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Forest disturbance and regeneration: a mosaic of discrete gap dynamics and open matrix regimes?

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Abstract

Question: Recent research in boreal forest suggests that an ‘open matrix’ model may be more appropriate than the traditional model of spatially discrete gap dynamics for describing forest disturbance and regeneration but what is the evidence from temperate broadleaved deciduous forests concerning the prevalence of these alternative models?

Location: Semi-natural temperate broadleaved deciduous forest in southern England.

Methods: Multi-temporal LiDAR data were used to monitor the changes in tree canopy height and canopy gaps over a 10 year period for a 130ha area of forest. Gap dynamics were characterised by quantifying new gap creation and gap expansion, and, by identifying the types and rates of canopy height transitions, observed gap contractions and closures were attributed to the processes of lateral crown growth and regeneration.

Results: Across the study site there was a zonation in canopy and gap properties and their dynamics. Many areas of the forest had the characteristics of open wood-pasture dominated by large, complex gaps being maintained under a regime of chronic disturbance. In these areas, several characteristics of the gap dynamics indicated that regeneration is restricted and this may be attributable to spatially-focussed overgrazing by large herbivores. In contrast, other areas were characterised by high, closed canopy forest with small, discrete gaps where gap creation and infill were balanced.

Conclusions: At the landscape-scale broadleaved deciduous forests contain a spatial mosaic of zones which conform to different models of disturbance and regeneration dynamics; discrete gap dynamics and open matrix regimes are juxtaposed. It is now important to elucidate the abiotic factors and biotic interactions which determine the spatio-temporal distribution of the different regimes and to examine whether such a 'regime mosaic' model is applicable in other forest types.

Keywords: Disturbance; Regeneration; Gap dynamics; Broadleaved Deciduous Forest; LiDAR.

Running head: A mosaic of disturbance and regeneration regimes

Introduction

The storm gap theory of forest dynamics was originated by Sernander (1936) based on observations of the loss of canopy trees during storm events which created sites where a systematic process of regeneration led to the restoration of a closed canopy. Subsequent research has refined the theory and demonstrated that gap creation affects canopy structure and the spatio-temporal properties of forest communities (White 1979; Pickett and White 1985). It is now recognised that canopy gaps can be caused by various factors, including meteorological vectors, insects, disease and the death of individual or multiple trees (McCarthy 2001). Subsequently, gaps can be filled by tree regeneration or lateral crown growth and the resulting canopy is then subject to further gap creation mechanisms; this entire cyclic process is termed gap dynamics (Brokaw & Busing 2000). The importance of gap dynamics in controlling a wide range of ecosystem properties and processes has been well documented for temperate broadleaved (Runkle 1982; Veblen 1989; Stewart et al. 1991; Ritter et al. 2005; Abd Latif & Blackburn 2010), boreal (Spies et al. 1990; Liu & Hytteborn 1991; Muscolo et al. 2007; Kathke & Bruelheide 2010) and tropical forests (Brokaw 1985; Van Dam 2001; Marthews et al. 2008; Gravel et al. 2010).

It has been demonstrated that various different properties of gaps can influence species composition and forest structure via their effects within the open and growth phases of the forest cycle (Denslow & Spies 1990; Elias & Dias 2009). In particular, it has been shown that the recruitment and establishment of tree species is a function of gap size, gap shape, gap age, number and causes of treefalls and canopy height (Barik et al. 1992; Arriaga 2000; Schnitzer & Carson 2001; Li et al. 2005; Lima & Moura 2008; Sapkota & Oden 2009). Hence, it has been suggested that quantifying gap characteristics is essential for understanding disturbance and regeneration dynamics and the consequent impact on ecological processes (Gagnon et al. 2004).

In temperate broadleaved deciduous forests, which are the focus of the present study, it has been recognised that the role of gap characteristics in the recruitment and regeneration of tree species is still not fully understood (Yang et al. 2009). Nevertheless, several studies have demonstrated the importance of a range of gap properties in maintaining the diversity and regeneration of species within broadleaved deciduous forests spanning the temperate zone, for example in Europe (Vetaas 1997; Ritter et al. 2005) and China (Li et al. 2005; Zang et al. 2005). Research has shown that gap size, shape and orientation (Dahir & Lorimer 1996), characteristics of gap creating species (Boettcher & Kalisz 1990) and the understorey species surviving in gaps (Taylor & Qin 1988) affect microclimate, species recruitment and regeneration rate in broadleaved deciduous forest.

The storm gap theory which forms the basis of our understanding of gap dynamics, implies that gaps are spatially discrete units that can be readily distinguished from surrounding closed canopy. However, the literature reveals that there is a wide variety of ways of defining and measuring gaps (see review by Schliemann & Bockheim 2011): some use simple thresholds in height difference between surrounding canopy and gap vegetation to characterise the ‘hole’ in the canopy (e.g. Brokaw 1982); others use more complex models of gap geometry (e.g. Ferreira de Lima 2005); while some emphasise the area which is influenced by the canopy opening (e.g. Porma et al. 1989). Furthermore, some researchers have questioned the entire notion of the canopy gap as a spatially discrete entity, indicating that the transition between gap and closed canopy is characterised by a continuum of change in environmental conditions (Lieberman et al., 1989). Most recently, Hytteborn & Verwijst (2013) argued that an ‘open matrix’ model may be more appropriate than the traditional theory of storm gap dynamics for describing forest disturbance and regeneration. Using evidence from three resurveyed plots in a boreo-nemoral forest, they found that the forest became dominated by an open tree matrix which had a low tree density and gaps were interconnected because gap creation rate was higher than closure rate. Consequently, rather than describing the dynamics of spatially discrete gaps within a surrounding closed canopy, the open matrix model explains how the fate of a single gap or canopy area depends upon the development of neighbouring gaps or canopy areas. Hytteborn & Verwijst (2013) suggest that the open matrix model may be applicable across the full range of forest types, from boreal to tropical rainforest. Hence, the present study aims to investigate whether discrete gap dynamics or the open matrix model provides suitable descriptions of disturbance and regeneration using evidence from temperate broadleaved deciduous forests.

Methods

Study site

The location for this research was Frame Wood and the adjoining Tantany Wood in the New Forest, southern England (1° 30'W, 50° 50'W). The New Forest is recognised as being of international importance to nature conservation; it is mostly Crown property and managed by the Forestry Commission. There are 4049 ha of unenclosed forests, of which the study site is one, where the dominant tree species are *Quercus robur* and *Quercus petraea*, *Fagus sylvatica*, *Betula pendula* and *Betula pubescens*. The unenclosed forests are permanently open to grazing by the ponies and cattle of the Commoners and wild deer. Historically there have been several periods of selective felling in Frame Wood and Tantany Wood. However, these stands are among the closest to 'old-growth' primary forests that exist in the UK, and among the standing trees, several generations have been identified with some individuals aged over 500 years (Flower 1977; Tubbs 1986). Gap vegetation consists predominantly of *Pteridium aquilinium* and grasses that have been maintained by grazing pressure to form a low, tight sward. Canopy gaps have mostly been created by natural treefalls, as result of tree death, disease and windthrow (Morgan 1987; Koukoulas & Blackburn 2005). In the New Forest Act 1877 the term 'Ancient and Ornamental Woodlands' was used to define this forest type which is widely distributed throughout the area (Forestry Commission 2008).

