Red squirrel habitat mapping using remote sensing

Silvia Flaherty

A thesis submitted in fulfilment of requirements for the degree of Doctor of Philosophy

School of GeoSciences
University of Edinburgh

2012

Declaration

I hereby declared that this thesis is of my own composition, and that it contains no material previously submitted for the award of any other degree. The work reported in this thesis has been executed by myself, except where due acknowledgments is made in the text.

Silvia Flaherty

Abstract

The native Eurasian red squirrel is considered endangered in the UK and is under strict legal protection. Long-term management of its habitat is a key goal of the UK conservation strategy. Current selection criteria of reserves and subsequent management mainly consider species composition and food availability. However, there exists a critical gap in understanding and quantifying the relationship between squirrel abundance, their habitat use and forest structural characteristics. This has partly resulted from the limited availability of structural data along with cost-efficient data collection methods. This study investigated the relationship between squirrel feeding activity and structural characteristics of Scots pine forests. Field data were collected from two study areas: Abernethy and Aberfoyle Forests. Canopy closure, diameter at breast height, height and number of trees were measured in 56 plots. Abundance of squirrel feeding signs was used as an index of habitat use. A GLM was used to model the response of cones stripped by squirrels in relation to the field collected structural variables. Results show that forest structural characteristics are significant predictors of feeding sign presence, with canopy closure, number of trees and tree height explaining 43% of the variation in stripped cones. The GLM was also implemented using LiDAR data to assess at wider scales the number of cones stripped by squirrels. The use of remote sensing -in particular Light Detection and Ranging (LiDAR) - enables cost efficient assessments of forest structure at large scales and can be used to retrieve the three variables explored in this study; canopy cover, tree height and number of trees, that relate to red squirrel feeding behaviour. Correlation between field-predicted and LiDAR-predicted number of stripped cones was performed to assess LiDAR-based model performance. LiDAR data acquired at Aberfoyle and Abernethy Forests had different characteristics (in particular pulse density), which influences the accuracy of LiDAR derived metrics. Therefore correlations between field predicted and LiDAR predicted number of cones (LSC) were assessed for each study area separately. Strong correlations (r_s=0.59 for Abernethy and 0.54 for Aberfoyle) suggest that LiDAR-based model performed relatively well over the study areas. The LiDAR-based model was not expected to provide absolute numbers of cones stripped by squirrels but a relative measure of habitat use. This can be interpreted as different levels of habitat suitability for red squirrels. LiDAR-based GLM maps were classified into three levels of suitability: unsuitable (LSC = 0), Low (LSC < 10) and Medium to High Suitability (LSC >=10). These thresholds were defined based on expert knowledge. Such a classification of habitat suitability allows for further differentiation of habitat quality for red squirrels and therefore for a refined estimation of the carrying capacity that was used to inform population viability analysis (PVA) at Abernethy Forest. PVA assists the evaluation of the probability of a species population to become extinct over a specified period of time, given a set of data on environmental conditions and species characteristics. In this study, two scenarios were modelled in a PVA package (VORTEX). For the first scenario (*Basic*) carrying capacity was calculated for the whole forest, while for the second scenario (*LiDAR*) only Medium-to-High suitable patches were considered. Results suggest a higher probability of extinction for the *LiDAR* scenario (74%) than for the *Basic* scenario (55%). Overall the findings of this study highlight 1) the importance of considering forest structure when managing habitat for squirrel conservation and 2) the usefulness of LiDAR remote sensing as a tool to assist red squirrel, and potentially other species, habitat management.

Acknowledgments

My biggest thanks are reserved for my supervisors Dr Genevieve Patenaude, for her support, patience and guidance throughout this project and Dr Peter Lurz, who very kindly adopted me as his student and very patiently helped me understand the squirrel world. I would also like to thank my co-supervisors Dr Tim Malthus and Dr Iain Woodhouse for their advice.

Without funding from the University of Edinburgh and the Forestry Commission Scotland this PhD would have not been possible. I would also like to acknowledge the support of the NERC Airborne Research and Survey Facility for acquiring and providing the LiDAR data. Thanks in particular to Mark Warren for his help with the pre-processing of the data.

Special thanks to Dr Juan Suarez, Dr Rachael Gaulton, Dr Alasdair MacArthur, Chris Place, Owen MacDonald, Dr Andrew Close and Dr Pablo Rosso for their advice in different moments of this PhD. Thanks also to Stewart Snape, Juliet Robinson, Dr Mel Tonkin, Jo Ellis, Andy Amphlett and all the individuals and organisations that contributed to this research.

Field work was possible thanks to the funding provided by the People's Trust for Endangered Species. I would also like to thank Wayne Fitter, Xavier De Lamo, Kushal Gurung and all the volunteers for their invaluable help and willingness to work during the field seasons.

Finally, my warmest thanks are due to my mother and my brother for their love and support, and to my friends, the ones in the UK and the ones overseas, for their love, support and encouragement.

Table of Contents

CHAPTER 1

General Introduction

1.1 Introduction

The red squirrel (*Sciurus vulgaris*) – the only squirrel species native to the UK- was previously widespread all over England, Scotland and Wales (Gurnell, 1987; Lurz *et al.*, 1995; Bryce *et al.*, 2005; Poulsom *et al.*, 2005). Intensive tree felling in the 17th and 18th centuries, causing habitat fragmentation and woodland loss, resulted in an severe reduction in the number of red squirrels. More recently, the introduction of grey squirrel (*Sciurus carolinensis*) from North America largely contributed to a further decline in red squirrel populations in Britain. Nowadays, the grey squirrel has replaced reds in most of England, Wales and Central Scotland (Lurz *et. al.*, 1995).

The decline in red squirrel populations has lead to concern about the conservation status of the species, which is now considered endangered, listed in the UK Biodiversity Action Plan and under legal protection (Schedules 5 and 6 of the Wildlife and Countryside Act 1981, Nature Conservation (Scotland) Act 2004; and WANE Act 2011). Today, long-term management of red squirrel habitats is a key goal of the UK Strategy for Red Squirrel Conservation (Bryce *et al.*, 2005)

Although the grey squirrel is currently thought to be the major threat, disease (i.e. squirrelpox virus) and habitat quality are also important factors affecting the future of red squirrels in the UK (Gurnell *et al.*, 2004; Rushton *et al.*, 2006a). Conservation efforts currently concentrate mainly in controlling grey squirrels and managing woodlands to favour red squirrels (Forestry Commission, 2012; Poulsom *et al.*, 2005; Mackinlay & Patterson, 2011)

The following section provides an overview of the main factors (e.g. competition with greys, squirrelpox virus) that currently threaten red squirrel survival in the UK. Research and main findings on the species habitat preferences leading to current habitat management strategy will also be reviewed.

1.1.1 Grey squirrels versus red squirrels

A great deal of research is dedicated to investigating the impact of exotic species introduction on native species (Tompkins *et. al.*, 2003). In the particular case of the red squirrel in the UK, the introduction of the grey squirrel from North America has largely contributed to a decrease in red squirrel populations in Britain. The largest number of grey squirrel was introduced in 1889, although there is evidence that a pair was brought to England in 1876. In Scotland, the grey squirrel was first introduced in 1892, and in Ireland in 1913 (Middleton, 1930). Since its introduction, the species has spread and replaced red squirrels in most of England, Wales as well as Central and Southern Scotland (Lurz *et. al.*, 1995; for red/grey squirrel distribution maps refer to: Naturally Scottish - Red Squirrels, SNH, 2010, pp 4-5). This phenomenon is not only limited to the UK but has also been observed in other countries where grey squirrels have been introduced, such as Ireland and Italy (Teangana *et al.*, 2000; Lurz *et al.*, 1995; Rushton *et al.*, 2000; Gurnell *et. al.*, 2004).

The mechanisms by which the greys are replacing reds are still being investigated and a number of hypotheses have been proposed. The grey squirrel is native to mixed forests rich in broadleaves in Eastern USA while the red squirrel is mainly adapted to living in conifer forests (Gurnell, 1987). These differences partly explain the way both species have evolved: grey squirrels are larger and heavier than reds and they spend most of their time on the ground, feeding on fallen seeds. Meanwhile reds are smaller and lighter and therefore can feed on cones in canopies, where they spend most of their time (approximately 70%), unlike grey squirrels which spend only 14% of their time in the canopy (Gurnell, 1987, Gurnell & Pepper, 1991). It must be highlighted however, that this is a general trend only: red squirrels have been observed to spend a larger amount of time feeding on the forest floor, while greys in Hamsterley Forest, for example, have been seen to spend most of their time in the canopy, where the food was more abundant (P.Lurz, pers. comm., 2012). The adaptation of the two species to their different habitats is also evident in other aspects of their ecology. For instance, grey squirrels appear more tolerant than reds to a toxic substance present in acorn, which explains why red squirrel densities are lower in deciduous forests dominated by oak (*Quercus*) trees (Lurz *et. al.*, 1995; Kenward & Hodder, 1998; Gurnell *et. al.*, 2004). This observation is further supported by Tompkins *et al.*, (2003) who reported that in years of good acorn crops in Norfolk, England, grey squirrel reach very high densities. This has consequences for reds, as large populations of greys also feed on other tree seeds, such as hazel nuts (*Corylus*), reducing in this way the red squirrel's source of food and thus, its survival (Tompkins *et al.*, 2003). It is worth emphasizing here that both squirrel species are capable of surviving in both broadleaved and conifer forests (Gurnell, 1987). Yet, the densities at which they live in the two different habitat types varies: while both grey and red squirrel densities fluctuate between 0.4 to 1.2 animals per ha in conifer forests, grey squirrel densities reach much higher values (2 to 8 per ha) in broadleaved forests (Gurnell & Pepper, 1991). This explains and highlights the importance of conifer forests in relation to red squirrel conservation in the UK. This will be discussed in more detail later in this chapter.

Mechanisms of competition between red and grey squirrel seem to be more subtle than direct aggressive interaction between the two species (Gurnell, 1987). Gurnell *et. al*. (2004) conducted a study in Hamsterley Forest, England (conifer forest) and Borgo Cornalese, Italy (mixed broadleaves and conifers). They compared two red-only with two red-grey sites, and their results indicate that the presence of grey squirrels negatively influence red squirrel in a number of ways. In habitats where reds coexist with greys, they observed a reduction in: red squirrel body mass; juvenile recruitment, number of females producing a second litter and summer breeding. Previous research by Wauters *et al.* (2002) reported that grey squirrels coexisting with reds were observed to pilfer their food catches, and as suggested by the authors, this probably is also the case in the UK. Red squirrels depend on seeds hoarded in autumn as a source of food for the following winter and spring, and a reduction in the amount of food recovered would reduce energy intake, and potentially lead to a reduced body mass in spring and the consequent reduction in fertility and reproduction (Wauters *et al.*, 2002). In terms of foraging behaviour, earlier studies by Wauters *et al.* (2001) conducted in two sites (red-only and red-grey) in Italy suggested that red squirrel feeding activity (*i.e.* time spent searching for food, time spent foraging) and food choice do not differ substantially between red squirrels that coexist with greys and those that do not share their habitat with greys. However, this does not match results from a study carried out in the Goathorn Peninsula, Dorset, where 14 red squirrels were released in a conifer forest dominated by Scots pine and with some oak and chestnut (*Castanea*), and where grey squirrels were also present (grey squirrel density is not reported, Kenward & Hodder, 1998). Out of the 14 initial squirrels, 11 died over the first 3 months, the majority due to predation, but a minority died of diseases that typically affect stressed individuals (adrenal hypertrophy, septicaemia, enteritis). The 3 red squirrels that survived the longest and settled among the greys had problems foraging (i.e. as indicated by an increase in their core areas) despite an abundance of food. These results suggest that grey squirrel could potentially interfere with red squirrel foraging behaviour (Kenward & Hodder, 1998). Some researchers have argued that the detrimental effects on red squirrel populations of competition with greys is density dependant and measurable effects increase with increasing number of grey squirrels (Bryce *et. al.*, 2005; Wauters *et al.*, 2002).

The findings summarised in this section show that competition between reds and greys is a major reason for the decreasing number of red squirrels in the UK. However, other factors such as disease have been investigated and are thought to play an important role in population decline (Tompkins *et al.*, 2003). Indeed, decrease in red squirrel population was observed in the past, before grey squirrel was introduced, and this was linked to disease (Middleton, 1930).

1.1.2 Squirrelpox virus

Previously known as parapox virus, squirrelpox virus (SQPV) is caused by a poxvirus and it is thought to be one of the reasons for the red squirrel population decline in the UK, in particular in England and Wales. More recently (2005), the first four cases of SQPV were detected in Scotland causing great concern, as Scotland is home to approximately 75% of the remaining red squirrel population in Britain (McInnes *et al.*, 2009).

It has been suggested that while SQPV severely affects and kills red squirrels, infected grey squirrels carry the virus but do not become ill thus acting as reservoir host for the virus (Rushton *et. al.*, 2000; Tompkins *et. al.*, 2003; McInnes *et al.*, 2009). Recent research by Fiegna (2011) reported that grey squirrels infected with SQPV nevertheless presented skin lesions (i.e. oral skin and lips). Their results also confirmed that skin lesions in grey squirrels were less severe than those in infected red squirrels.

The apparent severity in the way the disease affects red squirrels suggests that most individuals are likely to die before they can spread it to other populations, which reinforces the assumption that the virus is spread by infected yet asymptomatic grey squirrels (Rushton *et. al.*, 2000).

Direct contact between greys and reds rarely occurs and a number of possible transmission routes have been suggested. These include: anal dragging, saliva or scent marks left on branches by the two squirrels' species. This constitutes part of their olfactory communicational behaviour (Gurnell, 1987, Rushton *et al.* 2000).

Feeders used to provide red squirrels with supplementary food can also help to spread the virus, as well as trapping or any management that can potentially attract both red and grey squirrels to the same focal points (Bruemmer *et al.*, 2010). A study by Atkin *et al.* (2010) suggested that fleas could potentially be a transmission vector for SQPV.

Since grey squirrels densities are higher in broadleaf woodlands, this habitat type would potentially host more grey squirrels and therefore increase the possibility of encounters and thus virus transmission (Rushton *et. al.*, 2000). There are also other considerations for managing conservation areas: increasing habitat connectivity may also increase the risk of virus transmission and habitat de-fragmentation, usually thought to be beneficial (i.e. to avoid isolation of populations), can be harmful in this context (Tompkins *et. al.*, 2003, Rushton *et. al.*, 2000).

In large, non-endangered species populations, diseases play a regulatory role (Rushton *et. al.*, 2000). However, in the case of the red squirrel in the UK, SQPV coupled with the negative effects of competition with greys described above is speeding up both red squirrel decline and its ecological replacement by the greys (Tompkins *et al.*., 2003; Rushton et al., 2006a). More in-depth reviews of SQPV can be found in Rushton *et. al.*, 2000; Tompkins *et. al.*, 2003 and McInnes *et al.*, 2009.

