ward 1963). The number of groups was selected according to the cut-off point of the hierarchical dendrogram, when similarity measure made a sudden jump (Hair et al. 2006). Finally, the statistical significance of the structural typology was evaluated using non-parametric tests (Kruskal-Wallis and Mood's median) (Basterra et al. 2012; Montealegre et al. 2014).

1.5 Assessing storm damage

In order to evaluate the damage caused to the forest cover during the storms of 1973 and 1982, aerial photographs from 1956, 1977 and 1996 (the closest in time available for the two storm periods) were collected, geographically corrected, and compared for each period and landscape. Non-supervised classification was used to classify the aerial photographs to differentiate between vegetation and other land covers. Once the vegetation cover was defined for each year (i.e. 1956, 1977 and 1996), the amount of storm damage was estimated for each 25 × 25 m grid plot within the landscapes by identifying the pixels that had reduced their vegetation coverage between the years compared. In this way, the percentage of pixels per grid plot changing from "tree covered" to "non-tree covered" from 1956 to 1977 defined the amount of damage that occurred during the 1973 storm, and the change between 1977 and 1996 defined the amount of damage that occurred during the 1982 storm. Finally, each of the 3325 plots within the 208 ha occupied by the three landscapes was classified according to tree canopy cover change into: high damage (change greater than 66.6%), medium damage (change between 33.3% and 66.6%), and low damage (change less than 33.3%). Undamaged plots (i.e. plots showing nil or positive cover change) were considered as low damage. Additionally, management plans from the landscapes studied were examined to ensure that no management operations had been implemented after the storms, other than salvage logging of fallen or severely damaged trees.

1.6 Relating historical storm damage and current forest structure

Once the forest typology and damage level were estimated and mapped across the three different landscapes, the two sources of information were plotted in order to infer the role of past storm damage (considering its occurrence date and damage level) in determining current forest typology. For this purpose, the current abundance of the forest types within each landscape were related to level of damage and time since the disturbance took place with the use of observed and estimated frequencies of forest types. Additionally, chi-square tests (Cochran 1954) were performed for each landscape, in order to determine whether the abundance of the different forest types was independent of the occurrence and severity of past storms.

1.7 Spatial analysis

An estimation of different landscape metrics was implemented based on the defined forest typology and its spatial distribution, with the aim of identifying the impact of disturbances on shaping the spatial configuration of the forest landscapes. The different landscape metrics were obtained using the Patch Analyst extension of ArcGIS (Rempel et al. 2012) and include: number of patches (NumP) and mean

patch size (MPS) to characterize the size and abundance of forest patches, and mean shape index (MSI) as an indicator of patch form. The spatial arrangement of the landscape was assessed using Shannon's diversity index (SDI), which evaluates landscape heterogeneity from the diversity of fragments, and Shannon's evenness index (SEI), which reflects the homogeneity of the landscape.

2 Results

2.1 Structural characterization of forest types and distribution across the landscapes

Six structural types were defined from a subset of stand variables, and were used to classify the 3325 plots in our three landscapes (Fig. 3). Kruskal-Wallis non-parametric comparison tests on multiple independent samples ($P < 0.01$) and Mood's median test ($P < 0.01$) confirmed the independence between groups for the six structural types obtained. Forest types T1 and T2 corresponded to stands on early regeneration stages with dominance of FW (Table 1). The main difference between these types was the higher level of tree recruitment and the presence of some surviving large-size trees in T2, whereas T1 was characterized by the abundance of young trees over 7.5 cm in DBH. Forest type T3 matched young even-aged forest stands, with most of the trees being between 15 and 20 cm in DBH, but accompanied by a limited number of larger trees (Table 1). Type T4 corresponded to uneven-aged stands with the highest RD_H and a fairly balanced occupancy of FW, MW and TW classes. Finally, types T5 and T6 corresponded to adult forest stands with limited presence of regeneration (Table 1), the main difference between these two types being that T5 presented a higher degree of structural irregularity with shared dominance of MW and TW, whereas T6 was characterized by an overwhelming dominance of large trees classified as TW, combining mature and fully even-aged stands.

#Table 1 approximately here#
#Figure 3 approximately here#

Once the types were defined, their distribution across the three different landscapes was mapped (Fig. 4, Table 2). This revealed that most of the area in the analyzed landscapes corresponded to T5, T6, T4 and T3. By contrast, T1 was present in only 7% of the area, and T2 in not more than 1%. In landscape L1, the most representative type was T3, with 43% of the plots, followed by T4, T5 and T1, meaning that this landscape was mainly characterized by the dominance of young stands. Landscape L2 was characterized by the dominance of more mature structures (types T6 and T5), and lower presence of the remaining forest types. Finally, the most representative types were in landscapes L3, T5, T4 and T6, being present over 35%, 32% and 21% of the area respectively. Other types such as T3 and T1 also had a limited presence on this landscape, suggesting that landscape L3 occupied an intermediate position in between L1, younger, and L2, more mature.