Choice of methods for quantifying disturbance and regeneration dynamics

Disturbance and regeneration dynamics can only be quantified by analysing multi-temporal data, however, it has been noted that this can be difficult due to changes over time in gap and canopy definitions used, the accuracy of gap delineation and the methods employed for quantifying forest structure (Barden 1989). Moreover, measurement of forest disturbance and regeneration in the field is complex, costly, time consuming and limited to small spatial extents (Hu et al. 2009).

The synoptic view of remote sensing has the potential to provide a standardized approach for characterizing forest gap and canopy properties with high spatial and temporal resolution and comprehensive spatial coverage. Passive optical remote sensing has shown some promise in this respect (Blackburn & Milton 1996, 1997; Tanaka & Nakashizuka 1997), and, in particular, the availability of extended time series of aerial photography has enabled the analysis of repeated gap formation events (Torimaru et al. 2012). However, there are some limitations in identifying canopy gaps in passive optical imagery due to shadowing effects and spectral inseparability leading to inaccurate canopy height estimations especially in closed forests (St-Onge et al. 2004). LiDAR data has been widely used in forestry and ecological studies (Hyde et al. 2006; Falkowski et al. 2009) and specifically, in several studies of canopy gaps (Koukoulas & Blackburn 2004; Yu et al. 2004, Boyd et al. 2013), canopy height and forest structure (Lefsky et al. 2002; Naessat 2004; St-Onge et al. 2004) and for creating accurate digital terrain models (DTM's) (Krauss & Pfeiffer 1998; Hodgson et al. 2003; Clark et al. 2004). Thus, multi-temporal LiDAR appears to be an appropriate tool for assessing forest disturbance and regeneration.

Indeed, Vepakomma et al. (2008, 2011) recently established that multi-temporal LiDAR can be used to spatially characterise canopy gap dynamics in boreal forests. Gap creation at the site used in that study was mainly due to fire and spruce budworm outbreaks. An object-based technique was applied to small footprint LiDAR data to map canopy gaps of sizes ranging from a few square meters to several hectares. Gap dynamics over a five year period were quantified using LiDAR-derived canopy height models (CHMs) and this work indicates that there is considerable potential for developing LiDAR-based approaches for monitoring gap dynamics in other forest types. Hence, the present study used multi-temporal LiDAR data for mapping the changes in gap and canopy properties, in a temperate broadleaved deciduous forest.

LiDAR data acquisition and registration

LiDAR data were acquired in July 1997 and again in July 2007. The 1997 LiDAR data acquisition was carried out by UK Environment Agency (EA) using an Airborne Laser Terrain Mapping (ALTM) 1020 (Optech, Canada). The 2007 LiDAR data was acquired by the UK Natural Environment Research Council Airborne Research and Survey Facility (NERC ARSF) using an ALTM 3033 system (Optech, Canada). Both systems recorded single (first) returns only. Table 1 presents the key survey and LiDAR instrument parameters. While flight altitude differences were compensated for by the beam divergence differences, leading to approximately equal footprint sizes, the differences in pulse frequency lead to a notable difference in point density. Such differences are inevitable when using different generations of LiDAR instruments and our method for accounting for this disparity is discussed later. The 2007 data were used to generate a digital terrain model (DTM) because they were of higher point density and were collected using the NERC ARSF aircraft which had a more sophisticated inertial navigation system and higher rate GPS which, combined with post-processing using differential correction using GPS base station data, produces accurate elevations (NERC ARSF 2012). The 2007 point cloud was classified into ground and non-ground returns and the former were interpolated to a raster grid, to generate a DTM with a resolution of 1m. A differential GPS survey at 90 control points revealed levels of accuracy in elevation for the DTM (RMSE = 0.45m) comparable with previous studies (e.g. Hodgson & Bresnahan 2004) and this was considered acceptable for the present investigation.

[TABLE 1]

Digital surface models (DSM) were generated by interpolating the 1997 and 2007 LiDAR data to raster grids with a 1m resolution. An inverse distance weighted algorithm was used for interpolation as it was previously found optimal for generating elevation models and minimising errors due to point density differences in multi-temporal LiDAR data (Vepakomma et al. 2008). The pre-processing routines of both EA and NERC ARSF, using inertial navigation and kinematic GPS data, ensured that both datasets were georeferenced and this was confirmed by overlaying and visually comparing a vector map (from the UK Ordnance Survey) of the major infrastructural features of the study site (e.g. roads, railways, tracks and forest compartments) with the two DSM's. This revealed that the 1997 DSM had a small planimetric offset (typically in the order of 1-2 pixels) from the 2007 and OS data, which were in agreement. This offset may have resulted from factors such as the differences in pre-processing routines for the two data sets or variability in atmospheric conditions or GPS configuration during acquisition (Katzenbeisser 2003). Therefore, using ground control points distributed across the study site, the 1997 DSM was registered with the 2007 DSM using a second order polynomial transformation. Then to examine the correspondence in elevation values between the two DSMs, 50 bare ground locations across the study site were selected using the vector data for infrastructure such as forest tracks, with manual verification that these were bare surfaces, using a subset of locations. At the bare ground locations, elevation values were extracted from each of the DSMs and this revealed that there were no systematic offsets, with good overall agreement (RMSE = 0.26m) between the DSMs. Therefore, the DTM was subtracted from the DSMs from each year in order to derive two CHM's for the study site (Figure 1).

[FIGURE 1]

Gap delineation

In this study, gaps were considered as canopy openings and areas of low vegetation and caused by single and multiple treefalls. Hence, a minimum size threshold for a single treefall of 30m^2 was used to identify gaps for subsequent analysis and a height of 4m was used as the threshold for distinguishing gaps from canopy areas using the CHM. These thresholds were determined from previous work at the study site (Koukoulas & Blackburn 2004, 2005) and confirmed through further field verification undertaken as part of the present study. Consequently it was possible to implement a simple procedure for generating gap maps, by applying a threshold of 4m to the CHM's, above which areas were identified as canopy and below as gaps. The resulting binary map was filtered to remove any gap areas smaller than 30m^2. This procedure was validated by comparing 40 gaps extracted from the 2007 CHM with the same gaps digitised manually from digital colour aerial photographs (10cm spatial resolution) that were acquired concurrently with the LiDAR data. The sample of gaps was selected to cover a wide range of gap shapes and sizes (area range 42 to 460m^2). The results showed a good agreement between the two methods, with an RMSE value of 7.3m^2 (mean error = 3.2%) for area, which compares favourably with the variability in gap size when estimated using different field-based manual survey methods (Ferreira de Lima 2005) and is comparable with ground-based remote sensing methods (Hu et al. 2009).

Given that the 1997 LiDAR data was of a lower point density, it was important to examine whether the technique for delineating gaps (outlined above) was valid for the 1997 data. As there was no concomitant aerial photography for 1997 a direct validation was not possible. Furthermore, because of the likely changes in canopy height and spatial structure, it was inappropriate to directly compare the CHMs form 1997 and 2007. Therefore, characteristics of the 1997 data were simulated by spatially thinning the 2007 point cloud to generate a new point cloud with the same average point density as that of the 1997 data (i.e. 0.3 hits/m^2). The new point cloud was then interpolated to generate a DSM; the DTM was subtracted to generate a new CHM. The original 2007 CHM and the new CHM (reduced point density) were compared statistically and this revealed that overall, there was a high degree of correlation (R=0.95, sig.99%c.i.) with insignificant offset and bias. This minimal impact of reduced point density on canopy height estimates has been observed in other empirical and modelling studies (Goodwin et al. 2006; Disney et al. 2010). When the 4m threshold was applied to the new CHM, this was found to underestimate the total gap area across the study site by a small amount (1%). However, as observed by Vepakomma et al. (2011), such underestimation affects smaller gaps proportionally greater than large gaps (here typically 10% for a gap of 40m^2), and the underestimation may also lead to the artificial separation of gaps that are connected by narrow corridors. Hence, it was felt that further analysis was needed to fully account for the effects of differences in point density of the two LiDAR data sets.