1.1.3 Woodland cover

Habitat loss and modification are among the most important reasons why species become endangered. In many countries of northern Europe, intensive management of forests has affected biodiversity in a negative way. As a consequence, species whose habitats are natural forests have largely declined (Manton *et. al.*, 2005).

In the UK, forests went from covering 75% of the land surface area in the post-glacial period to approximately 5% at the start of the 20th century (Watts *et. al.*, 2005).

The loss of woodland and the fragmentation of forests reduced the amount of available habitat and increased the isolation of populations. This had serious consequences for the country's biodiversity. Nowadays, 15% of the species listed in the UK Biodiversity Action Plan inhabit forests (Watts *et. al.*, 2005).

In the case of the red squirrel, populations throughout the country were particularly affected by the felling of tree species such as Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) and their replacement by sitka spruce (*Picea sitchensis*) for commercial reasons (i.e. timber production) during the first half of the 20th century (Mackinlay & Patterson, 2011).

In recent years, more biodiversity-friendly forest policies have been implemented. Nowadays, 11% of the UK is covered by forest (Watts *et al.*, 2005). In Scotland, woodland cover increased up to 17% by 2006 as part of a governmental strategy aiming to reach 25% woodland cover by the end of the century (Scottish Forest Strategy 2006). This increase in woodland cover is expected to help reverse the loss of biodiversity (Watts *et. al.*, 2005). However, priority species such as the red squirrel require targeted and informed habitat management for their conservation.

More information on current research on landscape ecology and biodiversity in the UK can be found in Watts *et al.* (2005) and Watts *et al.* (2007).

1.1.4 Predation

Predation is one of the factors which can potentially influence red squirrel numbers in the UK. Main predators of red squirrel are goshawk (*Accipiter gentiles*), buzzard (*Buteo buteo*) and the pine marten (*Martes martes*) (Halliwell, 1997). Other predators include the red fox (*Vulpes vulpes*) and cats (*Felis* sp); Bosch & Lurz, 2012).

Two studies investigated the predation of red squirrel by goshawk in Kielder Forest (Petty *et al.*, 2003) and the pine martens in Ross-shire (Halliwell, 1997). Pine martens may prey on squirrels if other small mammals are not available, but in general, red squirrels are only a small proportion of marten diet. Furthermore, pine marten would also prey on grey squirrels (Bosch & Lurz, 2012).

In terms of predation of red squirrel by buzzards, a study carried out in Moray, Scotland (and cited in Halliwell, 1997), stated that 22% of remains found at buzzard nests were red squirrels.

Researchers arrived to similar conclusions: predation in general seems unlikely to cause the extinction of the species (Halliwell, 1997; Petty *et al.*, 2003). Yet, given the low densities of red squirrel due to other factors discussed previously (i.e. competition with greys, squirrelpox virus, habitat degradation) predation is assumed to accelerate the decline of the species populations (Halliwell, 1997).

1.2 Red squirrel habitat suitability

In order to design and implement effective management strategies, it is first necessary to assess red squirrel habitat requirements. A number of studies have been carried out to better understand red squirrel preferences in the UK. A summary of the most relevant findings is provided in the following sections. The first section provides a review of red squirrel habitat modelling studies, while the second section summarises results from studies investigating the species' preferences based on red squirrel field surveys (i.e. live-trapping, radio tracking).

1.2.1 Modelling habitat suitability for red squirrel in the UK

A number of studies have used modelling approaches to assess red squirrel habitat suitability and investigate the species preferences in UK forests.

Lurz *et al.* (1995) used a general linear model (GLM) to predict the number of squirrels in different habitat types in Spadeadam Forest, England. Squirrel densities were estimated based on live-trapping for 27 sites over a period of 3 years (1992 to 1994). The size of each area ranged from 21 to 60ha. The GLM was used to assess the relationship between squirrel densities and three independent variables: woodland area; proportion of Norwary spruce (NS) and Lodgepole pine (*Pinus contorta*, LP) relative to sitka spruce (SS; proportion of NS and LP = (NS+LP)/SP) and presence/absence of Norway spruce. Their results suggest that red squirrel densities increase when woodland area increases. Furthermore, the number of squirrels also increased with the presence of Norway spruce and with a higher proportion of Norway spruce and Lodgepole pine relative to sitka spruce: keeping the proportion of Lodgepole pine constant, red squirrel density per ha ranged from 0.02 when all the spruce-area was planted with sitka spruce, to 1.95 when 80% of the spruce-area was planted with Norway spruce. These results highlight the low suitability of sitka spruce for red squirrel in the UK and the importance of mixed conifers composition for red squirrel conservation.

Commercial forests in the UK consist predominantly of compartments and sub-compartments (i.e. management units), where each sub-compartment is composed of a particular tree species (and age). In Thetford Forest, England, the size of each sub-compartment ranges from 1 to 40ha. Using a GIS approach, Gurnell *et al.* (2002) investigated the suitability of the forest by analysing the suitability of sub-compartments. Thetford Forest consists mainly of Scots pine and Corsican pine (*Pinus nigra*), 10% of broadleaves and 5 % of other conifers. Based on live-trapping and published information, they assessed red squirrel habitat preferences within the forest, and assigned 3 habitat suitability levels: low, medium and high, where medium and high suitability sub-compartments consisted of tree species of an age that could support medium to high density of squirrels respectively; and low suitability sub-compartments (i.e. felled sub-compartments or plantations too young to produce food) were assumed not to support resident populations of squirrels.

One scenario combined sub-compartments of medium to high suitability with different linking distances (0, 50, 100 and 200m) to estimate different sizes of total suitable area (i.e. suitable sub-compartments linked together) for the whole forest. Another scenario estimated total suitable area at 5 years intervals (from 1995 to 2015) keeping linking distance constant (100 m) and considering felling and restocking plans for the forest. Results from this study showed little or not differences in the total size of suitable area of the reserve when combined with the different linking distances. This is probably due to sub-compartments being proportionally too large relative to the linking distances. Linking distances between suitable patches are important as red squirrels would move across patches of low suitability, provided their size does not exceed their home range (approximately 3 to 20 ha in conifer forests; Bosh & Lurz, 2012). This indicates the need for more research in this area to identify realistic linking distances. When considering felling and restocking plans, total suitable area increased from 39% (of the total woodland area) in 1995 to 67% in 2015, suggesting that management plans for the forest would increase the suitability for red squirrel. However, the results also suggested that if sitka spruce was planted instead of Corsican pine, the total suitable area would drop to 24% in 2015. Habitat preferences in terms of species composition and age resulting from red squirrel live-trapping carried out in this project are summarized in the next section.

The effects of forest management on red squirrel population in Kidland Forest, UK (55° 25’ N; 2° 10’ W), were explored by Lurz *et al.* (2003). Kidland Forest is a red squirrel reserve dominated by sitka spruce, with small proportions of Lodgepole pine, Scots pine and Larch (*Larix*). At the time the study was carried out, no grey squirrels were present in the forest. However, plans to restore biodiversity in the forest included re-planting 15 ha of oak, which could encourage grey squirrel incursion. In order to model the effects of felling plans for the forest and potential grey squirrel incursion, Lurz *et al.* (2003) used a spatially explicit population dynamics model. The first component of the model worked on a GIS platform (GRASS) and incorporated stock map data, future planting, felling plans and seed crops patterns (based on tree species). The second component of the model used life-history data to model red and grey squirrel population dynamics and viability based on species composition, tree age, felling/restocking plans and seed production patterns. All forest compartments that contained trees mature enough to produce seeds were considered suitable habitat. To model the oak-planting scenario, it was assumed that a small population of 20 grey squirrels was already present in the forest. Dispersal was modelled once a year, and grey squirrels were allowed to disperse to compartments where reds were present. Results suggested that poor sitka spruce seed crops in combination with felling could potentially lead to the extinction of red squirrels in Kidland Forest by 2012. Furthermore, in a mature-oak scenario, grey squirrel population could potentially increase to an average of 80 individuals by 2050. These results illustrate the need to carefully assess management strategies and objectives, in particular in forests where red squirrel conservation is a priority. Furthermore, priorities for red squirrel conservation and management may have to be set at the landscape scale to accommodate different priorities and to reduce potential conflicts e.g. management of red squirrels and planting of ancient woodland sites with native oak species.

1.2.2 Red squirrel habitat preferences

While arboreal squirrels live on a variety of different types of food (buds, tree flowers, fungi, berries), tree seeds remain their main diet. Hence squirrel densities have been observed to vary annually along with variations in tree seed production (Gurnell, 1987; Lurz *et. al.*, 1995). Furthermore, squirrels are known to prefer seeds with a high nutrient content (Gurnell, 1987). Given that different tree species produce seeds with different nutrient content (Grönwall, 1982), tree species composition and age (i.e. trees mature enough to produce food) are important factors determining red squirrel habitat preferences (Lurz *et al.*, 1995).

Studies carried out elsewhere (i.e. Belgium, Sweden and Finland) showed a strong preference of red squirrels for pine and spruce seeds (Lurz *et al.*, 1995). This is supported by results from a number of studies carried out in the UK. Bryce *et. al.* (2005) investigated tree species preferred by red squirrel in two forests in the UK: Clocaenog Forest in North Wales and Craigvinean Forest in Perthshire, Scotland. In this study, red squirrels were observed to select Norway spruce, Scots pine, Douglas fir (*Pseudotsuga*) and larch over sitka spruce. This supports results from the modelling studies discussed above, where model outputs suggested that red squirrel population would increase if a proportion of sitka spruce was replaced by Norway spruce in Spadeadam Forest, England (Lurz *et al.*, 1995).

In terms of pine species, the study by Gurnell *et al.*, (2002) showed that red squirrels preferred Scots pine to Corsica pine in Thetford Forest, England.

Lurz *et al.* (1995) compiled data from previous studies that reported densities of red squirrel per ha for different tree species in Northern Europe (i.e. England, Scotland, Russia, Belgium and Sweden). Observed densities were based on studies which had assessed trees selected by squirrels using feeding transects and live-trapping sampling techniques. A summary of their results is provided below:

- Pure Scots pine stands support higher densities of red squirrels than any other pure conifer species (0.33 to 0.8 red sq/ha)
- Plantations of pure sitka spruce support very low red squirrel population densities (near 0 red squirrels/ha)
- The combination of sitka spruce (SS) with Norway spruce (NS) and/or Lodgepole pine (LP) considerably improves habitat quality and increases carrying capacity (e.g. 0.21 red sq/ha for SS+NS; 0.35 red sq/ha for SS+NS+LP).
- The highest red squirrel carrying capacity was observed with the combination of Scots pine + Corsican pine + larch (1.01 to 1.41 red sq/ha)

Scots pine is one of the tree species most preferred by red squirrels in the UK because they provide high nutrient content seeds and good cover (Lurz *et al.*, 1995; Gurnell *et al.*, 2002). On the other hand, sitka spruce is less suitable for red squirrel as it offers a less reliable (i.e. less frequent and abundant) food supply (Gurnell & Pepper, 1991). It is important to highlight that most conifer species will produce a mast crop (i.e. large cone crop) every 3 to 5 years, usually followed by a poor cone crop year. This cycle is different for different tree species, and therefore, the number of tree species present in a forest is important to ensure a continuous food supply for red squirrels (Gurnell, 1987).

The age at which trees start and stop producing food is a crucial factor when considering habitat suitability for squirrels. The study carried out by Gurnell *et al.* (2002) in Thetford Forest showed that red squirrels preferred Scot pine younger than 49 year-old and Corsican pine between 25 and 34 year-old. Squirrels also preferred Scots pine to Corsican pine as the former has its first good seed crop 10 to 15 years earlier than Corsican pine. Furthermore, there is evidence of high numbers of red squirrel being present in the reserve between 1950 and 1960 when Scots pine planted in Thetford forest reached this favourable coning age (Gurnell *et. al.*, 2002).

It can therefore be concluded that a range of conifer species and tree ages is necessary to ensure food supply for red squirrel.

1.3 Forest management

The main reason for the continuous decline of the red squirrel in the UK is the introduction of the grey squirrel. However, controlling grey squirrel might not be feasible in the long term and therefore conserving red squirrel might strongly depend on managing forests in a way that favours reds without encouraging greys (Gurnell *et al.*, 2002).

Based on the factors that currently threaten red squirrel survival in the UK (i.e. grey squirrel, disease) and on the research carried out in the UK to investigate red squirrel preferences in terms of species composition and age (discussed earlier in this chapter) several management recommendations have been suggested by a number of researchers, which are summarized below:

- The main driver for squirrel populations is food availability so any habitat management intended to benefit habitat suitability for red squirrels should contemplate diversification of conifer species and tree ages that would ensure continuous supply of food for red squirrels (Lurz *et al.*, 1995; Gurnell *et al.*, 2002; Bryce *et. al.*, 2005).

- Large conifer forests (e.g. > 2000 ha) may represent an advantage for red squirrels and may help to reduce competition for food with greys. (Lurz *et al.*, 1995; Gurnell *et al.*, 2002; Bryce *et. al.*, 2005).

- In the UK, grey squirrels exhibit a strong preference for acorns. Thus, conifer forests with some oaks around are particularly vulnerable to grey squirrel invasion. The inclusion of oaks needs to be carefully considered and, if possible, avoided in forests managed for red squirrel conservation (Lurz *et. al.*, 1995).

- The proportion of large-seeded broadleaves (not only oak but also chestnut, beech (*Fagus*) and hazel) should be minimised in mainland forests managed for red squirrel conservation. Broadleaves scattered throughout a woodland might be more detrimental (i.e. would encourage grey squirrels throughout the forest) than an isolated cluster of these trees. (Bryce *et. al.*, 2005).

- A buffer (1 to 3 km) might help reduce grey squirrel incursion. Small-seeded broadleaves could be planted in those buffer areas (Bryce *et. al.*, 2005).

- Native Scots pine seems to support higher densities of red squirrels than Lodgepole pine and therefore it should be given preference (Lurz *et. al.*, 1995). Furthermore, Scots pine produce cones more regularly than Norway spruce. Thus, some stands of Scots pine combined with Norway spruce would considerably improve habitat suitability for red squirrel by ensuring food supply (Bryce *et. al.*, 2005).

- The presence of Norway spruce in stands of sitka spruce would be beneficial for red squirrels as it considerably increases food supply (Lurz *et al.*, 1995; Bryce *et. al.*, 2005).

- Current plans to expand and restore native woodlands in the UK need special consideration. Linking existing forests may be beneficial for red squirrel as it would allow dispersal and increase food availability. However, habitat management to reduce red squirrel mortality due to squirrelpox infection needs to be also contemplated. Keeping red squirrel populations in a relatively fragmented state would help avoid virus transmission between individuals of the same species, while maintaining red squirrel away from the greys would help to avoid both invasions by greys and virus transmission. Both these cases lead to the conclusion that developing forest networks need to be carefully considered (Poulsom *et. al.*, 2005).

- Plans to restore native broadleaves need careful consideration, particularly in areas designed for red squirrel conservation (Gurnell & Pepper 1993; Reynolds & Bentley, 2001).