#Table 2 approximately here#
#Figure 4 approximately here#

2.2 Damage assessment and relationship between forest types and storm damage

The comparison of aerial photographs from 1956, 1977 and 1996 allowed an assessment of the changes in forest cover between the two periods (Fig. 5, Table 3). During the first period (1956 to 1977), 7% of the total area was affected by high damage, 19% by medium damage, and 74% by low damage. During the second period (1977 to 1996), 3% of plots were affected by high damage, 36% by medium damage, and 61% by low damage. When the damage assessment was implemented separately for each landscape, it was observed that during the 1973 storm landscape L1 suffered the highest damage, landscape L2 remained unaffected, and landscape L3 suffered from significant damage over approximately 20% of its area. During the 1982 storm, landscape L1 was the least affected of the three, landscapes L2 and L3 suffered from medium storm damage over 40% of their area, and the presence of highly damaged stands was identified on 3% and 6% of the area respectively.

#Table 3 approximately here#
#Figure 5 approximately here#

The influence of storm damage on defining the current forest state was assessed from the relationship between the different levels of damage, the period when the damage occurred, and the relative abundance of the forest types over the different landscapes (Fig. 6). This evaluation showed that the highest levels of

damage occurred during the first period, translated by a higher presence of type T3 and to a lesser extent of T1. Medium levels of damage during this period led to types T3, T4, T5 or T1. Lower levels of damage during this first period were usually associated with a higher variation in the level of damage observed during the second one. Plots showing high and medium levels of damage during the second period appeared associated with the presence of types T4, T1 and T3, whereas forests that were mildly or not affected by storm damage during these two periods were characterized by the current dominance of types T5 and T6.

#Figure 6 approximately here#

The observed and expected frequencies (Table 4) showed the relationship between forest types and historical storm damage. Higher levels of influence were found for types T5 and T6, which were located in areas that had suffered the lowest damage levels in the study period. On the other hand, when high damage had occurred recently, types T1 and T2 were the most distinctive. However, when high damage occurred in the first period followed by no high damage, T3 was the more representative type, whereas type T4 appeared when landscapes were affected by medium damages in one of the periods, usually following or followed by a period of low damage. Finally, the homogeneity test gave values of χ^2 equal to 149, 328 and 343, respectively for each landscape, all significantly higher ($P < 0.05$) than the corresponding chi-square table value (56); this confirmed that the abundance of the different forest types was clearly dependent on the temporal pattern and damage level of past storms.

#Table 4 approximately here#

2.3 Spatial analysis

The assessment of landscape metrics revealed the critical role of the disturbances on the spatial distribution of the types across the landscapes (Table 5). Those landscapes where high or medium levels of damage were common (L1 and L3) presented (independently of the time when damage occurred) a more complex pattern, and higher levels of spatial heterogeneity, with smaller patch sizes, higher MSI, SDI and SEI. By contrast, the least affected landscape (L2) enclosed, on average, the largest and most regular patches, the lowest SDI and a SEI closer to zero, so that it can be considered the most homogeneous of the three landscapes. The size of the landscapes seemed to be the most important feature defining the number of patches per landscape, so that that no clear relation between this metric and the level of damage could be inferred.

#Table 5 approximately here#

3 Discussion

In recent years, the comparison of aerial photographs and the analysis of LiDAR data have been successfully used to assess, respectively, vegetation cover changes associated with natural disturbances (e.g. Foster et al. 1999; Haire and McGarigal 2010), and forest successional patterns (Zimble et al. 2003; Falkowski et al. 2009). In this study we combined the two methods to analyze post-disturbance successional pathways, and in particular the role of the temporal pattern and damage level associated with storms on forest structure and landscape configuration (Kwak et al. 2010; Vepakomma et al. 2010). The results of our study show how forest development is clearly influenced by its particular history of disturbances, their associated damage, and the time since the disturbance took place (Fig. 7). Although the disturbance recurrence on a specific site can modify successional pathways, the current state of the forest is mostly defined by the most severe disturbance. Disturbances causing small levels of damage were found to have a relatively low impact on the forest development in terms of structural attributes, with mature forest structures (T5 and T6) being the most common in areas without significant levels of damage. By contrast, those forests affected by higher levels of damage usually regressed towards earlier stages of development (T1), or transitional stages (T3) if the disturbance took place early enough to let the forest evolve from the previous early stages of development. For T2 (the least common of the types defined), it was difficult to identify the factors determining its origin. This type, dominated by trees in an early stage of development and a small number of remnants of mature reservoir individuals, could originate from a high, but non-complete, damage disturbance, but also from recurrent disturbances causing medium damage, or by a medium damage disturbance causing a destabilization or debilitation of the surviving trees with subsequent delayed tree mortality.