By examining the two CHM's together with height transects across gap zones and the gap delineations resulting from application of the 4m threshold, it was found that at the edge of gaps there was typically a rapid decrease in height over the transition from tree canopy to gap in the original 2007 CHM, whereas in the reduced point density CHM the rate of decrease in height was lower. This indicated that the higher point density data was able to provide a better representation of the full extent tree crowns that surrounded gaps. In testing various methods for accounting for this, it was found that a simple and effective technique was to adjust the height threshold used for gap delineation. By iteratively adjusting the threshold and observing the change on gap area delineated, it was found that an optimum threshold of 4.059m generated the equivalent gap area when applied to the reduced point density CHM as compared to the 4m threshold applied to the original CHM (Figure 2). Hence, this optimised threshold for reduced point density was applied to the CHM generated from the 1997 LiDAR data to generate a binary gap and canopy map. Using the 1997 and 2007 gap and canopy maps, the area and perimeter of each gap was determined and gap shape was quantified using the perimeter to area ratio (P:A). Several workers, such as

Battles et al. (1996) have identified the P:A ratio as a useful indicator for assessing the irregularity of canopy openings.

[FIGURE 2]

Characteristics of gap dynamics

The multi-temporal LiDAR data were used to determine important characteristics that describe the processes involved in gap dynamics. Within the study area, the characteristics defined were canopy openings (new gap and gap expansions), canopy closures (regeneration and lateral closure) and continuous gaps, using a similar technique to that of Vepakomma et al. (2008). A transect running through the 1997 and 2007 CHM's demonstrates the various forms of gap and canopy change (Figure 3). A new gap is defined as a gap in the canopy that is present in 2007 but not in 1997 (A). A gap expansion is when a gap existing in 1997 becomes enlarged in 2007 (B). Regeneration is where a gap area is lost because there is an increase of vegetation height from beneath 4m in 1997 to over 4m in 2007, but the increment in height is less than 6m (i.e. the maximum vertical growth of broadleaved deciduous tree crowns which could be expected over the study period (*n.b.* the 'Gap dynamics' subsection below explains how the value of 6m was derived)) (C). Lateral closure is classified as closure from expansion of tree crowns at the gap edge, identified by an increment in height of more than 6m (i.e. a height increase that is greater than that which is possible by growth of regenerating trees within gaps) (D). Continuous gap areas are present consistently in 1997 and 2007 (E).

[FIGURE 3]

Results

Gap characteristics

Definable canopy gaps present in 1997 and 2007 are shown in Figure 4. Table 2 summarises the changes that have taken place in the gap and canopy properties across the study site as a whole. The maximum canopy height increased slightly, however there were more extensive changes in gap properties. There was an increase in number of gaps and total gap area, and, accordingly, the proportion of canopy coverage decreased. Similarly the mean gap area increased, particularly because there were several cases where a number of smaller gaps expanded and coalesced to form considerably larger gaps. Hence, the mean gap perimeter increased but the P:A ratio changed little, and the complex shape of gaps was maintained.

[FIGURE 4]

[TABLE 2]

Gap dynamics

Figure 5 is a spatial representation of the gap and canopy changes that have taken place over the ten year period. In addition to continuing gap areas, the upper map shows areas of gap expansion and entirely new gaps that were created between 1997 and 2007. The lower map shows the areas of gaps present in 1997 that have contracted by 2007 and entire individual gaps that were closed over the study period. Table 3 summarises the area and number of gaps involved in various types of change during the study period. The results demonstrate that the total gap area created was considerably higher than total gap area lost over the study period. The gains in gap area mainly resulted from the expansion of existing gap areas and most gaps (86%) showed some areas of expansion, resulting from the loss of whole trees or branches at the periphery of gaps. A considerable number of entirely new gaps were created; these were distributed throughout the study site and ranged in area corresponding with the loss of individual and multiple trees. In contrast, a smaller number of gaps were completely closed during the study period and this covered less than half the area of new gaps. Most of the gaps present in 1997 (81%) showed some areas of contraction, but the dominant process is that of gap expansion. Of the gaps present in 1997, 221 had a net decrease in area, 23 no change and 528 had net increase in area. This process of expansion has created areas in the northern and south western parts of the study site that have developed an open wood pasture structure (Forestry Commission 2009), with similar proportions of gap and canopy areal coverage. However, there are extensive areas in the central to eastern parts of the study area that are dominated by high (see Figure 1), closed canopy, where there are fewer continuing gap areas and gap dynamics are dominated by the creation and closure of individual gaps with a size corresponding to that of individual trees (see Figure 5).

[FIGURE 5]

[TABLE 3]

Following the approach of St-Onge & Vepakomma (2004) it was possible to distinguish gap areas that have filled due to regeneration (i.e. due to vertical growth of young trees within gaps) and from lateral canopy expansion (predominantly horizontal growth of mature crowns). The method used here was to define a threshold for the increment in canopy height, below which the increase in height would be within the range possible given the growth rate of broadleaved deciduous trees; above which the increase in canopy height could only be explained by the lateral expansion of mature crowns. Higo *et al*. (1992)

reported that the maximum growth rate of broadleaved deciduous trees in temperate regions was approximately 0.51m.year^{-1}. Thus, we might expect a maximum increment in canopy height of between 5 to 6m over the ten year period of the present study. In order to confirm whether this was an appropriate threshold, a histogram showing the difference between the CHM's from 1997 and 2007 was plotted (Figure 6). The Jenks natural breaks classification algorithm was used to identify the 6m break point in the distribution of canopy height increments (as highlighted on the histogram). Hence, given the evidence from the literature concerning maximum growth rates and the break point in the histogram, a height increment of 6m was identified as a threshold for separating gap areas that have filled due to regeneration and lateral canopy expansion.

[FIGURE 6]

On this basis, Figure 7 represents gap areas that have contracted due to regeneration and lateral crown expansion. Lateral crown expansions were generally located along the edges of continuing gaps while regeneration mostly occurred within gaps away from the periphery, where maximum light levels were available for promoting the growth of young trees. However, some regeneration occurred along the periphery of continuing gaps. As Table 3 shows, a greater proportion of the contraction of existing gaps was due to lateral crown expansion than regeneration. Table 3 also demonstrates that of the small proportion of the total gap area lost due to entire gap closure, lateral crown expansion and regeneration were equally responsible for this closure, with most gaps closing due to a combination of both processes (only 9 of the 133 closures was entirely due to lateral crown expansion and 17 entirely due to regeneration).