- Regarding felling and thinning operations, the study carried out in Clocaenog Forest shows that squirrels leave their home ranges when thinning operations are taking place but they stay nearby (200 m) and return afterwards. However, since it is also known that good seed crops are important for red squirrels, avoiding felling in good seed years would be beneficial (Bryce *et. al.*, 2005).

- In order to maximise seed production, aspects such as fringe planting and woodland irregular shapes to increase periphery need also be considered (Gurnell, 1987; Pepper & Paterson, 2001)

1.4 Red squirrels strongholds and forest structure

As part of the Scottish Government strategy for red squirrel conservation, 18 selected sites or strongholds have been selected. The main aim of these strongholds is to provide a refuge for long-term conservation of red squirrels in case grey squirrels continue to spread. These strongholds were identified using Geographic Information System (GIS), and the criteria used to select these sites were mainly based on the absence/presence of red and grey squirrel in or near the site, the proportion of broadleaves found and an assessment of conflict with other conservation objectives. For an in-depth description of the selection process, the selection criteria, the list of proposed strongholds and maps refer to *Red squirrel strongholds* (Forestry Commission, 2009).

Habitat management for red squirrel conservation in these woodlands will be a priority and will require an informed strategy. The importance of tree species composition and food availability for squirrel abundance has been discussed early in this chapter. However, a suitable place where a species can live should not only entail food availability or the distribution of suitable nesting sites but it should also present reduced risks of predation and limited competition (Gurnell, 1987; Gurnell *et al.*, 2002).

With respect to the red squirrel in the UK, a study carried out by Gurnell *et al.* (2002) in Thetford Forest, England, showed that old stands of Scots pine that had been subjected to intensive thinning were avoided by red squirrels despite the presence of food. After late or final thinning is carried out in old stands, gaps among trees become too large for the squirrels to move (Gurnell *et al.,* 2002). This suggests that even when food is present, other factors shape red squirrel preferences in terms of habitat and that further research is necessary to understand and quantify the relationship between red squirrel habitat use and forest structural factors such as canopy connectivity, tree densities and height heterogeneity. The relationship between vegetation structure and birds or small mammal distribution has been investigated and a review of relevant literature is provided in Chapter 2. However, evaluating and monitoring vegetation structure at the stand level is expensive and time consuming. This highlights the need for research into methods that can extract and utilise structural data to derive habitat suitability information over large forest areas.

1.5 Remote sensing for biodiversity and habitat mapping

In recent years, there has been an increasing need for mapping habitat and monitoring wildlife over large areas. Traditional methods of field data collection are expensive and time consuming, and therefore, advances in technology such as Geographical Information Systems (GIS) and remote sensing have become widely used (McClain *et. al.*, 2000). Both remote sensing and analytical GIS have proven to be powerful tools for habitat mapping when time and budgets are limited (Weiers *et. al.*, 2004).

The list of studies that have used remotely sensed data to assess biodiversity and/or to map habitat quality is long and it would be impossible to review all of them here. Instead, a summary of the main and most used approaches is provided, and their advantages and disadvantages are discussed. Table 1.1 provides some additional examples.

Remotely sensed data have mainly been used to assess biodiversity and species distribution by creating land-cover maps which represent species habitats (i.e. forests, grasslands, wetlands). The combination of species habitat requirement and land-cover maps allows for the assessment of, for example, potential species presence or richness (Turner *et al.*, 2003).

Visual interpretation of aerial photographs is probably one of the first remote sensing methods used to assess species habitat. When performed by highly skilled interpreters, visual interpretation of aerial photograph is very valuable and allows the generation of accurate land-cover/land-use maps, detection of gaps, assessment of habitat fragmentation and estimation of canopy cover. However, the manual nature of the method makes it highly time consuming and only feasible when applied to small areas (McDermid *et al.*, 2005).

Multispectral satellite remote sensing such as LANDSAT TM or ETM + (6/7 spectral bands, 30m spatial resolution, see Table 1.1) provided an alternative to map land-cover over large areas. Land-cover classification has been the object of a great deal of research and several classification techniques have been developed. An in-depth review of image classification can be found in Mather, 2004 or Lillesand, Kiefer & Chipman, 2004. Satellite imagery classification provides land-cover maps that can be integrated into a GIS along with other ancillary data (i.e. topography) to assess, for example, habitat suitability for a particular species (McClain and Porter, 2000). Gaps and habitat fragmentation can also be detected as long as they cover several pixels (McDermid *et al.*, 2005).Although widely used and providing relatively accurate and easy to understand outputs, land-cover maps generated from multispectral LANDSAT TM/ETM+ data can be too coarse, lack detail or simply be unable to discriminate classes (i.e. vegetation types) due to the limited spatial or spectral resolution of multispectral data (McDermid *et al.*, 2005).

Hyperspectral remote sensing is a relatively new technology that can improve land-cover classification and therefore species habitat assessment. Satellite hyperspectral detects reflected radiation across a continuous spectrum usually covering a minimum of 100 spectral bands (Turner *et al.*, 2003). This fine spectral resolution allows for finer discrimination of land-cover types, in particular those related with vegetation (i.e. tree species) improving in this way the assessment of the relationship between species and habitat type (Turner *et al.*, 2003). However, hyperspectral data can be expensive and requires expertise to perform the pre-processing of the data, in particular to remove atmospheric interference.

On the other hand, high spatial resolution remotely sensed data, such as IKONOS or QuickBird, typically provide 4-band multispectral imagery with a spatial resolution of approximately 2-3m, and a panchromatic band with a spatial resolution of around 1 m (see Table 1.1). These data allow the identification of individual features, for example trees (Gougeon and Leckie, 2006). Although there is still a need for more research in this subject, high spatial resolution data also allows for direct detection and monitoring of species such as large marine mammals (i.e. whales) in Roatan Island, Honduras (Abileah, 2001). Due to a limited spectral resolution, high spatial resolution data offers little advantages in terms of land-cover mapping, but can improve habitat mapping by, for example, providing accurate delineation of individual trees, gaps and canopy cover (Turner *et al.*, 2003).

Data fusion and synergistic use of remote sensing data involve the combination of multi-source remote sensing data. This provides an opportunity to complement data with different characteristics and obtain more reliable results (Wang *et al.*, 2009). A good example of data fusion would be the combination of data from hyperspectral sensors with high spatial resolution data, which would allow for more detailed description –in terms of both spectral and spatial resolution- of the area being observed.

It is important to highlight that in all cases remotely sensed data should be validated against field data to assess its accuracy (McDermid *et al.*, 2005).

To the author's knowledge, no peer-reviewed studies have used -or acknowledged the use of- remotely sensed data to assist habitat quality assessment for red squirrel in the UK. In most studies that have assessed or modelled habitat suitability for red squirrel, land cover information and tree species composition have been obtained from the National Inventory of Woodlands and Trees (NIWT; e.g. Poulsom *et al.*, 2005) and forest stock maps (e.g. Lurz *et al.,* 1995; Gurnell *et al.*, 2002).

Two studies by postgraduate students at the University of Edinburgh have used remote sensing to map aspects of red squirrel habitat quality. Cristina García (unpublished work, 2006) used high spatial resolution data (QuickBird imagery) to map tree species composition at Kielder Forest, England. Tree species maps were incorporated into a GIS system to identify suitable habitat for red squirrel based solely on tree species composition and age (extracted from forest stock maps); while Xavier de Lamo (unpublished work, 2010) used medium-spatial resolution multispectral data (IRS-P6, 4 spectral bands, 23 m spatial resolution) to map canopy closure in Aberfoyle Forest, Scotland, as a potential predictor of red squirrel presence. A strong correlation (r_s= 0.72) was found between field measured canopy closure and Normalised Difference Vegetation Index (NDVI) which illustrates the potential of remote sensing to extract one forest parameter (canopy closure) potentially related to red squirrel habitat preferences. Results from these studies are not conclusive and therefore they only provide an example of potential uses of remote sensing to assist red squirrel habitat management

One limitation that all passive (i.e. optical) remote sensing data have in common is the incapability to successfully characterize and describe vertical forest structure. Active remote sensing, in particular LiDAR, can be used to directly measure structural characteristics of forest stands such as canopy cover, canopy height and height variability (Bradbury *et. al.*, 2005; Turner *et al.*, 2003).

This section has provided an overview of the most common applications of optical remote sensing to habitat suitability mapping and biodiversity assessment. More in depth reviews can be found in Turner *et al.*, 2003; McDermid *et al.*, 2005; Wang *et* *al.*, 2009 and Singh *et al.*, 2010. Furthermore, a description of LiDAR remote sensing and a detailed review of its use for species habitat mapping can be found in Chapters 3 and Chapter 4 respectively.

Table 1.1: Literature examples showing some of the applications of remote sensing to habitat mapping

Application	Sensor (data type)	Resolution (spectral/spatial)	Species	Reference
Land-cover, visual interpretation	Aerial photograph	1:10000	Iberian lynx (*Lynx pardinus*)	Palma *et al.*., 1999
Land-cover classification	LANDSAT TM & ETM+ (passive)	6 spectral bands 0.45 – 2.35 µm/ 30m Panchromatic 0.52-0.9 µm/15 m	Giant panda (*Ailuropoda melanoleuca)*	Jian *et al.*, 2011
Land-cover classification, multi-temporal (change detection)	QuickBird (passive)	4 spectral bands 0.45-0.90 µm/ 2.6 – 2.8m Panchromatic 0.445-0.90 µm/ 0.6 -0.7 m	Littoral vegetation	Heblinski, *et al.*.; 2011
Individual items detection (data fusion)	Ikonos (passive)	4 spectral bands 0.445 - 0.853 µm/ 4m Panchromatic 0.45–0.90 µm/ 0.8m	Marine mammals	Abileah, 2001
Tree species classification	ATM (passive)	11 spectral bands 0.42 - 13 µm / 2m	Broadleaves, temperate forest	Hill *et al.*., 2010
Tree species classification/ synergistic approach	QuickBird (passive) & LiDAR (active)	-----	Mixed deciduous/conifer forest	Ke *et al.*., 2010

1.6 Thesis aims and scope

This thesis presents a multi-disciplinary approach which aims to address two critical gaps in understanding red squirrel habitat suitability in the UK. First, the thesis investigates the impact of forest structure on red squirrel habitat use. Second, it assesses the potential of LiDAR remote sensing as a key management tool for habitat assessment and mapping. The study is based on two forests located in Scotland: Abernethy and Aberfoyle Forests, and focuses on Scots pine.

The key aims of this thesis are:

- To assess and quantify the relationship between field measured forest structural parameters and habitat use by red squirrels

- To evaluate the importance of considering forest structure when managing forests for red squirrel conservation
- To examine the potential for using LiDAR remote sensing to map habitat suitability for red squirrels based on forest structure
- To provide recommendations both in terms of red squirrel management and for the use of LiDAR in this context

To achieve these aims, the following objectives will be addressed:

- To collect field data on forest structure and squirrel feeding activity at two study areas: Abernethy and Aberfoyle Forest
- To develop statistical relationships between key stand structural variables and squirrel feeding behaviour for Scots pine
- To extract forest structural parameters that relate to red squirrel habitat suitability from LiDAR data and assess their accuracy
- To extrapolate the analysis using LiDAR derived explanatory variables and generate habitat suitability maps, and finally
- To assess the population viability and probability of extinction of red squirrel when forest structure parameters are considered

By achieving these aims, this thesis contributes new underpinning knowledge which supports an integral approach to red squirrel management that considers forest structure along with other known habitat requirements, as reviewed in this thesis.

1.7 Thesis structure

All chapters in this thesis are intended for publication (Chapter 2 is already published). As a result, some information may be repeated between chapters. A list of literature cited throughout all chapters is provided at the end of the thesis in a single reference section.

Chapter 1 provides an introduction to red squirrel conservation in the UK. It provides an overview of the research that has been carried out regarding red squirrel conservation with an emphasis on those studies that led to the current management strategy in forests designated as red squirrel strongholds in Scotland. An overview of the main approaches used to assess habitat mapping using optical remote sensing is also provided.

Chapter 2 provides a review of previous research on the importance of forest structure for animal species (i.e. birds and small mammals) including arboreal squirrels. A description of the two study areas is also provided as well as detailed information on field data collection and statistical analyses. The development of the model that relates forest structure (i.e. canopy cover, number of trees and tree height) to red squirrel feeding behaviour is explained. Results are presented and discussed and management implications identified

Chapter 3 provides an introduction to LiDAR remote sensing and a review of literature relevant to the retrieval of forest structural parameters from LiDAR data. The methodology used to retrieve tree height, canopy cover and number of trees is described. Accuracy assessment is performed and discussed.

Chapter 4 provides a review of the use of LiDAR remote sensing for habitat mapping. The methodology used to implement the statistical model (developed in Chapter 2) in the two study areas and to generate habitat suitability maps is described in detail. Accuracy assessment is performed by comparing LiDAR-based model predictions with field-based model predictions. Results are discussed as well as implications for management.

Chapter 5 integrates the findings from the previous Chapters in a population viability analysis (PVA). LiDAR derived habitat suitability data are use to refine the estimation of carrying capacity (K) in Abernethy Forest. This K in turn is used as an input in PVA. Population size and probability of extinction are projected and compared to a non-LiDAR scenario. Implications for stronghold habitat management are discussed.

Chapter 6 summarises the findings of this research and discusses the limitations of the approach. Further research needs and potential applications beyond the scope of this thesis are also highlighted. Overall conclusions and key recommendations are provided.

CHAPTER 2

The impact of forest-stand structure on red squirrel habitat use

---

The native Eurasian red squirrel is considered endangered in the UK and under strict legal protection. Long term habitat management is a key goal of the UK conservation strategy. Current selection criteria for reserves and subsequent management mainly consider species composition and food availability. However, there exists a critical gap in understanding and quantifying the relationship between squirrel abundance, their habitat use and forest structural factors. This is partly a result of limited availability of structural data along with cost-efficient data collection methods. We investigated the relationship between structural characteristics and squirrel feeding activity in Scots pine. Field data were collected from two study areas: Abernethy and Aberfoyle Forest. Canopy closure, diameter at breast height (DBH), tree height, and number of trees were measured in 52 plots. Abundance of squirrel feeding signs was used as an index of habitat use. We used a GLM to model the abundance of cones stripped by squirrels in relation to field collected stand structural variables. Stand structural characteristics are significant predictors of feeding sign presence. Canopy closure and number of trees per plot explain 43% of the variation in abundance of stripped cones. Our findings highlight the need to consider stand structure in effective management for red squirrels.

2.1 Introduction

The Eurasian red squirrel (*Sciurus vulgaris* L., hereafter “red squirrel”) is the only squirrel species native to the UK. While previously widespread over England, Scotland and Wales (Shorten 1953; Gurnell 1987), the population of red squirrels has declined significantly as a result of the introduction and spread of the Eastern gray squirrel (*Sciurus carolinensis* G., hereafter “grey squirrel”; Gurnell *et al,* 2004). Today, the red squirrel is considered endangered, is listed in the UK Biodiversity Action Plan, and benefits from legal protection (Schedules 5 and 6 of the Wildlife and Countryside Act 1981, Nature Conservation (Scotland) Act 2004; and WANE Act 2011). Long-term management of red squirrel habitats is now a key goal of the UK Strategy for Red Squirrel Conservation and the future of the species will depend largely on the careful management of suitable reserves or strongholds. The selection and management of these strongholds require an informed and strategic selection of tree species composition and forest structural characteristics (Gurnell and Pepper 1993; Pepper and Patterson, 2001; Parrott, *et al.* 2009).