#Figure 7 approximately here#

The results of the landscape spatial configuration analyses agreed in general with those reported in similar studies regarding the marked relationship between landscape heterogeneity and the occurrence and damage of natural disturbances (Lindemann and Baker 2001; Hayes and Robeson 2011). As observed by Mori and Lertzman (2011) in their study on subalpine Canadian forests, we found highest landscape heterogeneity and patch richness in areas where the impact of storms in terms of forest damage was highest (L1 and L3).

On the other hand, landscapes suffering low damage by storm disturbances (L2) showed in general relatively untouched forests and a higher spatial homogeneity. It is noteworthy that all the storms studied caused local adverse effects rather than severe damage over large areas. In the latter case, more homogeneous landscapes would be expected in the disturbed areas.

A better understanding of the impact of natural disturbances on forest landscapes, combined with proper assessments of the future evolution of the forest according to these disturbances, should allow significant improvements in current forest management and planning strategies. Ability to quantify forest damage and changes in forest structure should permit a better estimate of the future evolution of associated services (wood products, scenic beauty, biodiversity and others) and reduce uncertainty when forest management is oriented toward maximizing their production (von Gadow 2000; Gonzalez et al 2005). Also, better comprehension of the storm regimes and their consequences on important attributes such as landscape heterogeneity could be used to implement new forest management models oriented toward reducing the impact of human interventions (see for example Bergeron et al. (2002) and Kamimura and Shiraishi (2007) on close-to-nature management) or new management strategies aimed at enhancing resilient forest attributes to face future disturbances and long-term environmental changes (Bolte et al. 2009; Puettmann et al. 2009; Stephens et al. 2010).

Studies analyzing the influence of disturbances on forest evolution are often focused on the impact of a single large disturbance (Batista and Platt 2003; Kupfer et al. 2008; Wang et al. 2010; Allen et al. 2012). However, forests in the Pyrenees seldom suffer from damage linked to large extreme disturbances, these being important in only a few dispersed specific locations (López-Moreno et al. 2008; Muntán et al. 2009). This characteristic disturbance regime provides the opportunity to compare similar forest systems (located not far from each other) that have suffered storms that took place at different times and caused different levels of damage (Martín-Alcón and Coll, 2008), and where no post-disturbance management operations modified the natural evolution of the forest. However, our study presented some limitations. First, a limited set of historical aerial photographs were available for the study area. These photos were obtained some years after the storm events and so may underestimate its associated damage, since the development of some regeneration in the first years following the disturbance event would be expected. Another limitation arising from our study is that although high resolution data was found to be extremely useful for defining the current forest structure, it was not accurate enough to provide information on standing deadwood, an important variable to define a stand's structural heterogeneity (Pesonen et al. 2008; Martín-Alcón et al. 2012). Finally, we note that using LiDAR multi-temporal data from well-differentiated years, instead of data from a single LiDAR flight, would enhance our knowledge of the evolution of forest and its dynamics after natural disturbances (St-Onge and Vepakomma 2004; Vepakomma et al. 2011).

In conclusion, we have evaluated the utility of combining LiDAR data, aerial photography and spatial pattern analysis to assess forest successional stages after natural disturbances. The definition of three degrees of damage associated with historic storms on two study periods made it possible to infer successional pathways on mountain forests affected by recurrent storms. The combination of forest structural typology with damage estimation and their temporal and spatial distribution explained the evolution of forests since the storm took place, and how landscape heterogeneity naturally emerges as a consequence of this type of disturbance regime. This is relevant to the future definition of forest management and planning strategies.

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- 1   **Figure Legends**
2
3   **Fig. 1** Flowchart of the method
4   **Fig. 2** Location of the study area
5   **Fig. 3** Graphical description of different forest types
6   **Fig. 4** Spatial distribution of the forest
7   **Fig. 5** Spatial distribution of the damage for the periods 1956–1977 and 1977–1996
8   **Fig. 6** Relative abundance of the forest types per damage level and landscape
9   **Fig. 7** Potential forest successional pathways

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Fig. 1 Flowchart of the method
159x141mm (300 x 300 DPI)

Fig. 2 Location of the study area
149x130mm (300 x 300 DPI)

Fig. 3 Graphical description of different forest types
192x224mm (300 x 300 DPI)

Fig. 4 Spatial distribution of the forest
233x229mm (300 x 300 DPI)

Fig. 5 Spatial distribution of the damage for the periods 1956–1977 and 1977–1996
302x427mm (300 x 300 DPI)

Fig. 6 Relative abundance of the forest types per damage level and landscape
254x338mm (300 x 300 DPI)

Fig. 7 Potential forest successional pathways
190x142mm (300 x 300 DPI)