[FIGURE 7]

Discussion

The purpose of this study was to understand the spatio-temporal characteristics of disturbance and regeneration in broadleaved deciduous forests and thereby evaluate the applicability of alternative conceptual models of these processes which have been developed in different forest types. In this respect it is useful to provide some context for the present findings, by comparing our observations of gap dynamics in broadleaved deciduous forests with those found in boreal forests. In the broadleaved deciduous forest gaps tended to be larger than those in the boreal forest found in the recent study by Vepakomma et al. (2008). In the present study 45% of gaps had an area of 100m^2 or less, whereas in the boreal forest 85% of gaps were 100m^2 or less. These differences may be attributable to differences in the size of individual tree crowns and the nature of gap creation and regeneration or infilling. Almost all gaps in the broadleaved deciduous forest experienced some contraction due to combined lateral crown expansion and regeneration, whereas in the boreal forest only around half of the gaps experienced contraction or closure. This may be because of the larger size of gaps within the broadleaved deciduous forest providing opportunities for both crown expansion and regeneration. However, it might be argued that such differences could also result from the longer time period over which the present study monitored gap and canopy changes (compared to the 5-year sampling period of Vepakomma et al. 2008) and the variation in growth rates between the two biomes. However the long term investigation by Hyyeborn and Verwijst (2013) confirmed that in boreal forest gaps tended to be smaller than those of the broadleaved deciduous forest and that gaps which did experience total or partial infilling were significantly larger than those not experiencing infill. Hyyeborn and Verwijst (2013) noted that the dominant coniferous trees of boreal forest have very slow rates of lateral growth or lack the capacity entirely. This evidence therefore starts to suggest that there may be fundamental differences between broadleaved deciduous and boreal forests in terms of the disturbance and regeneration regimes. However, other information highlights the similarities.

The key process that has been recorded in this study is that of the expansion of existing gaps, which is much greater than new gap creation or gap loss. This has resulted in many areas of the forest being dominated by many large, complex gaps which are created by the maintenance and progressive enlargement of existing gaps, rather than rare large-scale disturbances such as windthrow which usually results in gaps with a simple shape (Franklin et al. 1987). Therefore the large, complex gaps could be considered as 'chronic disturbance patches' (Forman & Godron 1986), whereby once a gap is created, it is perpetuated by repeated disturbance. In the present study it was found that most large gaps experienced some regeneration around the periphery and evidence for the suitability of gap edges for regeneration has been found in previous field-based investigations in broadleaved deciduous forests (Canham 1988; Mountford et al. 2006). However, the results show that gap edges are also susceptible to disturbance, resulting in the loss of major branches or entire tree crowns. Recent work by Torimaru et al. (2012) using a time series of aerial photography observed cycles of crown expansion followed by branch or crown loss at gap edges and this supports the concept of gaps in temperate broadleaved forest being maintained by chronic disturbance as found at the present study. These observations are consistent with the open matrix model observed by Hytteborn & Verwijst (2013) in boreal forests, whereby gap expansion and coalescence results in a forest consisting of an open tree matrix rather than discrete gaps within a closed canopy.

A series of observations indicate that regeneration is failing across many areas of the study site: the total gap area gained was 41% greater than the gap area lost; the number and area of new gaps created was greater than gaps closures, by 79 % and 120%, respectively; and where gaps did contract the process of lateral crown expansion dominated, being responsible for 53% greater contraction than regeneration. A field-based investigation at nearby site has indicated that reduced regeneration rates in the unenclosed woodlands of the New Forest are likely due to overgrazing by large herbivores (ponies, deer, cattle) (Mountford and Peterken 2003). That study compared vegetation along transects in areas where herbivores were present and had been excluded and investigated changes over a 40 year period. While the present study covers a shorter period of time, it is spatially comprehensive and provides canopy structural evidence that is complementary to the field data and confirms the limited regeneration in many areas of the study site. There is recent evidence that in temperate broadleaved deciduous forests where grazing by large herbivores has restricted regeneration, removal of the herbivores can promote recovery but this is a slow process and is dependent upon adequate seed sources to ensure full tree canopy regeneration (Tanentzap et al. 2011). However, there is evidence that even before the onset of human impacts across the landscapes of lowland Europe, the primary forests were strongly influenced by grazing. While the longer established 'high-forest' hypothesis suggests that the primary forest was dominated by a high, closed canopy of mixed deciduous species (Bradshaw et al. 2003; Mitchell 2005) the more recent 'wood-pasture' hypothesis suggests that grazing by large herbivores was important in maintaining an open landscape with a mosaic of grassland, scrub and forest (Vera 2000). Modelling by Kirby (2004) has demonstrated that a herbivore-driven dynamic process is able to maintain over extended periods of time intimate mixtures of closed canopy and open wood-pasture at the scale of a few hundred metres. Such a mixture has been observed in the present study, with the northern and south-western parts of the study site being wood-pasture with persistent large complex gaps and the central to eastern part mainly high, closed canopy where gap creation and closure appear balanced. Thus, as figure 8 shows, the study site can be considered to be mosaic of zones within which disturbance and regeneration takes the form of either the open matrix model or the spatially-discrete gap dynamics model.

[FIGURE 8]

The long-term maintenance of a mosaic of open and closed canopy areas has been demonstrated by Palmer et al. (2004) using field evidence. In temperate oak forest it was shown that grazing by large herbivores had a strong influence on regeneration in some parts of the study sites but little influence on regeneration in areas of dense mature tree canopy, where light availability was the limiting factor. The local variations in canopy structure and gap dynamics at the present study site appear to support this idea. Consequently, it is possible to conceive of a mechanism which initiates and sustains a mosaic of different disturbance and regeneration regimes. Within a small geographical area, such as that covered by the study site, which has limited topographic variation, it is unlikely that there will be large spatial variations in tree growth rate (i.e. access to resources) or disturbance rate which can create a mosaic in which there are zones with very different disturbance and regeneration regimes within close proximity. Instead, it may be that subtle environmental variations (e.g. in soil or hydrological conditions) initially create spatial variations in tree productivity and viability which in turn affects susceptibility to disturbance and gap creation. A process of positive feedback can then continue to differentiate spatial zones within the forest. Where tree growth is more successful, the zone may be less favourable to grazers (particularly large herbivores) due to restricted accessibility and limited ground forage, and a dense closed canopy reduces the susceptibility of individual trees to windthrow. In these zones tree death results in spatially-discrete gaps which are quickly filled by lateral crown growth or regenerating trees which are subjected to reduced grazing intensity. Where tree growth and viability is more limited, the zone may be more favourable to grazers particularly due to more extensive understorey and ground layers, meaning that grazing becomes spatially-focussed within these zones. The suppression of regenerating tree seedlings and the increased susceptibility to windthrow around gap edges or of isolated trees sustains an open tree matrix structure in these zones. Thus the development or maintenance of a disturbance and regeneration 'regime mosaic' depends upon the characteristics of the component zones and the juxtaposition of zones with different regimes within the mosaic.

Greater evidence is now required in order to substantiate the mosaic model proposed above. In addition to further understanding the mechanisms which initiate and sustain different disturbance and regeneration regimes, it is important that we investigate the interactions between zones with different regimes. Interesting questions arise concerning what factors may influence the dominance of one regime over the other and their relative expansion and contraction over time; what size of forest area is required in order to support an interacting mosaic of different regimes; and, how are dynamics of the forest mosaic influenced by adjacent vegetation or landuse types. As recognised by Kuuluvainen & Aakala (2011) in the context of boreal forest, there is a lack of evidence concerning forest disturbance and regeneration dynamics across a range of spatial scales, with most evidence coming from small survey plots. The present study has highlighted the importance of placing our understanding of local scale dynamics within a wider landscape context, because survey plots would not be large enough to capture the spatial extent of the mosaic of disturbance and regeneration regimes that was found in this research. The results confirmed that LiDAR data are valuable for mapping canopy gaps and monitoring long term dynamics in a spatially-comprehensive manner over a large area; this would be virtually impossible using field techniques. The time span covered by available LiDAR data is currently restricted and such data cannot replace long-term repeat surveys of permanent forest plots. Nevertheless, the growing availability of multi-temporal LiDAR datasets presents an important opportunity to provide a spatio-temporal framework for further studies investigating disturbance and regeneration in order to fill gaps in our understanding of these processes within forest ecosystems (see Seidl et al., 2011).