The relationship between spatial heterogeneity, species diversity and species abundance remains a fundamental question in ecology. Many studies have investigated, for instance, the effect of microhabitat variables such as vegetation composition, density and structure, on avian habitat selection (Carrascal and Telleria 1988; Goetz, *et al.* 2010; Lesak *et al.* 2011). Findings support the hypothesis that structural characteristics of the environment are determinants of the distribution and density of birds. Structural characteristics related to the existence of understory vegetation also significantly influence habitat selection: for some bird species, since understory vegetation provides essential nesting sites and a protection from predators. The importance of forest structure is not limited to avian fauna and extends to mammalian species. Sullivan *et al.* (2009), for example, investigated the impact of structure in Lodgepole pine (*Pinus contorta* Douglas) plantations on abundance and diversity of forest-floor small mammals. The results showed that pre-commercial thinning and fertilization of young (20-25years) forest stands increased abundance, species richness and diversity of small mammals to those levels found in mature and old-growth forests. Milazzo *et al.*, (2003) investigated the habitat preferences of the Fat dormouse (*Glis glis italicus*) in Sicily, Italy and demonstrated the species' preference for deciduous woodlands with trees taller than12 m and dense understory. Edelman *et al.* (2009) investigated habitat preferences of the invasive Abert's squirrel (*Sciurus aberti* Woodhouse) and the native Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis* Allen) in Piñaleno Mountains, Arizona. The native squirrel preferred higher canopy closure and tree density compared to the invasive Abert squirrel which tended to nest in more open forests. However, knowledge of squirrel preferences for forest structural characteristics is limited. A few studies suggest that forest structural characteristics play an important role in habitat selection. In a study conducted in the Rocky Mountains (USA), McKinney and Fiedler (2010) found that arboreal squirrels tend to prefer mature mixed conifer habitats with tall closed canopies. Nelson *et al.* (2005) also highlighted the importance of forest structural parameters such as tree height, canopy closure and understory vegetation for Delmarva fox squirrel (*Sciurus niger cinereus* L) in

Maryland’s Eastern Shore, USA. They found that Delmarva fox squirrels prefer dense forest with closed canopies (canopy closure > 80%), average canopy height greater than 30 m, and open understories. Arboreal squirrels also select stands with tree species that produce high energy content cones (McKinney and Fiedler 2010).

In the particular case of the red squirrel in the UK, the importance of tree species composition and food availability for squirrel abundance has been extensively demonstrated (e.g. Gurnell 1983, Lurz *et al.* 2000). However, a suitable place where a species can live should not only entail food availability or the distribution of suitable nesting sites but it should also present reduced risks of predation and limited competition. Studies utilising radio-tracking approaches suggest that red squirrels tend to avoid thinned open stands of trees, even though these stands are located close to the squirrels’ observed areas of activity and contained seed food (Gurnell *et al,*. 2002). This suggests the need for further understanding and quantifying of the relationship between red squirrel habitat use and forest structural factors such as canopy connectivity, tree densities and height heterogeneity. In this paper, we attempt to address this knowledge gap by empirically exploring the importance of stand structure on red squirrel habitat selection in a semi-natural Scots pine forest (Abernethy) and a Scots pine plantation (Aberfoyle). We use General Linear Modelling to relate key stand structural variables to squirrel feeding behaviour and discuss the implications of this research for the selection and management of strongholds in the UK.

2.2 Methodology

2.2.1 Study area

Field work was carried out at Abernethy Forest in October 2009 and at Aberfoyle in May 2010. Abernethy Forest (57° 15’ N, 3° 40’ W, Figure 2.1) is owned and managed by the Royal Society for the Protection of Birds (RSPB) and lies between 200 m and 500 m altitude with a total area of 28 km^2 (Summers and Proctor 1999). Two thirds of the forest (19 km^2) is native forest and one third is plantation (Figure 2.1). The dominant tree species is Scots pine (*Pinus sylvestris).* A few broadleaves, mainly birch (*Betula pendula*), can also be found. Ground vegetation is mainly composed of heather (*Calluna vulgaris),* bearberry (*Arctostaphylos uva-ursi),* blueberry *(Vaccinium corymbosum*), bracken (*Pteridium aquilinum*), a range of mosses (*Sphagnum* sp.) and there is an extensive shrub layer of juniper (*Juniperus communis).* Abernethy Forest hosts large populations of birds, including Capercaillie (*Tetrao urogallus)*, Crested tits (*Lophophanes cristatus*), Scottish Crossbill (*Loxia scotica*) and in the summer Ospreys (*Pandion haliaetus*). The forest is also home to mammalian species such as red deer (*Cervus elaphus)* and pine marten (*Martes martes).* The presence of red squirrels (*Sciurus vulgaris*) in the area has previously been confirmed by Summers and Proctor (1999) who investigated foraging competition levels between red squirrels and crossbills.

Aberfoyle (56° 10” N, 4° 22” W) is managed by Forestry Commission Scotland. The forest is part of the Loch Lomond and Trossachs National Park, located in the west of Scotland, approximately 25 km North-West of Glasgow (Figure 2.1). Total forest area estimated from Forestry Commission stock maps is slightly less than 12000 ha. Tree species present in the forest are predominantly conifers and include Scots pine, sitka spruce (*Picea sitchensis*), Lodgepole pine (*Pinus contorta*) and Norway spruce (*Picea abies*). A number of semi-natural stands consisting of oak (*Quercus petraea*), birch, alder (*Alnus glutinosa*) and ash (*Fraxinus excelsior*) are also present. Scots pine covers 944 ha of the total forest area (McInerney *et. al*., 2010). The terrain varies in altitude from 50 to 700. Ground vegetation consists mainly of heather, bearberry, blueberry, bracken, a range of mosses. In terms of fauna, bird species such as sparrowhawk (*Accipiter nisus*), hen harrier (*Circus cyaneus*), red kite (*Milvus milvus*) and golden eagle (*Aquila chrysaetos*) are common in the area. Among the most common mammalian species that can be found in this National Park are otter

(*Lutra lutra)*, red fox (*Vulpes vulpes*), badger (*Meles meles*) hedgehog (*Erinaceus europaeus*), roe deer (*Capreolus capreolus*) and red deer. Both red and grey squirrels have been present, although recent grey squirrel sightings have been localised and sporadic and none were near the study sites (K. Freeman, FC Officer, pers. comm.). Red squirrels were seen by the authors in both study areas and on several occasions during this study.

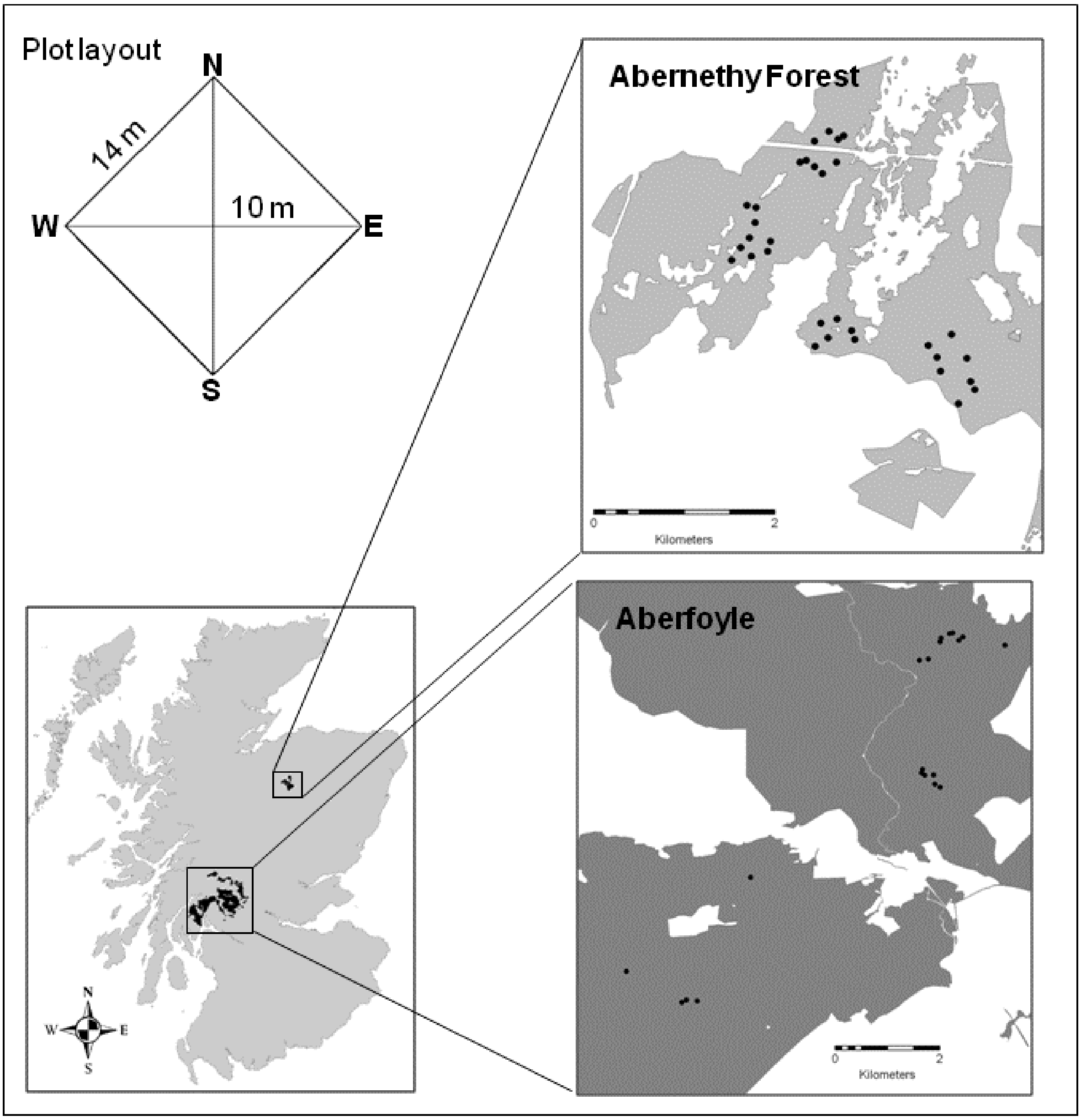


Figure 2.1: Study areas and sample plots: Abernethy Forest and Aberfoyle, Scotland. Black dots represent the location of the sample plots. Upper left: diagram showing the design of the plots in the field. Map source: Edina (University of Edinburgh, 2010)

2.2.2 Stands selection and sampling strategy

Sample areas at Aberfoyle and Abernethy were selected using the Forestry Commission stockmap data as well as available digital forest data respectively (ArcMap GIS; RSPB 2009). The stands were chosen to be representative of available mature seed-producing habitat types for red squirrels: namely semi natural woodlands, plantations, and a mix of both. We employed a stratified random sampling approach. Stands were stratified by habitat type within which plots were randomly selected. At both sites, 14 m x 14 m plots were sampled: a total of 20 in Aberfoyle and 32 in Abernethy (Figure 2.1). Plots were pre-selected, mapped and located on the ground using a compass and GPS (Garmin GPS map 60CSx). Within each plot, we recorded diameter at breast height (DBH), canopy closure using a spherical densiometer (Robert E. Lemmon Model C), and tree height using a Silva ClinoMaster Clinometer/Heightmeter (CM-1015-2025 A). Canopy closure measurements were made at the central point and at each of the 4 corners of the plot, and subsequently averaged. DBH was recorded for all trees per plot. For tree height, all trees were measured. In plots where the number of trees was greater than 30, the height of the four trees with largest DBHs was measured and recorded.

Squirrel presence and local abundance was assessed using cone transect lines (Gurnell *et al.* 2009). Our interest was in plot-level squirrel activity. We therefore used feeding remains (cones stripped by squirrels) within each plot as an index of micro-habitat selection by red squirrel. Grey squirrels have not yet spread to Abernethy (Lurz & Cole, 2010, pp. 49). In Aberfoyle, although both red and grey squirrels are present in the area, recent grey squirrel sightings have been localised and sporadic and none were near the study sites (K. Freeman, FC Officer, pers. comm.). Given the dense ground vegetation found in the plots and the semi-natural arrangement of trees (absence of parallel plantation structure), a quadrat-based approach (2 m x 2 m) was employed (Wauters *et al.* 2004). A total of 200 and 320 quadrats were sampled in Aberfoyle and Abernethy, respectively. This represents a standard effort of 10 quadrats per plot. We counted both eaten and un-eaten cones. All sampled plots contained a cone crop. This was important as the absence of food would clearly bias the adopted approach.

2.2.3 Data analysis

Abernethy Forest

In an early stage of the project, a preliminary analysis was carried out considering Abernethy Forest data only. A General Linear Model (GLM) was used to relate the number of stripped cones (dependent variable, count data) to the stand structural variables measured in the field, namely: total number of trees; mean tree height (m); mean DBH (m); and mean canopy closure (%). However, the use of one study site only does not allow for a generalisation of the results. Thus, the final analysis was carried out considering both Abernethy and Aberfoyle data together as described in the following section

Abernethy and Aberfoyle Forest

We used a General Linear Modelling approach and modelled the response of the dependent variable (cones stripped by squirrel) as a combination of three independent variables collected in the field: canopy closure, tree density and tree height. Linear models are commonly used to explain the relationship between a single normally distributed dependent variable Y, and one or more independent variables (Faraway, 2005). Generalized linear models (GLM) are an extension of linear regression commonly used to model dependent variables that are not continue or normally distributed (Agresti, 2002).

The number of stripped cones is a count (a positive integer). Poisson regression is usually used with count data (Zuur *et al.*, 2007). If the variance is greater than the mean, the data are considered over dispersed. In most real ecological applications, this assumption is violated (Faraway, 2006). In such instance, a GLM model with a quasi-Poisson error structure should be used. We tested our field data and found them to be over dispersed. Therefore, we used a general linear model with a quasi-Poisson error structure for our analysis. All analyses were carried out in the software package ‘R’ version 2.11.1.

We also tested our data for collinearity. If the relationship between the response variable and the covariates is not very strong (usually the case in ecological studies) even a small amount of collinearity might affect the results of the regression (Zuur *et al.*, 2012, in preparation). Furthermore, the general recommendation is to have at least 15-25 observations per covariate (Zuur *et al.*, 2012, in preparation). The current number of observations (i.e. 52) is on the low side for four covariates but is sufficient for three. Thus, in addition to testing for collinearity, we also assessed the relationship between the covariates and the response variable in order to decide which variables could be disregarded (Zuur *et al.*, 2012, in preparation).