1 **Table 1** Summary of the stand variables defining the forest types

T	TCC (%)	G (m ² ·ha ⁻¹)	D _M (cm)	N (stems·ha ⁻¹)	N _m (stems·ha ⁻¹)	FW (%G)	MW (%G)	TW (%G)	RD_H	H _M (cm)	H ₀ (cm)
T1	34.8	6.0	12.0	425.9	350.3	87.3	3.1	0.0	0.1	698.0	815.2
T2	43.4	3.5	14.7	192.1	1875.8	51.5	26.6	6.9	0.1	768.4	851.5
T3	74.0	21.9	16.7	952.7	28.9	82.0	15.3	2.7	0.2	899.5	1081.9
T4	44.1	15.7	20.7	402.6	152.4	29.0	28.6	42.4	0.4	1014.2	1451.9
T5	67.9	28.0	29.5	439.3	22.5	13.9	30.8	55.3	0.3	1296.8	1633.3
T6	89.4	41.4	43.1	283.9	5.9	0.6	6.1	93.2	0.1	1686.5	1913.5

2 TCC: tree canopy cover; G: basal area; D_M: mean diameter; N: stocking density; N_m: recruitment; FW:
3 basal area of fine wood; MW: basal area of medium wood; TW: basal area of thick wood; RD_H: relative
4 difference in heights; H_M: mean height; H₀: dominant height. T: structural type.

Table 2 Relative abundance of the forest types within each landscape in percentage of the landscape occupied

Landscape	Structural Type					
	T1 (%)	T2 (%)	T3 (%)	T4 (%)	T5 (%)	T6 (%)
L1	12	0	43	27	17	1
L2	5	1	5	9	25	55
L3	4	0	7	32	35	21
Total	7	1	18	22	26	26

Table 3 Relative abundance of the damage levels per landscape and storm occurrence period

	1 st period				2 nd period			
	L1 (%)	L2 (%)	L3 (%)	Total (%)	L1 (%)	L2 (%)	L3 (%)	Total (%)
High	19	0	1	7	0	3	6	3
Medium	38	2	18	19	15	46	47	36
Low	43	98	81	74	85	51	47	61

Table 4 Observed versus expected frequencies of the forest types (Obs / Exp), per damage combination and landscape

	1 st period	2 nd period	T1	T2	T3	T4	T5	T6
Landscape 1	Low	Low	28/34	0/1	86/119	84/75	78/47	1/2
		Medium	13/11	0/0	24/40	41/25	14/16	1/1
		High	3/0	0/0	0/1	0/1	0/1	0/0
	Medium	Low	33/36	1/1	133/125	84/79	38/49	3/2
		Medium	8/4	0/0	10/13	10/8	3/5	0/0
		High	0/0	0/0	0/0	0/0	0/0	0/0
	High	Low	21/20	2/1	116/70	13/44	12/28	0/1
		Medium	0/0	0/0	0/0	0/0	0/0	0/0
		High	0/0	0/0	0/0	0/0	0/0	0/0
Landscape 2	Low	Low	22/25	2/7	33/28	36/47	152/133	292/297
		Medium	13/23	5/7	22/26	46/43	104/123	309/276
		High	12/1	8/0	2/2	5/3	2/7	0/16
	Medium	Low	1/1	0/0	0/1	5/2	11/5	4/12
		Medium	0/0	0/0	0/0	2/0	2/1	1/3
		High	0/0	0/0	0/0	0/0	0/0	0/0
	High	Low	2/0	0/0	1/0	1/0	0/1	0/2
		Medium	0/0	0/0	0/0	0/0	0/0	0/0
		High	0/0	0/0	0/0	0/0	0/0	0/0
Landscape 3	Low	Low	4/19	0/1	15/29	69/144	210/158	146/94
		Medium	19/25	0/1	38/38	216/185	177/203	123/121
		High	20/4	2/0	6/6	55/28	4/31	1/19
	Medium	Low	8/8	0/0	20/12	62/59	77/65	15/38
		Medium	7/3	0/0	9/5	37/23	13/25	4/15
		High	0/0	0/0	0/0	0/0	0/0	0/0
	High	Low	1/1	0/0	3/1	3/4	5/4	0/3
		Medium	0/0	0/0	0/0	1/0	0/0	0/0
		High	0/0	0/0	0/0	0/0	0/0	0/0

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1   **Table 5** Landscape configuration variables of forest calculated with the Patch Analyst program

Landscape	Plots (%)	NumP	MPS	MSI	SDI	SEI
L1	26	112	0.47	1.36	1.32	0.74
L2	33	119	0.57	1.29	1.23	0.69
L3	41	178	0.47	1.37	1.38	0.77

2   NumP: number of patches; MPS: mean patch size; MSI: mean shape index; SDI: Shannon’s diversity
3   index; SEI: Shannon’s evenness index.

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