Conclusions

This study aimed to use evidence from temperate broadleaved deciduous forest to determine whether disturbance and regeneration was best described using the recently-developed open matrix model or a traditional model of discrete gap dynamics. By using multi-temporal LiDAR remotely-sensed data we were able to quantify disturbance and regeneration over a 10 year period with fine spatial resolution across a landscape scale. We found that both open matrix and discrete gap dynamics models could be applied but they were each relevant to different zones within a mosaic that was distributed across the landscape. Some zones were dominated by the maintenance and expansion of existing large and complex gaps under a regime of chronic disturbance, resulting in a low tree cover. Several characteristics of the gap and canopy changes indicated that regeneration was restricted and this may be attributable to spatially-focussed grazing by large herbivores within these zones. Other zones contained closed canopy forest, where gap creation and infill were approximately in balance and constrained to discrete spatial units. It is now important to elucidate the abiotic factors and biotic interactions which facilitate the development of such a mosaic and influence its spatio-temporal characteristics within broadleaved deciduous forests and to examine whether such a ‘regime mosaic’ exists in other forest types.

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Table 1. Specifications of the two LiDAR instruments used for data acquisition.

Specification	1997	2007
Model of Optech LiDAR	ALTM 1020	ALTM 3033
Flight altitude (m AGL)	730	1000
Divergence (mrad)	0.3	0.23
Pulse frequency (Hz)	5000	33,333
Max. scan angle (degrees)	20	20
Point density (hits/m^2)	0.3	1

Table 2. Descriptive statistics for canopy gaps in 1997 and 2007.

Statistics	1997	2007
Total study area (m^2)	1009488	1009488
Max canopy height (m)	31.3	32.0
Number of gaps	905	989
Total gap area (m^2)	211044	237096
Percent of total area covered by gaps (%)	20.9	23.5
Mean gap area (m^2)	4077	8369
Max gap area (m^2)	23372	40252
Mean perimeter (m)	1390	3107
Max perimeter (m)	7884	14716
Mean P:A	0.47	0.49
Max P:A	2.00	2.00
Min P:A	0.17	0.20

Table 3. Gap dynamics expressed using the area involved in various types of change during the study period. Minimum area recorded for all changes was 1m^2 i.e. the spatial resolution of the CHM. The numbers of gaps experiencing the various types of change are not mutually exclusive, as any single gap can experience more than one type of change.

	Gap gain			**Gap loss**						
	Area of entirely **new gaps**	Area of **expansion** from existing gaps	Total gap area gained	Area of entire gap **closure**			Area of **contraction** from existing gaps			Total gap area lost
				Due to lateral crown expansion	Due to regeneration / vertical growth	Total area of closure	Due to lateral crown expansion	Due to regeneration / vertical growth	Total area of contraction	
Total area (m^2)	10328	79116	89444	2380	2312	4692	35504	23196	58700	63392
Max area (m^2)	404	532	532	68	108	216	128	96	296	296
Mean area (m^2)	79.5	74.5	75.0	19.1	22.8	54.8	16.6	11.8	36.5	37.9
No. of gaps experiencing this change	238	780	*N/A*	116	124	133	704	640	734	*N/A*

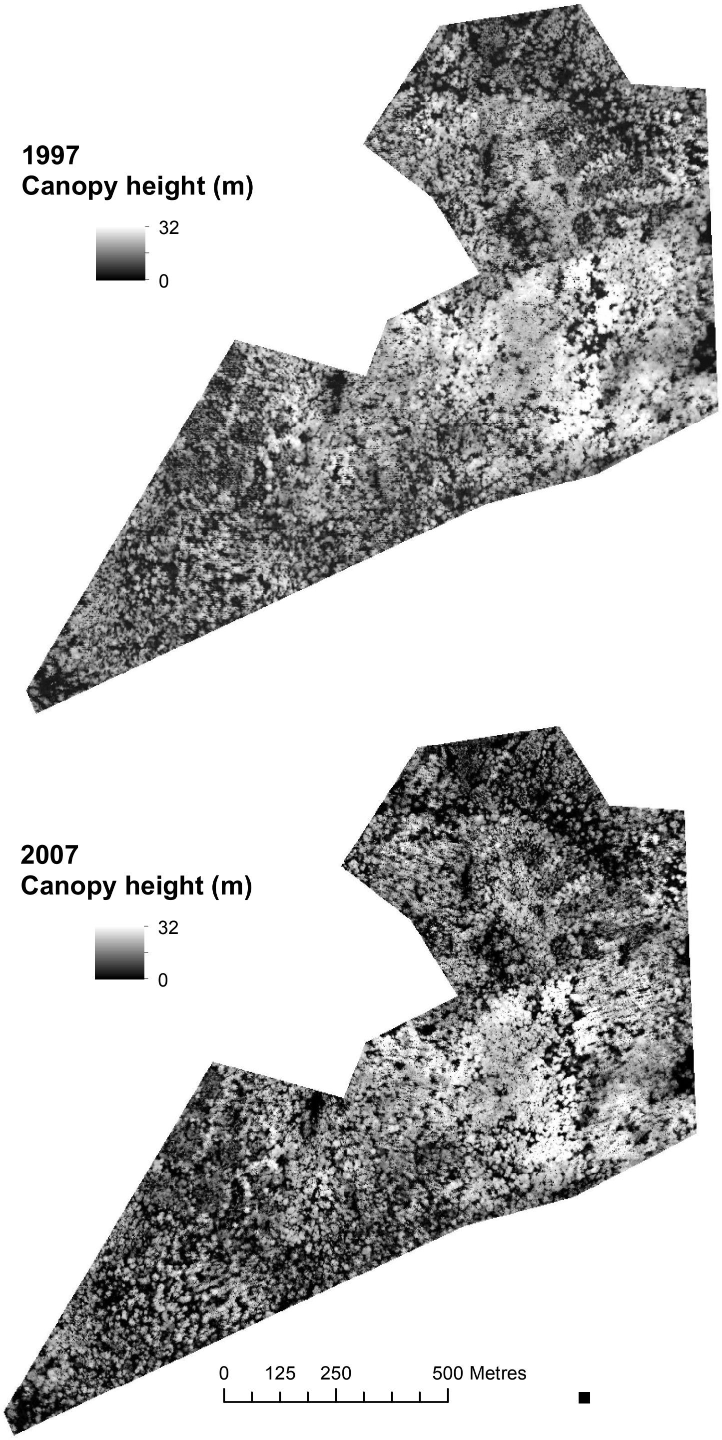


Figure 1. CHMs of the study area for 1997 and 2007, derived using LiDAR data from the respective years.