Finally, the correlation between total cone crop per plot (i.e. whole cones plus cones stripped by squirrels) and stripped cones was also performed in order to assess the relationship between food abundance and habitat use by red squirrel,

2.3 Results

In Abernethy, the total number of trees per plot ranged from 3 to 74 (average 19.2 +/- 15.4 95% CI); mean DBH, from 12 cm to 79 cm (average 26.9 +/- 8.5 95% CI); mean percentage canopy closure, from 61% to 93% (average 88.1 +/- 5.5 95% CI) and mean tree height from 7m to 26m (average 17.6 +/- 3.1 95% CI). In Aberfoyle, total number of trees ranged from 7 to 26 (average 16.2 +/- 7.5 95% CI); mean percentage canopy closure from 54% to 94% (average 85.4 +/- 7.7 95% CI); mean DBH from 16cm to 37cm (average 29.3 +/- 7.5 95% CI) and mean tree height from 15m to 24m (average 20.5 +/- 2.3 95% CI). Table 2.1 presents values for both sites, including the total number of trees, mean DBH, mean tree height, and mean percentage canopy closure per plot. For all these variables, we also provide averages, standard deviations and 95% confidence interval of the mean for all plots combined. In Table 2.1 we also present the number of stripped cones per plot. Total cone crop ranged from 14 to 293 (average= 98.4; SD =57.7) at Abernethy and 21 to 222 (average = 83.7; SD=56.7) at Aberfoyle.

Table 2.1 Total cone crop, Total number of stripped cones, Total number of trees, Average DBH, Average tree height, and % canopy closure per plot for both Abernethy Forest (Abern) and Aberfoyle (Aberf), Scotland.

Plot number	Total cone crop	Total number of stripped cones	Total number of trees	Average DBH (cm)	Average tree height (m)	Canopy Closure (%)
Abern1	121	61	32	22.5	20.4	91.3
Abern2	81	4	4	26.7	15.2	61.5
Abern3	119	15	34	16.9	16.0	91.4
Abern4	119	9	22	22.9	22.4	92.0
Abern5	99	42	22	18.1	19.5	93.2
Abern6	36	4	21	23.3	23.1	93.5
Abern7	64	12	19	21.9	21.1	88.5
Abern8	108	27	15	25.8	18.8	88.0
Abern9	37	0	12	23.3	19.2	89.8
Abern10	41	4	9	12.1	6.4	73.3
Abern11	293	91	5	78.6	25.5	94.8
Abern12	100	20	12	20.2	12.0	94.2
Abern13	135	5	15	18.6	9.1	76.8
Abern14	166	14	42	15.1	8.8	77.2
Abern15	113	35	74	14.7	17.9	91.3
Abern16	25	11	23	15.4	15.9	92.2
Abern17	152	47	67	14.1	13.8	91.8
Abern18	90	17	33	17.1	14.6	88.6
Abern19	143	16	12	34.4	14.0	92.4
Abern20	88	0	7	39.5	16.2	85.2
Abern21	87	44	14	37.2	20.9	92.9
Abern22	183	18	23	23.4	15.5	91.5
Abern23	113	9	13	27.1	17.0	90.7
Abern24	58	16	7	32.3	19.2	89.0
Abern25	193	60	11	25.8	20.0	93.5
Abern26	32	3	7	28.8	15.9	91.9
Abern27	64	5	10	34.9	20.9	90.7
Abern28	57	5	11	30.8	21.6	90.4
Abern29	14	2	3	41.5	20.4	69.9
Abern30	62	32	11	33.0	18.3	92.6
Abern31	85	55	15	31.5	24.5	91.4
Abern32	72	3	11	34.0	19.1	89.2
Aberf33	35	18	14	35.3	23.0	87.6
Aberf34	21	0	13	27.0	16.1	54.4
Aberf35	80	11	7	35.1	22.3	93.1
Aberf36	76	0	22	22.9	15.6	90.2
Aberf37	49	6	18	32.5	21.0	93.6
Aberf38	41	4	18	27.4	19.2	93.1
Aberf39	222	0	9	35.2	24.1	84.4
Aberf40	93	48	11	37.3	22.7	86.5
Aberf41	139	7	16	26.2	21.3	91.1
Aberf42	88	2	11	35.1	21.7	80.7
Aberf43	183	3	12	35.3	21.5	83.3
Aberf44	68	2	8	34.7	21.9	77.3
Aberf45	118	21	9	32.6	21.7	80.0
Aberf46	57	22	9	32.2	23.3	88.0
Aberf47	176	4	12	35.5	22.8	81.1
Aberf48	27	1	28	21.7	18.5	93.8
Aberf49	38	3	30	18.6	16.2	84.8
Aberf50	38	25	30	18.4	19.5	87.2
Aberf51	78	57	36	16.8	17.1	89.6
Aberf52	46	12	11	26.0	21.4	87.8
Mean	**92.8**	**17.9**	**18.1**	**27.8**	**18.7**	**87.1**
SD	**57.2**	**20.4**	**13.9**	**10.5**	**4.1**	**8.2**
95% CI	**31.9** **(76.8-108.7)**	**11.1** **(12.4, 23.5)**	**7.5** **(14.3, 21.8)**	**5.8** **(24.9, 30.7)**	**2.2** **(17.6, 19.8)**	**4.5** **(84.8, 89.3)**

Abernethy Forest

We checked the data for collinearity and we found that mean tree height and mean DBH were significantly correlated (r_s= 0.55, n=32, $p \leq 0.001$). Correlations between mean tree height/mean DBH and the number of stripped cones were also assessed and found to be very similar (r_s = 0.37 and 0.38; $p < 0.04$ and 0.03 respectively, n =32). Between tree height and DBH, only the latter was used in the General Lineal Model (GLM) analysis.

The results of the GLM analysis indicate that mean DBH, mean canopy cover and total number of trees per plot were significant predictors of the number of cones stripped by squirrels ($p < 0.006$, 0.01 and 0.03 respectively). DBH is the independent variable which contributes the most (coefficient = 2.6) followed by canopy cover and number of trees (coefficients = 0.09 and 0.02 respectively). The resulting model (presented below) explains 46% ($R^2 = 0.46$) of the variation in the field measured data.

$$\boldsymbol{SC = -6.6 + (2.6)\,DBH + (0.09)\,\mathrm{CC} + (0.02)\,NT}$$

Where *SC* is the total number of stripped cones, *DBH* is mean diameter at breast height, *CC* is mean canopy closure and *NT* is total number of trees.

Abernethy and Aberfoyle

Combining the data from the two sites, we tested the relationship between the number of stripped cones -as an indicator of squirrel habitat use- and the different stand structure variables.

The data was checked for collinearity and it was found that mean DBH was significantly correlated with the number of trees (r_s= -0.58, n=52, $p \leq 0.001$) and with mean tree height (r_s = 0.59, n=52, $p \leq 0.001$). We assessed the relationship between these three covariates and the response variable in order to decide which variables not to use for the model. Mean DBH did not show a stronger correlation with the number of stripped cones (r_s= 0.23, n=52, $p \leq 0.009$) than the number of trees (r_s= 0.25, n=52, $p \leq 0.008$) or tree height (r_s= 0.21, n=52, $p \leq 0.014$). Therefore, DBH was not used in the GLM analysis. No other correlations were observed among the variables.

With respects to food abundance, correlation between total cone crop and number of stripped cones was low to moderate (r_s=0.37, n=52, p<0.007).

The results of the GLM analysis indicate that forest structural variables measured in the field were significant predictors of the number of cones stripped by squirrels (Table 2.2).

Mean canopy closure and total number of trees per plot are the variables which contribute the most to the incidence of cones stripped by squirrels ($p \leq 0.01$ and 0.03 respectively; Table 2.2). Squirrels are known to prefer seeds with high nutrient content (Gurnell 1987), and nutrient content in Scots pine has been found to increase with tree height (Grönwall 1982). Thus, mean tree height was considered to be an important biological predictor of red squirrel tree selection and was retained ($p \leq$ 0.058).

Table 2.2: Results for the GLM model (with a quasi-Poisson error structure) relating number of stripped cones to forest structure parameters

Regression parameters	**Slope coefficient**	**Standard Error**	***t* value**	***p* value ≤**
Constant	-6.503725	2.935908	-2.215	0.0315*
Mean canopy closure	0.083300	0.032195	2.587	0.0128*
Number of trees	0.017996	0.008096	2.223	0.0310*
Mean tree height	0.083209	0.043005	1.935	0.0589**
Significance code (alpha level): * 0.05 - **0.1				

The resulting GLM is presented below, where *SC* is the total number of stripped cones, *CC* is mean canopy closure, *NT* is total number of trees and *TH* is mean tree height.

$$SC = -6.5 + (0.083)\, CC + (0.018)\, NT + (0.083)\, TH$$

The model explains 43% ($R^2 = 0.43$) of the variation in the field measured data. Figure 2.2 shows the scatter plot of observed vs. predicted number of cones stripped by red squirrels.

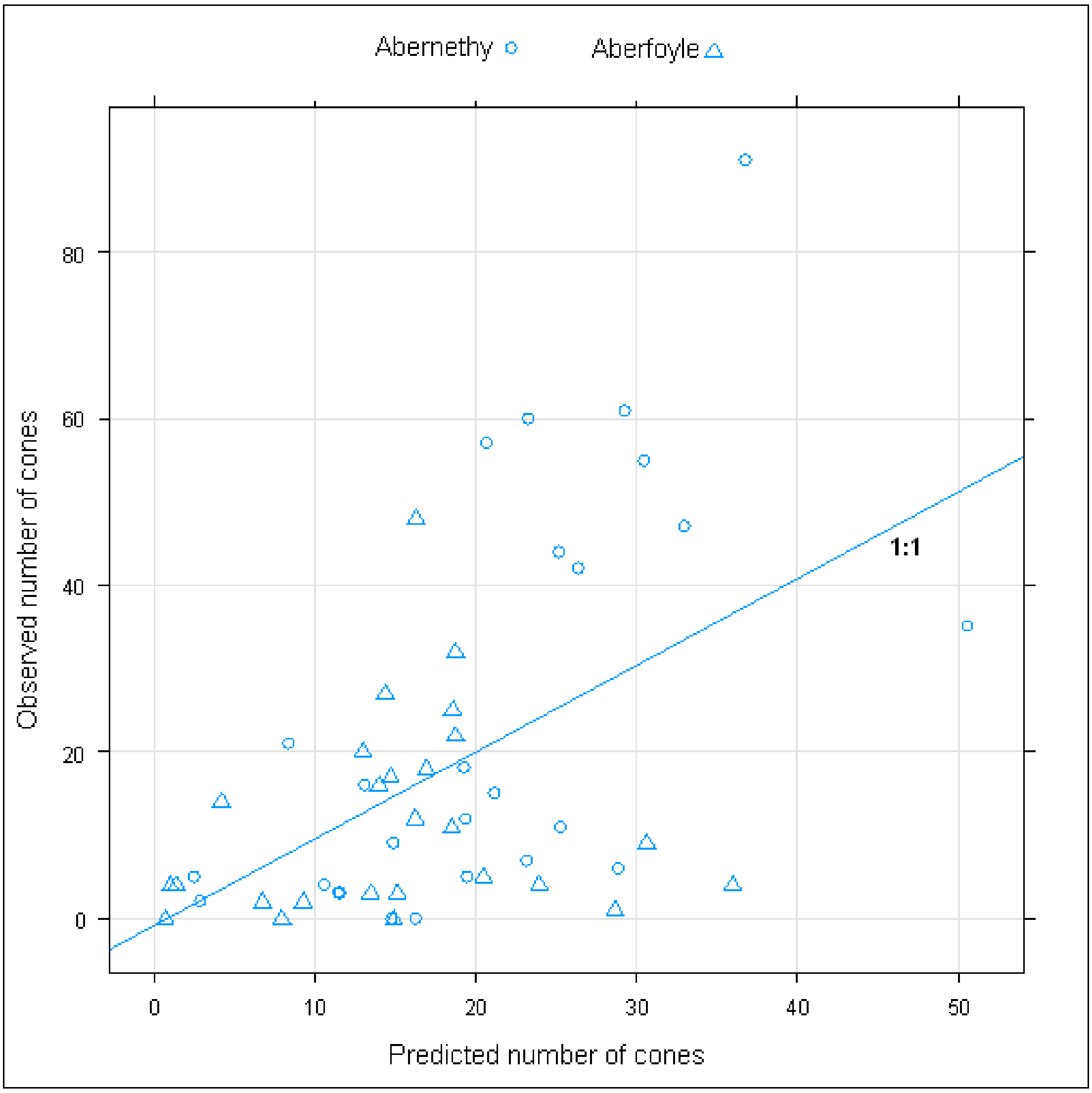


Figure 2.2: Scatter plot. *Observed* versus *Predicted* values of number of Scots pine cones stripped by squirrels using the GLM : $Y = \mu + \beta c + \beta d + \beta h + \varepsilon$, where Y is the dependent variable and βc, βd, βh are covariates describing Canopy Closure, Tree Density and Tree Height respectively. The Residual Error is described by ε. Line of unity (1:1) is shown in blue.

2.4 Discussion

Our results show that forest structural characteristics are significant predictors of the number of cones stripped by squirrels and therefore suggest that canopy closure, tree density (and potentially tree height) are important factors in influencing foraging behaviour of red squirrels. This has implications for conservation management. The current strategy for red squirrel conservation with respect to forest management is based on the selection of a set of suitable strongholds sites (see for example http://www.forestry.gov.uk/forestry/infd-7q3ft8), where viable red squirrel populations can be sustained over the long term (Parrott *et al*., 2009). Management recommendations currently focus on overall woodland size (e.g. > 2000 ha), tree species composition and age structure to provide a dependable seed food supply, guidance on forest operations such as thinning and felling to reduce detrimental impacts on local populations, monitoring to detect population trends and changes in distribution of both grey and red squirrel, grey squirrel control to prevent or reduce the risk of disease spread and reducing the potential for grey squirrel competition by excluding large-seeded broadleaves in and around stronghold areas (Gurnell & Pepper 1993, Gurnell *et al.* 2009, Lurz *et al.* 1998, Pepper & Patterson 1998, Bruemmer *et al.* 2010).

Our findings extend these recommendations by stressing the need to consider forest structure at the sub-stand level when implementing conservation measures. More specifically, our findings highlight and for the first time quantify the importance of mean canopy closure and total number of trees per plot as key structural variables. This suggests a preference of red squirrels for denser stands which concords with previous research carried out in the UK, where red squirrels were observed to avoid thinned, open stands of trees (Gurnell *et al.* 2002). Studies conducted elsewhere on arboreal squirrels' habitat preferences also reach comparable conclusions: Smith *et. al*. (1994) found that Mount Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) midden sites (i.e. sites were cones are stored for winter food supply) were located in areas of high tree densities and high canopy closure (> 70%) in Piñaleno Mountains, Arizona. Moreover, Nelson *et al*. (2005) highlighted the importance of closed canopies for the Delmarva fox squirrel (*Sciurus niger cinereus* L), while McKinney and Fiedler (2010) found that basal area, canopy closure and canopy height were significant predictors of the distribution of arboreal squirrels in the Rocky Mountains (USA). Besides, a habitat suitability index model developed by the Fish and Wildlife Service, Department of the Interior (U.S.A, 1987) to predict grey squirrel habitat, regarded canopy closure and tree density as variables directly related to the provision of cover for squirrels. It is important to note however, that these preferences are not generic to squirrels, but species specific. Whilst our results allow an assessment of habitat suitability for red squirrels in Scots pine habitats, there is a need to improve our understanding of these preferences in other habitat types and their underlying causes. Canopy cover and tree density may be linked to optimal foraging by allowing speedy movement through tree crowns without a need to descend to the forest floor; and reflect a need for cover to reduce predation risks. Tree height was marginally significant in our GLM model ($p \leq 0.058$), but may be an important predictor of seed quality. Grönwall (1982) studying habitat selection in red squirrels in Sweden found a significant correlation between tree height (and age) and seed nutrient content (e.g. crude protein, phosphorus, magnesium).

Our findings suggest that not all structural characteristics are *equally* important for habitat selection, and indicate a ‘hierarchy’ for red squirrel habitat selection. In Table 2.3 we present a basis for building such hierarchical framework for red squirrel habitat selection in the UK. We start from the premise that decision-making is a result of processes involving a succession of choices, themselves influenced by preferences. Hierarchically, food availability and quality are the most important factors influencing habitat choice and determining red squirrel habitat use. If food is available, our results show that stand structure is then a critical second factor in determining where squirrels forage.

Table 2.3: Habitat design for red squirrel conservation In a hierarchy of decision, food availability is the most important component determining red squirrel abundance and habitat use. Our results show that when food is available, stand structure is a critical factor in determining red squirrel habitat use

Habitat suitability	**Forest management option**	**Reference**	**Currently accounted for in management?**
Habitat type	Conifer species diversity	Gurnell 1983 & 1987; Lurz *et al.* 2000; Poulsom *et al.* 2005	YES
Seed availability & quality	Suitable age structure	Gurnell 1983 & 1987; Lurz *et al.* 2000; Poulsom, *et al.* 2005	YES
Stand structure	Fringe planting	Pepper & Paterson, 2001	YES
	- Closed canopy - High tree density - Tall trees	This study	NO

Our results indicate that open forests (or late stage thinned) may be of limited suitability for red squirrels. This has significant implications for further developing the UK strategy for red squirrel conservation as well as for improving the management of woodlands to support red squirrel populations. Current forest design for red squirrels contemplates diversification of conifer species and age class to ensure continuous food supply and the avoidance of large-seeded broadleaved species, such as oak (*Quercus petraea*), chestnut (*Castanea*), beech (*Fagus*) and hazel (*Corylus*). This paper highlights the importance of considering as well the structural characteristics of forest stands and the need to provide dense stands and maintain a contiguous canopy cover in parts of the forest. For management, these results identify the need for methods to extract and utilise structural data (notably canopy closure and total number of trees) to derive habitat suitability information over large forest areas. These are needed to assess current suitability of strongholds and to plan conservation management actions for red squirrels and other endangered forest dwelling species. One potential future research avenue would be to link field data on habitat selection with forest structural data extracted using remote-sensing approaches (e.g. LIDAR, Patenaude *et al.*, 2004).

CHAPTER 3

LiDAR data processing for red squirrels habitat mapping

The importance of forest structural parameters for red squirrels habitat mapping was addressed in the previous Chapter: Canopy closure, number of trees and tree height were found to be significant predictors and to explain 43% of the variation in cones stripped by squirrels. However, the analysis is restricted to a few sample plots due to a limited availability of structural data along with cost-efficient data collection methods. The use of remote sensing -in particular Light Detection and Ranging (LiDAR) - enables cost efficient forest structure assessment at large scales.

This chapter provides a brief introduction to LiDAR remote sensing as well as detailed description of methodologies used to retrieve the three parameters that relate to habitat suitability for red squirrels: *mean canopy cover*, *mean tree height* and *total number of trees*. Accuracy assessment is performed by comparing LiDAR retrieved structural parameters to field measurements at the plot level, and results are presented and discussed. The relationship between field measured canopy closure and LiDAR estimated canopy cover is also discussed.

3.1 Introduction

3.1.1 LiDAR remote sensing

LiDAR (Light Detection and Ranging) is an active remote sensing technology that uses the time that a laser beam takes to travel to and from a target to calculate distances. Laser pulses descend to the ground and form a circular footprint where the pulse hits the ground. These pulses are reflected by objects on the ground or by the ground itself and the distance between these targets and the sensor is calculated by multiplying the return time (i.e. time elapsed between the laser beam leaves the sensor, hits a target and returns to the sensor) by the speed of light and divided by two (Mather, 2004). Detailed technical description of LiDAR can be found in Baltsavias (1999). The main characteristic and advantage of LiDAR remote sensing in forestry is that it allows for direct retrieval of canopy height (Brovelli *et al.*, 2002).

LiDAR sensors can be categorised as *discrete return* or *full-waveform*. The main difference between these two systems is how they sample three-dimensional structure. Full-waveform systems record reflected energy over equal time intervals, and the level of detail in a laser footprint is given by the number of recording intervals. On the other hand, discrete systems record either one (single-return systems) or a small number (multiple-return systems) of returns for each pulse sent to the ground from the aircraft (Lim *et al*, 2003). Both LiDAR systems consist of a combination of three pieces of equipment which are mounted on an aircraft: laser emitter-receiver, Global Positioning System (GPS) and Inertial Navigation System (INS) (Brovelli *et al.*, 2002).

The utility of each system depends on the size of the footprint. For most discrete return systems, footprints are in the order of 0.2 to 0.9 m, while for full waveform systems, footprint size ranges from 8 to 70 m (Lim *et al*, 2003). Therefore, if used for forest applications, full waveform LiDAR system will be more likely to provide information on a forest area including multiple elements while discrete return will be capable of characterizing individual trees (Lim *et al*, 2003). In this project, only data acquired by discrete return LiDAR system were used as it provides the spatial resolution needed.

3.1.2 LiDAR data processing for red squirrel habitat mapping

LiDAR data consists of a collection of points where the *x, y* and *z* coordinates of the points are known. This cloud of points consists of terrain -or bare Earth - and off-terrain (i.e. objects on the surface) points. The first step in LiDAR data processing is usually generating a *digital terrain model* (DTM) which involves the filtering of returns in order to identify those that correspond to the ground (bare Earth points) (Brovelli *et al.*, 2002). The general approach to generate a DTM from LiDAR data consists on taking the lowest value within a grid cell, where the size of the cell will depend on the spatial resolution of the data (i.e. pulses/m^2). The missing values are then estimated by interpolation (Maltamo *et al.*, 2004). The approach to generate a *digital surface model* (DSM) from LiDAR data is similar to the described above: in this case, the highest value within each grid cell is detected and the missing values are calculated by interpolation (Maltamo *et al.*, 2004). Finally, *canopy height model* (CHM) is calculated by subtracting the digital terrain model from the digital surface model. It is beyond the scope of this Chapter to critically review the several filtering techniques to discriminate between ground and above ground points and algorithms that exist to generate digital terrain and canopy height models. More detailed summaries can be found in Kraus & Pfeifer (1998); Brovelli *et al* (2002), Reutebuch *et al*, (2003); Meng *et al* (2010) and Sulaiman *et al.* (2010). Furthermore, detailed reviews of the use of LiDAR for forest applications can be found in Lim *et al* (2003), Næsset *et. al*, (2004), Hyyppä *et al* (2008).

This chapter will focus on the use of LiDAR data to retrieve forest structural parameters that relate to red squirrel habitat suitability at the plot level, namely *mean canopy cover*; *mean tree height* and *total number of trees* (see Chapter 2). Several researchers have explored different approaches to generate these products using LiDAR data. A review of previous studies is presented in the following sections; while a summary of the use of LiDAR for habitat assessment is provided in Chapter 4.

3.1.2.1 Canopy cover

The most common approach used to estimate canopy cover from LiDAR data consists of calculating the proportion of returns that hit the canopy, where canopy is defined as vegetation above a specific height threshold (Korhonen *et al.*, 2011). This is analogous to the method used by ecologists to estimate ground vegetation cover, which consists of dividing the number of points covered by vegetation by the total number of sampled points within a reference frame (i.e. quadrat; Jennings *et al.*, 1999).

In the case of LiDAR remote sensing, the approach involves dividing the canopy portion of the returns by the total of the returns (i.e. canopy returns + ground returns). Usually only first returns are considered as last and intermediate returns provide little useful information. The height at which field measurements of canopy cover are taken (i.e. breast height) can be used as threshold to discriminate canopy from non-canopy (Korhonen *et al.*, 2011).

This approach has been used by several researchers. Hyde *et al.*, (2005) estimated canopy cover using waveform LiDAR for a mixed-conifer woodland in Sierra National Forest, California. They separated the ground and canopy portions of the waveform and calculated canopy cover by dividing the canopy portion of the waveform by the total energy in the waveform. In their study, Hyde *et. al.* (2005) also used optical data: they classified the Quickbird Near-Infrared (NIR) band into forest and non-forest (based on visual observation); then the ratio between the two classes was computed, and the result (i.e. 1.6) was used to assist in the discrimination between canopy and non-canopy in the image resulting from the ratio between the canopy portion/total energy in the waveform. In this study, the accuracy of canopy cover estimated from LiDAR was evaluated by assessing the correlation between field measured and LiDAR derived canopy cover which showed an agreement of 81% (0.81, root mean square error (RMSE) =9.4%, n =40, P<0.00). Canopy cover was measured in the field using a Moosehorn densiometer.

LiDAR canopy cover has also been used in studies without direct field validation. For instance, Stephens *et. al* (2012) used canopy cover derived from LiDAR along with other LiDAR metrics in a linear regression to predict carbon content at the plot level in 246 plots randomly distributed in forests throughout New Zealand for which both LiDAR and field inventory data were available. Results showed that LiDAR canopy cover and 30th percentile of height explained 74% of the variation in carbon content (R^2 =0.74, n=246, P<0.05).

The disadvantage of using the proportion of laser beams that hit the canopy to estimate canopy cover is that large LiDAR scan angles can produce slightly biased canopy cover estimates (Korhonen *et al.*, 2011). However, previous research on this issue has shown that at the scan angles LiDAR data is usually acquired (not larger that 18°), bias does not represent a problem. For instance, Morsdorf *et al.* (2008) carried out a study to assess the effects of LiDAR scan angles on biophysical forest parameters derived from LiDAR data. In their study, they only used LiDAR data that had been acquired with a scan angle of +/- 7.5, and their results showed that -at those small scan angles- the effects on canopy cover estimates are negligible. Furthermore, Richardson *et al.*, (2009) and Ahokas *et.al.*, (2005) tested the effects of larger scan angles on forest products derived from LiDAR. They found that scan angles up to 10° and 15° respectively had no or very little influence on canopy cover estimates.

3.1.2.2 Individual tree delineation

In order to estimate the number of trees in a given area it is necessary to detect individual trees first. Several algorithms have been developed to delineate individual trees using LiDAR data (Vauhkonen *et al.*, 2012).

The watershed technique is one of the approaches that have been widely used to delineate individual trees. This approach is based on detecting the edges (valleys) of each crown in the canopy model, and the top (peak) of individual trees (Doo-Ahn Kwak *et al.*, 2007).

Gougeon's (1995) algorithm, based on the watershed technique, works by detecting the lowest pixels (or local minima) in a given *n* x *n* window, and then it follows the "valley pixels" -or pixel with values that are lower than their neighbours- until it delimitates a crown. A threshold, to allow for the detection of the local minima, is required to be defined by the user. This threshold or reference value represents the average height of the lower part of the crowns for a given study area and can be estimated from a histogram as shown in Figure 3.1 (Rahman & Gorte, 2009) or from empirical data. García *et al.* (2007) applied this algorithm to a sitka spruce plantation in Scotland and found that it delineated individual trees with an accuracy of 77.9 %, where the trheshold was estimated by averaging the height of the lowest part of the tree crowns measured in the field (García *et al.*, 2007).

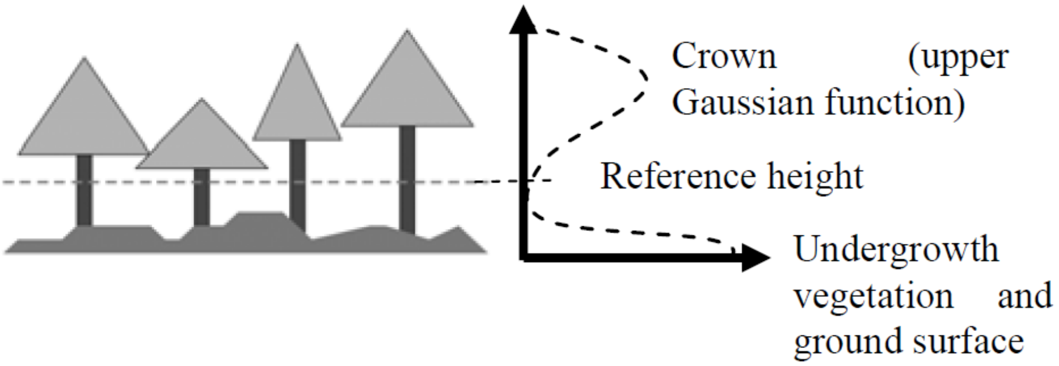


Figure 3.1: LiDAR data histogram (height (m) Vs frequency) showing how the height of the lowest part of the crowns (reference height) can be estimated (Rahman & Gorte, 2009)

However, most algorithms are based on the local maxima approach, which consists in finding the pixel with the highest value within a *n* x *n* window or kernel (Popescu *et al.*, 2003; Vauhkonen *et al.*,2012) The local maxima technique is based on the assumption that those local maxima or pixels with highest values represent the top of a tree crown (Popescu *et al.*, 2003). Most of these algorithms use the canopy height model as the input file (Rahman & Gorte, 2009).

Popescu *et. al.* (2003) developed an algorithm which applies the local maxima technique using a variable-size window. This method requires maximum and minimum crown diameters and allometric relationships between tree height and crown diameter which are used to determine the appropriate window size. To finally delineate the tree crown, a fourth-degree polynomial function is used, allowing for the modelled crown to have a concave shape. When applied to a sitka spruce plantation in Scotland, this algorithm delineated trees with an accuracy of 89.3% (García *et al.*, 2007).

A local maxima technique has also been combined with segmentation to delineate trees in boreal forests. Hyyppa *et al.*, (2001) developed an algorithm which combined local maxima and segmentation to delineate individual trees. The algorithm works by applying a filter to the canopy height model first to suppress noise. Then a local maximum (or seed point) is detected, and from there the crown is delineated by incorporating pixels using a seeded region growing method[1]. The crown is considered to be delineated when a minimum threshold, defined by the user, is reached. This algorithm was applied to a study carried out in a semi-natural boreal forest in Finland by Maltamo *et al.* (2004). Tree species present in the forest were Norway spruce (*Picea abies* L.), Scots pine (*Pinus sylvestris*) and silver birch (*Betula pendula* Roth.). In this study, out of 682 trees, 265 were correctly identified (approximately 39%) using LiDAR. When only dominant trees (i.e. trees or shrubs with crowns receiving full light from above) are considered, the accuracy increased to 83% (i.e. 245 out of 295 dominant trees).