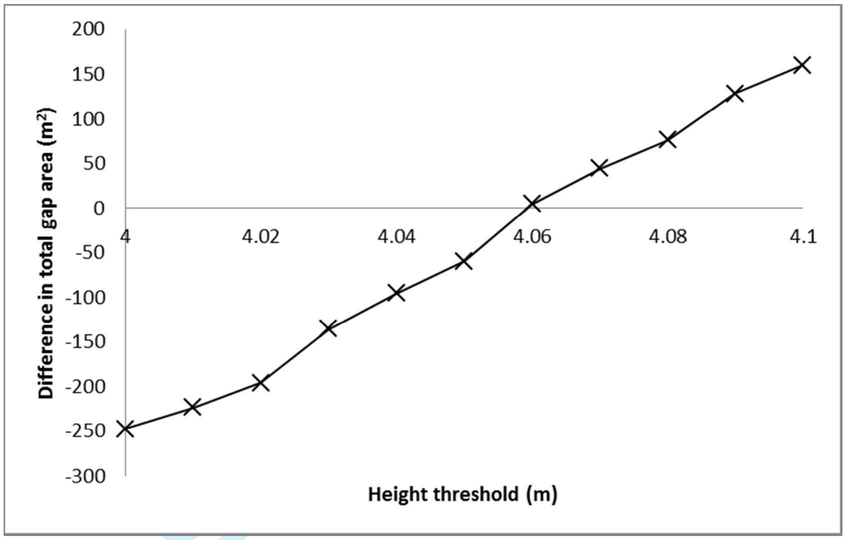


Figure 2. Difference in total gap area delineated between the original 2007 CHM and the reduced point density CHM when applying different height thresholds to the reduced point density CHM for gap delineation.

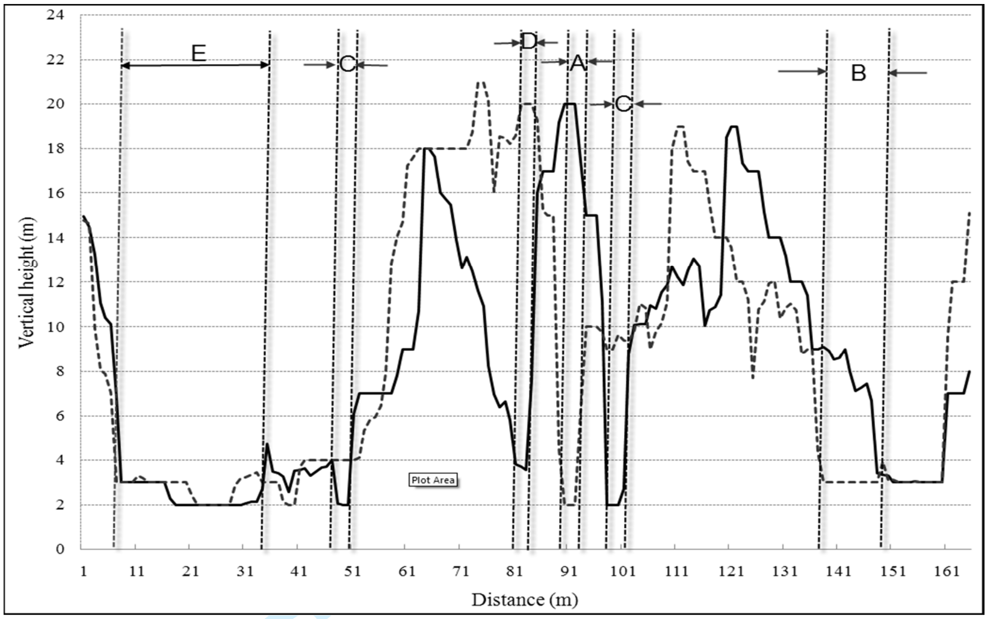


Figure 3. CHMs showing vertical profile changes between 1997 (bold line) and 2007 (dashed line). (A) new gap; (B) gap expansion; (C) gap closure from below due to regeneration; (D) gap closure due to lateral expansion of tree crowns; (E) a continuous gap area, existing in 1997 and 2007.

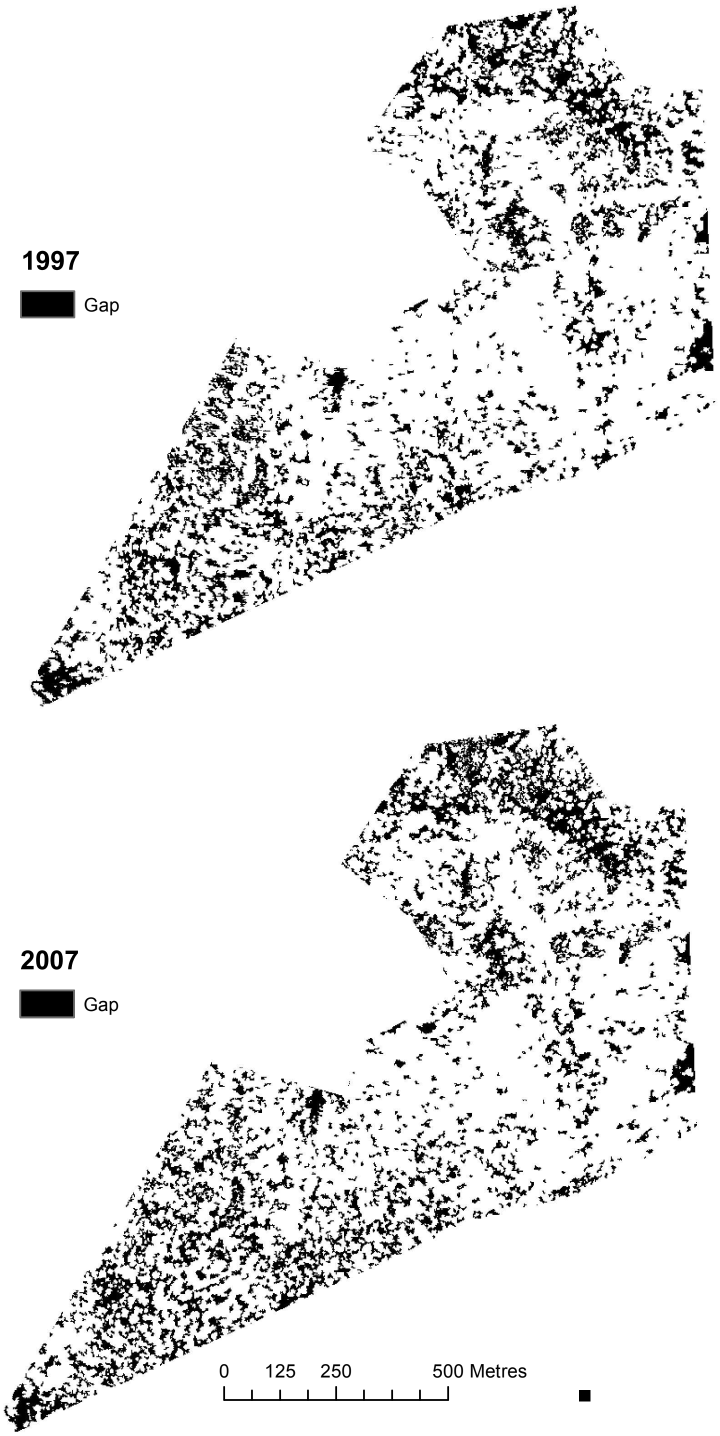


Figure 4. Distribution of canopy gaps in the study area in 1997 and 2007.