Lee *et al* (2010) used a similar approach (i.e. local maxima plus segmentation) to detect trees in two managed forests composed of the same pine species (loblolly pine, *Pinus taeda* L.) in North-Central Florida, USA. Individual trees were detected with an overall accuracy of 95.1%.

The question of which algorithms produce more accurate results has also been addressed: In a recent study, Vauhkonen *et al.* (2012) compared the accuracy of a number of tree-detection algorithms under different types of forests. They applied six tree-detection different techniques to both conifer and deciduous forests in Brazil (deciduous: *Eucalyptus*), Germany (conifers: Scots pine and deciduous: oaks *Quercus rubra*, European beech *Fagus sylvatica* and silver birch *Betula pendula*), Norway (conifers: Scots pine and Norway spruce) and Sweden (conifers: Scots pine and Norway spruce). Airborne data point density (i.e. pulses/m^2) were 1.5 (Brazil), 7 (Norway), 30 (Sweden), 7 and 16 (Germany). An in depth description of each

---

[1] Seeded region growing method can be summarised in 3 steps: 1) Choose the seed pixel or local maxima; 2) Check the neighbouring pixels and add them to the region if they meet the criteria (usually a threshold is used); 3) repeat step 2 until no more pixels can be added to the region (Jain *et. al.*, 1999).

algorithm can be found in Vauhkonen *et al.*, (2012). Summing up, the algorithms worked as a combination of: local maxima and crown segmentation based on point clustering (algorithm #1); voxel[2] space and morphological algorithm (i.e. crown boundaries detection, algorithm # 2); segmentation based on tree spacing (algorithm # 3); local maxima adjusted by residual tree height (algorithm #4); segmentation based on tree crown models (algorithm # 5) and adaptive filtering based on CHM height values (algorithm # 6). Algorithms 1 and 2 used point data while the others used the CHM (i.e. raster file). In general, the different algorithms performed similarly under the different forest conditions. It is beyond the scope of this thesis to provide the exact tree detection rates of each algorithm for each study area and for each point density. Instead, the main findings are summarised as follow: a) the general success of tree detection was strongly linked to the tree density and spatial distribution of trees; b) an increase in laser data point-density improved the performance of tree detection algorithms, in particular for the point-based ones; and c) all algorithms performed better in conifer forests.

Local maxima algorithms have also been found to fail to identify small trees surrounded by bigger and higher ones (i.e. suppressed trees) and individual trees in deciduous woodlands where the crowns of the trees are not clearly separated from one another, and when there is considerable overlapping between crowns (i.e. very young conifer plantations) (Hyyppa *et al.*, 2001). However, these limitations are not exclusive to the local maxima approach. In their comparison of six different algorithms, Vauhkonen *et al.*, (2012) found that while all algorithms successfully detected the same dominant trees, they failed to detect most of the suppressed trees. This seems to reinforce the concept that tree detection is likely to be more dependent on tree density and spatial distribution than on the algorithm itself.

3.1.2.3 Mean tree height

LiDAR remote sensing has been widely used to estimate canopy height. Several authors have explored different approaches to retrieve individual tree height from LiDAR data and have assessed the accuracy of those estimations. Results suggest that LiDAR derived canopy height tends to underestimate height, due to two main reasons: laser pulses missing the top of the trees and ground height overestimation

---

[2] Voxel: Volumetric Pixel or Volumetric Picture Element

(low number of pulses reaching the ground). For detailed reviews on LiDAR derived tree height see Suarez *et al* (2005); Maltamo *et al* (2004), Koukoulas *et al* (2005).

This section will focus on the estimation of mean canopy height at the plot level as this is the parameter which relates to habitat preferences by red squirrels (see Chapter 2). Previous studies have shown that using arithmetic mean of laser heights leads to underestimation of field mean tree height, in particular in those plots where large gaps exist (i.e. low number of trees) and that upper percentile heights correlate well with field plot-level mean and top tree height (Naesset, 1997; Lefsky, 2010; Patenaude, 2004). In particular, 90th percentile which has been found to correlate well with mean tree height, and 99th percentile, often used for top tree height (Rosette *et al*, 2009; Hopkinson *et. al*. 2008).

The correlation between LiDAR percentiles and field tree height has been explored by a number of researchers. For instance, Popescu *et al* (2002) used linear regression to relate LiDAR estimated with field measured parameters in a mixed deciduous – conifer forest in Virginia, US. They found that 90th percentile was a significant predictor of mean tree height ($P< 0.05$) and explained 35% of the variation in field data ($R^2 = 0.35$; $n=24$).

Hopkinson *et al* (2008) performed Pearson correlation between LiDAR metrics and field measurements in a forest of heterogeneous species composition, 50km north of Toronto, Canada. Results showed strong correlation between LiDAR 90th percentile and field mean tree height ($r = 0.63$, $P< 0.01$, $n=19$). However, 90th percentile is not the only LiDAR metric that has been successfully associated with mean tree height: Correlation between LiDAR 95th percentile and field mean height was also assessed by Hopkinson *et al* (2008) and found to be also strong ($r = 0.59$, $P< 0.01$, $n=19$). Furthermore, Holmgrem *et al.* (2004) carried out a study in a forest in Norway, mainly composed of Norway spruce and Scots pine. They found a high correlation ($r=0.995$, $n=29$, $P< 0.00$) between laser-predicted and field-measured mean tree height, where laser mean height was predicted using 95th percentile.

In this Chapter, both 90th and 95th percentiles of LiDAR canopy height will be compared to mean field tree height at both Abernethy and Aberfoyle forests to assess which of these metrics better represent mean tree height at the plot level.

3.1.3 FUSION

FUSION (Version 2.90) was developed by the United States Department of Agriculture and it is distributed free of charge.

This package was developed to visualize, analyse and process LiDAR data. FUSION allows users to display, import/export LiDAR data in different formats, and to create products such as digital terrain models, digital surface models, canopy height models and canopy cover.

The accuracy of products generated using FUSION has been tested by a number of researchers. For instance, Reutebuch *et. al.* (2003) compared digital terrain model derived from LiDAR to 347 checkpoints elevation measured in the field. Checkpoints were located in different areas of a conifer forest in a mountainous area, ranging from clear cut to dense vegetation. Their results showed that elevation values obtained from LiDAR were highly accurate. Differences between LiDAR DTM and elevation measured in the field ranged from –0.63 to 1.31 m and the mean of the difference was 0.22 ± 0.24 m (mean ± SD).

FUSION allows for individual trees to be manually identified and measured. In a study carried out by McGaughey *et al.* (2004), a total of 112 trees were measured in the field, manually identified in a LiDAR canopy height model and measured within FUSION and their heights were compared. Mean height difference was -0.29 m and SD = 2.23.

FUSION based tree heights were also compared to those generated using other packages (TIN, ArcGIS) by Gaulton (2008). Both canopy height models were compared and found to be very similar, with a largest difference of 1 m in maximum tree height (34.50 m for FUSION; 35.52 for TIN). In this study, FUSION based tree heights were closer to the height measured in the field (mean difference = -0.06m and -1.08m and RMSE = 1.43m and 1.91m for FUSION and TIN respectively, n=49). FUSION has been widely used and more exhaustive descriptions of its application than are possible here can be found in the FUSION website (http://forsys.cfr.washington.edu/JFSP06/index.htm). The main advantage of FUSION is that it allows for operational processing of large amounts of LiDAR data at no cost. However, critical reviews of FUSION advantages and limitations remained yet to be published at the time this thesis was written.

3.2 Methodology

3.2.1 LiDAR data processing

LiDAR data at Abernethy Forest and Aberfoyle Forest were acquired and delivered by different providers and in different format files, as follow:

Abernethy Forest

LiDAR data at Abernethy Forest was collected by the NERC Airborne Research Facility (ARSF). Data provided consisted of eight (8) text files, one for each LiDAR flight-line. Before being delivered to the final user, LiDAR data quality is tested for noise and points are classified with the number 1 or 7, where points classified with the number 7 are suspected to be "noise" or returns outside the range of realistic elevations (i.e. caused by atmospheric aerosols, birds, or low-flying aircraft). These points are not removed by the provider but a program is delivered with the data which creates new text files where the noise has been removed.

Aberfoyle Forest

LiDAR data for Aberfoyle Forest was provided by Infoterra. Data was delivered as a number of XYZ files (tiles in ASCII format). Noise had already been removed. The program *XYZConvert* (FUSION) was used to convert XYZ files into a format that could be processed within FUSION.

LiDAR data characteristics are summarised in Table 3.1

Table 3.1: Characteristics of the LiDAR data for both Abernethy and Aberfoyle, Scotland

	Abernethy	**Aberfoyle**
Date	27th November 2009	8th May 2008
Resolution (pulses / m^2)	2 pulses / m^2	1 pulses / m^2
Data provided	First, second, and last return- intensity	First and last return
Scan angle	+/- 18°	+/- 20°
Average flight altitude	1760 m	1310 m

Both LiDAR datasets (i.e. Abernethy and Aberfoyle) were mapped to a geographic co-ordinate system (British National Grid) using on-board attitude and positional information with additional ground control points. Data was compared to Ordnance

Survey Maps and judged to be accurately positioned and no further corrections were applied.

3.2.2 DTM and CHM

Once LiDAR data from both Abernethy and Aberfoyle Forests had been converted into a format that could be processed within FUSION, the following step is to generate a digital terrain model (DTM) by filtering those returns that are more likely to correspond to bare Earth. The software used to generate the DTM was FUSION (Version 2.90). Creating a DTM within FUSION requires the use of two programs. First, *GroundFilter* creates a surface where only returns that correspond to bare earth are kept. The algorithm used, which is described in detail in Kraus and Pfeifer (1998), is based on linear prediction and works iteratively. First, an average surface (i.e. a surface between top of the vegetation and ground) is created from all input points. On a second stage, weights are computed for each point, according to the distance from the average surface and direction (given by the positive or negative sign of the residuals). On a final stage, and given a threshold *g,* points with residuals smaller than *g* are given a weight of 1, and points with residuals larger than *g* are given a weight of 0. In the final iteration, those points -that were given a weight of 1- whose distance from the average surface is less than a user-specified tolerance are classified as bare earth points.

The number of iterations was set to 30, the tolerance was set to 0.1m (default value) and the rest of the parameters were also defined according to recommended defaults (McGaughey, 2009).

In the second part of the process, the program *GridSurfaceCreate* is used to finally create the DTM. This program uses the file created by *GroundFilter* and interpolates the values identified as bare earth. *GridSurfaceCreate* computes the elevation of each grid cell using the average elevation of all points within the cell. The option to smooth the data is given but it is not recomemended for vegetated areas since it can result in loss of surface detail (McGaughey, 2009). Based on LiDAR data spatial resolution (i.e. 2 pulses/m^2 at Abernethy and 1 pulse/m^2 at Aberfoyle) cell size was set to 1 m for both forests. The resulting files were exported as ASCII files and imported into ArcGIS (V 9.0) to create raster files.

FUSION was also used to create a canopy height model. The program *CanopyModel* creates a canopy height model (CHM) by assigning the elevation of the highest return within each grid cell, where the size of the cell is given by the user. The algorithm uses both the file which contains all the returns and the DTM (bare earth surface) to subtract the ground elevations and generate a CHM (McGaughey, 2009). Cell size was again set to 1m, and the files created in FUSION were also exported as ASCII files and imported into ArcGIS to create raster files.

Table 3.2 presents a summary of the tools and programs used and files created in every stage of the LiDAR data pre-processing.

Table 3.2: Summary of LiDAR data pre-processing described in this section

Process	**Program**	**Output file**
"Noise" filtering (only for Abernethy Forest data)	pt_cloud_filter (NERC- ARSF)	Text file free from noise
Format conversion (only for Aberfoyle data)	*XYZConvert* (FUSION	FUSION format file - first and last returns
Bare earth points filtering	GroundFilter (FUSION)	FUSION format file with only points identified as bare earth
DTM creation	GridSurfaceCreate (FUSION)	Digital terrain model
Canopy Height Model creation	CanopyModel (FUSION)	Canopy height model
ASCII files creation	FUSION	DTM and CHM ASCII files
Raster files creation	ArcGIS	DTM and CHM raster files

DTM validation

As part of this study, elevation measurements in the field were not required. Albeit the fact that the equipment required was not available at the time that the field work was being conducted, absolute accuracy of digital terrain model (i.e. elevation above the sea level) is not of interest for this project: the main aim is to assess whether spatial changes in elevation are well represented, as these would influence canopy height. For this purpose, the fact that several studies have already provided evidence that LiDAR produces accurate digital terrain models under dense forest canopy (for example, Kraus & Pfeifer; 1998; Reutebuch *et al*, 2003) is considered sufficient. Nevertheless, an assessment of the consistency of LiDAR retrieved DTM was conducted by comparing results with the Ordnance Survey (OS) DTM. The purpose of this evaluation is to assess whether gross systematic errors can be detected and, if possible, whether this error can be attributed to LiDAR or OS DTM. This evaluation was conducted for both Abernethy Forest and Aberfoyle Forest.

Ordnance Survey (OS) DTMs are created using the height information contained in contour files. These contours were surveyed by photogrammetry – stereo interpretation of aerial photography – in an initial capture programme which was completed in 1987. The results achieved depend on the density of height data contained in each contour file. OS DTMs are provided with 1 m height resolution and 10 m horizontal grid interval. The general height accuracy is +/- 2.5m to 5m; although in mountain and moorland areas the accuracy can be lower. In some flat areas where there is little height information, contours and spot heights may be a great distance apart, this can cause irregularities in the DTM which appear as slight terracing of the terrain (Ordnance Survey, 2001).

The comparison between the LiDAR and OS DTMs was performed as follow:

- A map of the difference between LiDAR and OS DTMs was created within ArcGIS and differences were classified into 3 intervals: -5 to -2.5, -2.5 to 2.5m and 2.5 to 5 (Figure 3.4). These thresholds were based on the OS DTM accuracy range (+/- 2.5m to +/- 5m).
- Ground elevation retrieved from LiDAR data was compared to the OS DTM at the plot level. Both DTM values (LiDAR and OS) were extracted for the plots' central points (i.e. 32 in Abernethy and 52 in Aberfoyle) and the correlation between the two sets of values was explored.
- The mean difference between LiDAR and OS DTM was statistically tested to assess the presence of systematic error.

3.2.3 Canopy Cover

Canopy cover was estimated as the proportion of laser beams that hits the canopy, where canopy is defined as vegetation above a specific height threshold (Korhonen *et al.*, 2011). The programme *Cover* (FUSION) was used to calculate canopy cover by dividing the number of first returns above a given height threshold (*height-break*) by the total number of returns over a specific area (*cell size*). Height break was set at 1.3m (following literature recommendations; Korhonen *et al.*, 2011); cell size must be large enough (i.e. larger than individual tree crowns) in order to provide a reasonable sample area to assess vegetation cover. For most forest types, cell sizes of 5m to 15m produce good results (McGaughey, 2009). To allow for comparison between LiDAR derived canopy cover and field measured canopy closure, the cell-size used was the size of the field plots (i.e.14 m). Output file values range from 0 to 100 percent.