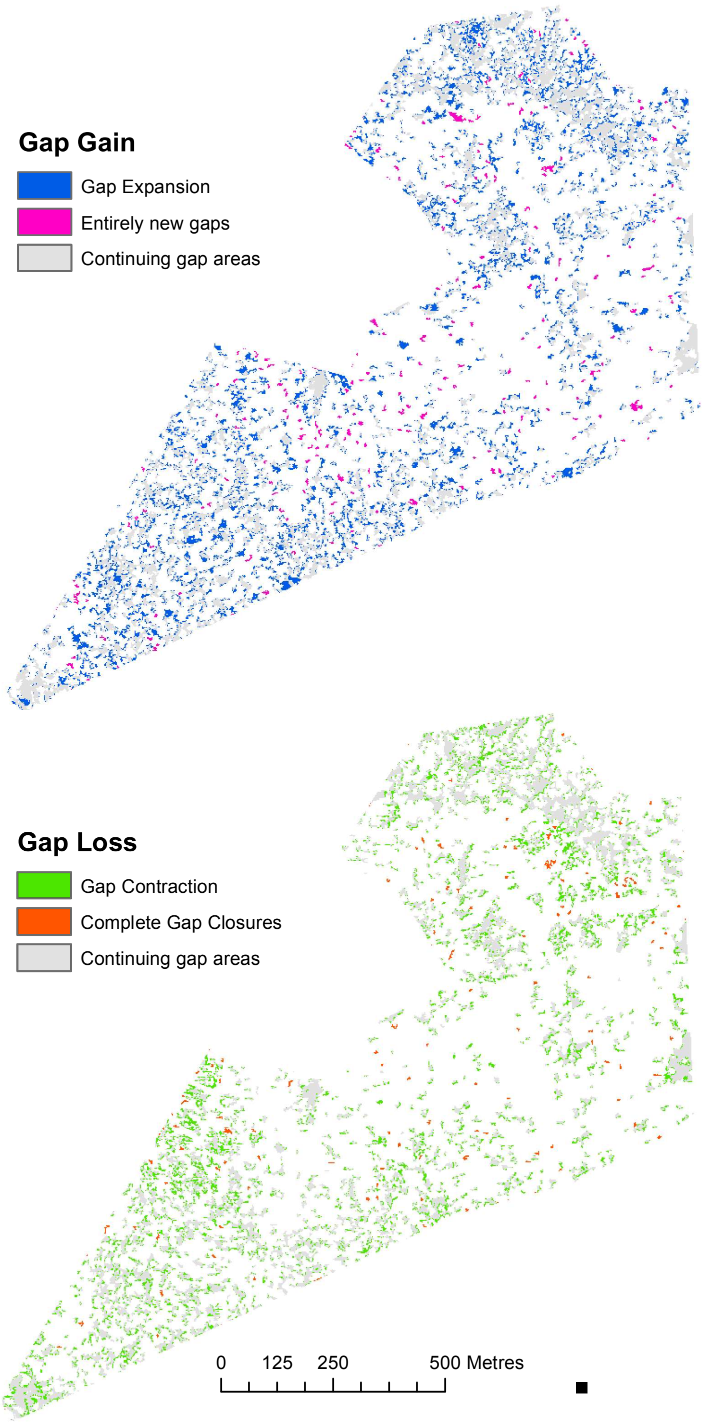


Figure 5. Spatial representations of loss and gain in gap areas between 1997 and 2007.

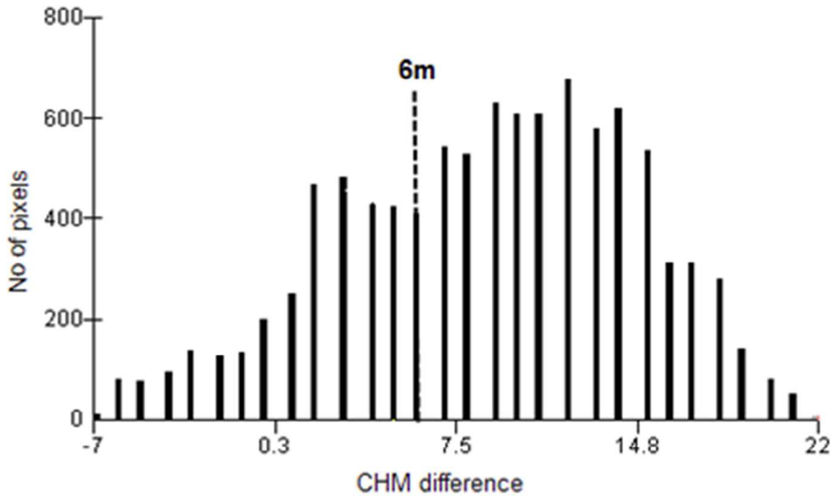


Figure 6. Histogram showing the difference between the CHM's from 1997 and 2007. A threshold of 6m was identified using natural breaks algorithm in ArcGIS, to distinguish between height increments due to regeneration and those due to lateral crown expansion.

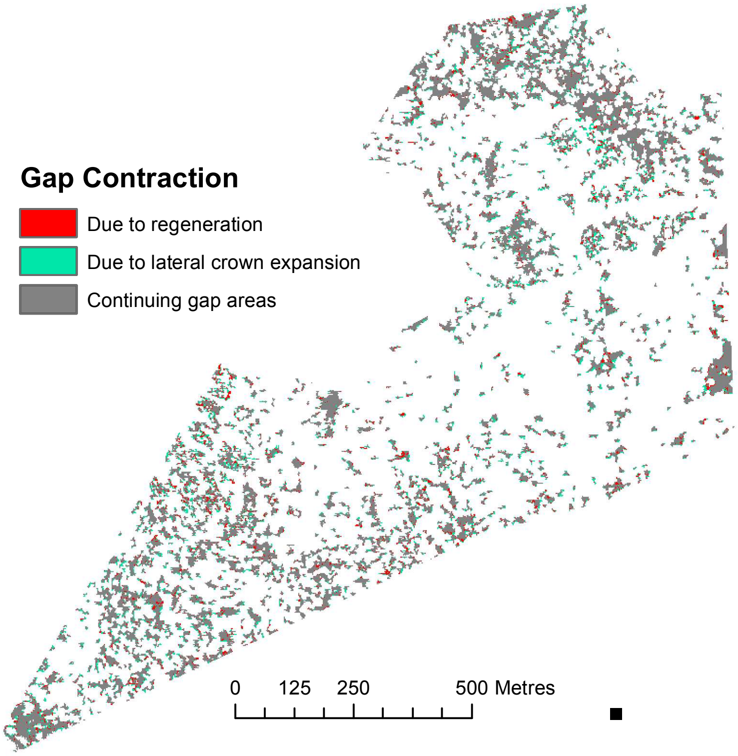


Figure 7. Gap areas that have contracted due to regeneration and lateral crown expansion.

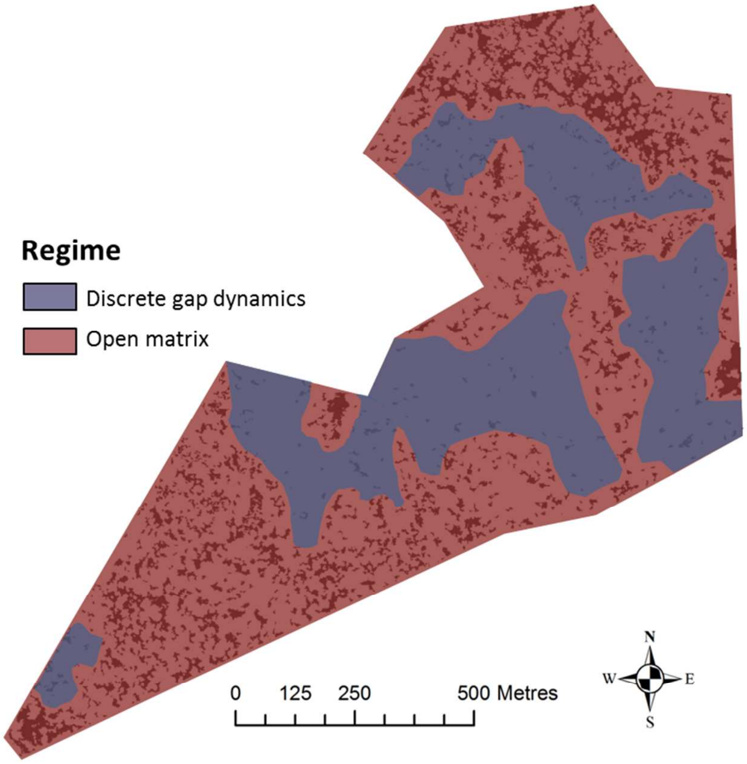
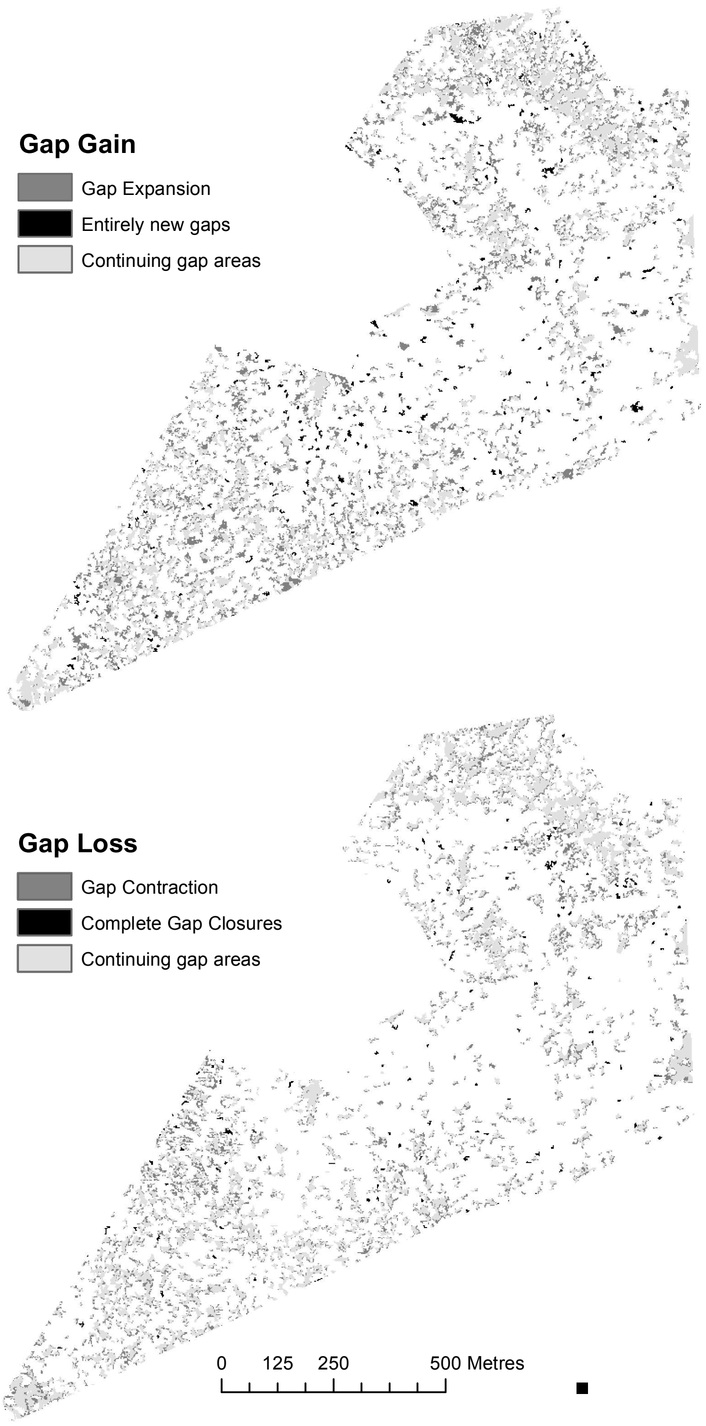


Figure 8. The mosaic of different disturbance and regeneration regimes. Zones have been delineated by applying a series of spatial filters to the map of continuing gap areas (which is shown beneath the regimes map).

GREY-SCALE FIGURES FOR PRINT VERSION



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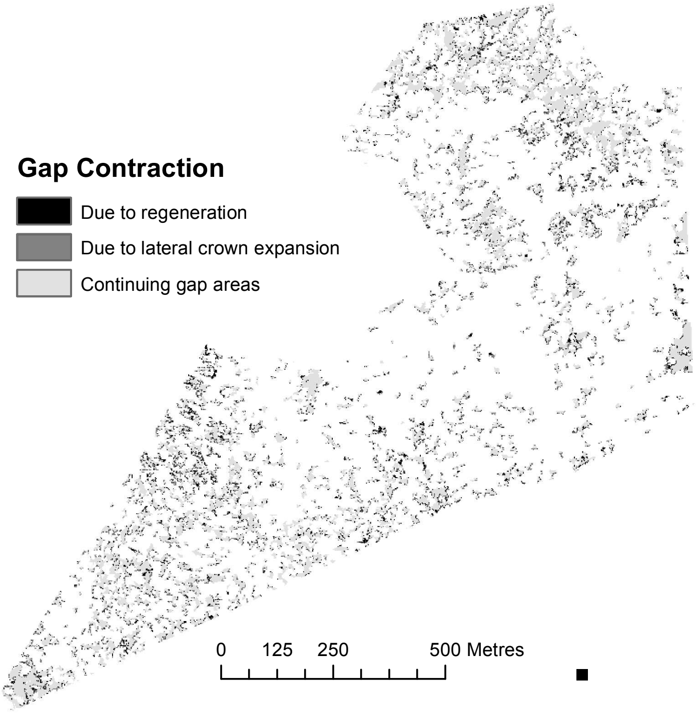
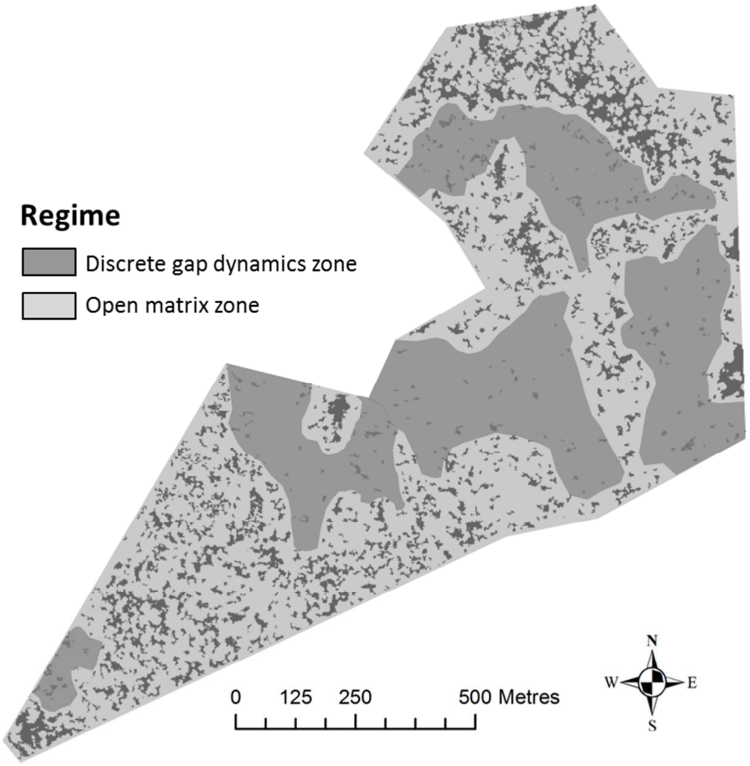


Figure 7. Gap areas that have contracted due to regeneration and lateral crown expansion.



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