Canopy closure was measured in the field using a concave spherical densiometer (Robert E. Lemmon Model C). Measurements were made at each of the 4 corners and at the central point of the plot and subsequently averaged.

Although canopy cover and canopy closure have been frequently used as synonymous, it is important to remark here that there is a clear difference between these two ways of quantifying forest canopies: While canopy closure represents *the proportion of the sky hemisphere obscured by vegetation when viewed from a single point* (Jennings *et al*., 1999), canopy cover reflects *the proportion of the forest floor covered by the vertical projection of the tree crowns* (ibid). In other words, canopy cover is a vertical measure of gaps between crowns; while canopy closure includes all gaps in the field of view (Figure 3.2).

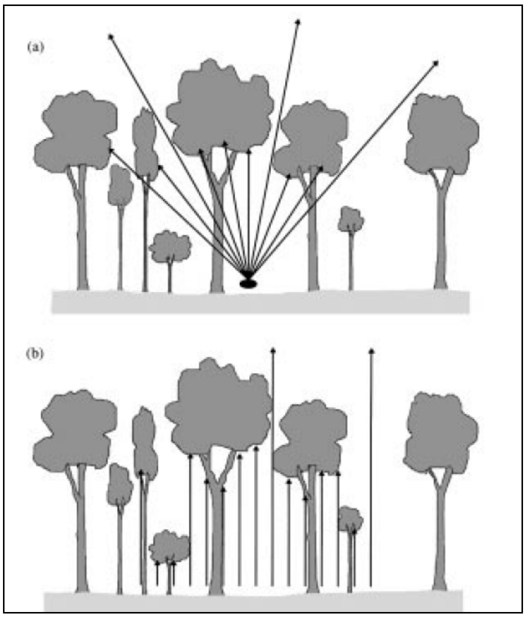


Figure 3.2: a) canopy closure, b) canopy cover (Jennings et. al., 1999)

Canopy closure –and not canopy cover- was measured in the field for this project as this is the variable most traditionally associated with ecological applications such as habitat assessment and monitoring (Paletto & Tosi, 2009). In this study, canopy closure more closely measures light penetration as it is experienced by the animal (diffuse light received from hemispherical directions, rather than only vertically). Moreover, previous studies that have investigated habitat preferences of arboreal squirrel have found a positive relationship between canopy closure and squirrels presence (Smith and Mannan, 1994; Nelson *et al.*, 2005).

On the other hand, remotely sensed data provides an estimation of vertical canopy cover. Canopy closure over a given area of a forest might not be correlated with canopy cover of the same area (Jennings *et. al.* 1999). However, an open canopy allows more light to penetrate and that reflects on measurements no matter whether canopy cover or closures is being measured. Thus it would be expected that a correlation does exist between both variables. Yet, both terms have been frequently used as synonyms causing significant confusion (Jennings *et. al.* 1999): hence the difficulty in finding studies where the correlation between canopy cover and canopy closure is explored. One such study was found: Cook *et. al.* (1995) compared measurements made using a concave spherical densiometer (canopy closure) and Moosehorn densiometer (canopy cover) - and found they were correlated as a negative exponential (correlation coefficient not reported, n=39, $P < 0.001$). Furthermore, Rosette *et. al.* (2009) found a strong correlation between canopy cover derived from airborne LiDAR and canopy closure measured in the field using hemispherical photography (r=0.77, n = 15, RMSE = 0.02).

The extent to which LiDAR canopy cover could potentially be used as a surrogate for field canopy closure to map habitat suitability for red squirrels has been assessed in this study. To achieve this, the correlation between LiDAR canopy cover and field measured canopy closure was investigated as follow: LiDAR canopy cover created within FUSION was exported and a raster file was created within ArcGIS. Mean canopy cover (%) was extracted from the raster image for each plot and the correlation with mean field canopy closure was assessed at both Abernethy Forest and Aberfoyle.

3.2.4 Individual trees

The local maxima approach was selected for this project for being an operational approach. Furthermore, levels of accuracy achieved when using this approach are comparable to those achieved when using more complicated and time consuming procedures (see Table 3.6).

In practical terms, the local maxima algorithm works by applying a moving window -to either the CHM or the cloud of points- and the maximum value within that window is assumed to be the top of a tree. The moving window can be squared (n x n) or circular (radius = n; where n is the size in meters).

The size of the moving window is an important factor to be considered. If the window is too large, i.e. larger than tree crowns, the number of trees could be underestimated due to some trees being omitted (error of omission). On the other hand, a window that is too small would have the opposite effect and the number of trees would be overestimated (error of commission). The size of the windows then should be as approximate as possible to the crown size.

A study by Mäkelä & Vanninen (2001) reports that crown width for young, mature and old Scots pine in a forest in Finland ranged from 0.7m to 4.75m (mean not provided, n=24); while Ene *et al* (2011) reports crown diameters between 0.9m to approximately 7m (mean=3.3m; n=266) for young and mature Scots pine in Norway. Based on these figures, a number of window-sizes were tested and the results assessed to determine which one produced the best results. Local maxima approach was applied to both the canopy height model (CHM) and to the cloud of points.

Canopy height model approach

ArcGIS *Spatial analyst* tools were used to identify individual trees by detecting the highest value within a moving window on the canopy height model (CHM) created within FUSION. Three different window sizes were tested: 4m, 3m and 2m. To avoid ground points being identified as “local maxima”, only cells with values above a given threshold were considered for the analysis. The value used for this threshold was the minimum tree height measured in the field (7 m for Abernethy Forest and 10m for Aberfoyle Forest).

Cloud of points approach

By working directly with the cloud of points, the loss of information caused by the process of creating a CHM (i.e. interpolation) is minimized and therefore, the likelihood of detecting smaller trees increases (Gaulton, 2008).

A modification of the algorithm used by Gaulton (2008) was used to apply the local maxima technique to the cloud of points. A detailed description of this algorithm can be found in Gaulton (2008). Originally developed to delineate canopy gaps, the algorithm works as follow:

- identifying the local maxima
- removing returns below a given threshold
- clustering of canopy returns
- merging and delineating of clustered points to delineate canopy gaps

A simplified version of this algorithm was used to identify the highest returns by comparing them to their near neighbours. A fixed radius for the search window and a number of neighbours are used. As the process is time consuming, the number of points was reduced (before applying the algorithm) by considering only those points which height was above a given threshold. The threshold used for this was also the minimum tree height measured in the field and it was assumed that no tree crowns were likely to be found below those thresholds. As the aim was identifying tree tops only, the stages of the algorithm where canopy returns are clustered and merged were not used.

3.2.1 LiDAR 90th & 95th percentiles

Mean field height was compared to both 90th and 95th percentiles of LiDAR canopy height to determine which of these metrics better represent mean tree height at the plot level.

In order to perform this comparison, height values were extracted from the 1 m resolution CHM for both Abernethy and Aberfoyle datasets. All plots were used and a set of data consisting of one height value per square metre was created for each plot (approximate size of the plots is 200 m^2). In order to eliminate the effect of shrubs and understory vegetation, the minimum tree height measured in the field was used as a threshold and only height values > 7m for Abernethy Forest, and > 10m for Aberfoyle were considered. Finally, 90th and 95th percentiles of LiDAR heights were computed for each plot and compared to mean tree height measured in each plot.

3.3 Results

3.3.1 Digital terrain model

Results of the comparison between LiDAR and OS DTMs are presented below:

Abernethy Forest

Figure 3.3 shows the DTM created within FUSION and ArcGIS. White circles represent plots surveyed during the field season in Abernethy Forest, Scotland, October 2009.

The classification of the difference between LiDAR and OS DTMs showed that 80% of the total area lies within a range of values between -5m to 5m (outer limits of the OS DTM accuracy interval) while 60% of the area lies within values between -2.5 m to +2.5m (inner limits of the OS DTM accuracy interval).

OS DTM was visually assessed to evaluate its quality and irregularities (i.e. a large area with the same elevation value) were found. These irregularities are shown in Figure 3.5.

The correlation between DTM values (LiDAR and OS) at the plot level (Figure 3.6) is close to one, with a Pearson coefficient (r) of 0.998, $P < 0.001$ and root square mean error (RMSE) of 3.01m ($n = 32$). Furthermore, average difference (2.0m) was statistically tested and found to be significantly different from 0 (*t-test*, $P<0.001$, Figure 3.7)

Except for 5 values (plots 4, 5, 8, 25 and 32) where negative differences are observed, differences between both DTMs are consistently positive and fluctuate between 0 to 9 m (Table B.1, Appendix B). Points 11, 13, 14, 15, and 22 present differences higher than 5m. All these plots are located in an area of the OS DTM where no variation in elevation is observed over a large region (Figure 3.5), which suggests poorer quality of the OS DTM. The rest of the differences between OS and LiDAR DTM were considered to be reasonably within the OS DTM accuracy (+/-2.5m to 5m).

Aberfoyle Forest

In the case of Aberfoyle Forest, the image supplier (Infoterra) provided –along with the LiDAR data- a Ground Truth Report. Two different sets of points (site 1 and site 2) were used to assess the accuracy of LiDAR ground elevation values. Mean height difference for site 1 was -0.032m (*n*=42, *SD*=0.6, RMSE = 0.068) and -0.009m for site 2 (*n*=39, *SD*=0.041, RMSE=0.042). In addition to this, comparison with OS DTM was also carried out.

Figure 3.8 shows the DTM created within FUSION. White circles represent plots surveyed during the field season at Aberfoyle in May 2010. A total of 56 plots were surveyed (see Chapter 2)

The classification of the difference between OS and LiDAR DTM showed that 94 % of the total study area falls within a range of values between -5m to 5m, while 74% of the total area lies within a difference between -2.5m to 2.5m.

The correlation between DTM values (LiDAR and OS) at the plot level is close to 1, with a Pearson coefficient of 0.999, $P< 0.001$ and root square mean error (RMSE) 3.02m ($n = 56$).

In general, observed differences (Table B.2, Appendix B) are small and both positive and negative. Values fluctuate between -7m to 5m. Points 3, 6, 9, 11, 24 and 47 (highlighted in blue in Figure 3.8 & 3.9) show differences higher than -5m, the rest of the values are within -5m to 4m which lie within the accuracy of the OS DTM (+/- 2.5 to 5m).

The mean difference (-0.19) was found to be not significantly different from 0 (*t-test*, P<0.646, Figure 3.11).

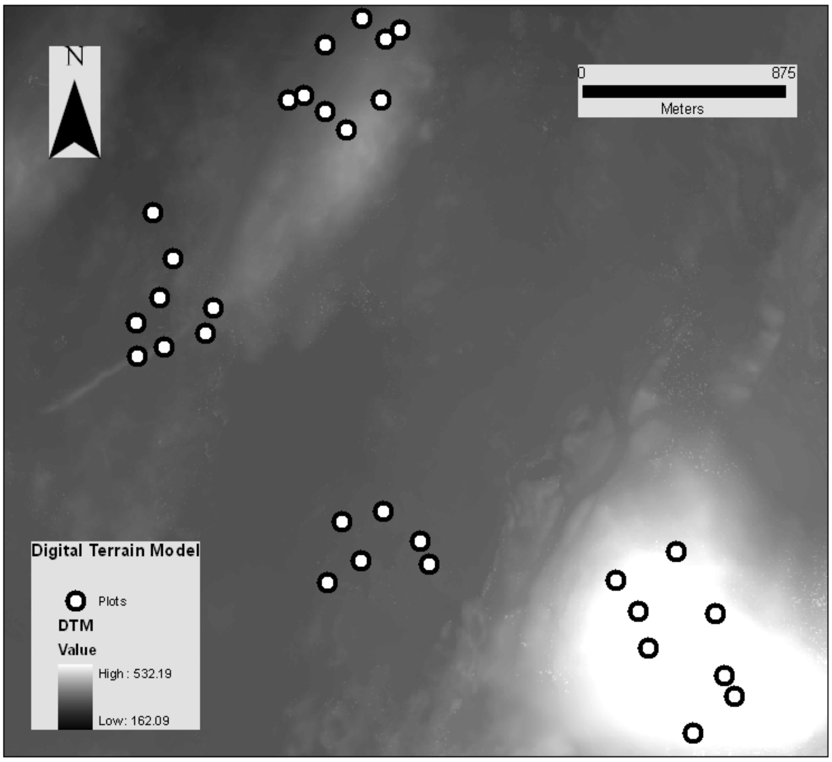


Figure 3.3: Digital terrain model (DTM) derived from LiDAR data and plots (white circles) surveyed during the field campaign, Abernethy Forest, Scotland.

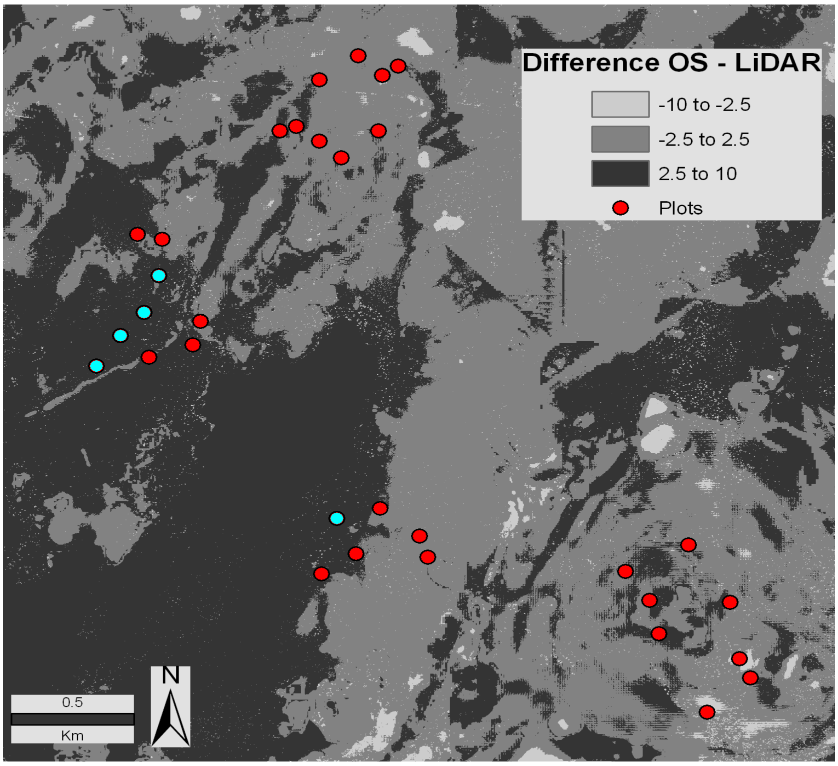


Figure 3.4: Map showing the result of the difference between the OS and LiDAR DTMs for Abernethy Forest, Scotland. Circles represent central points of the plots where field work was carried, points where the difference between both DTMs is > +/-5 are highlighted in blue.

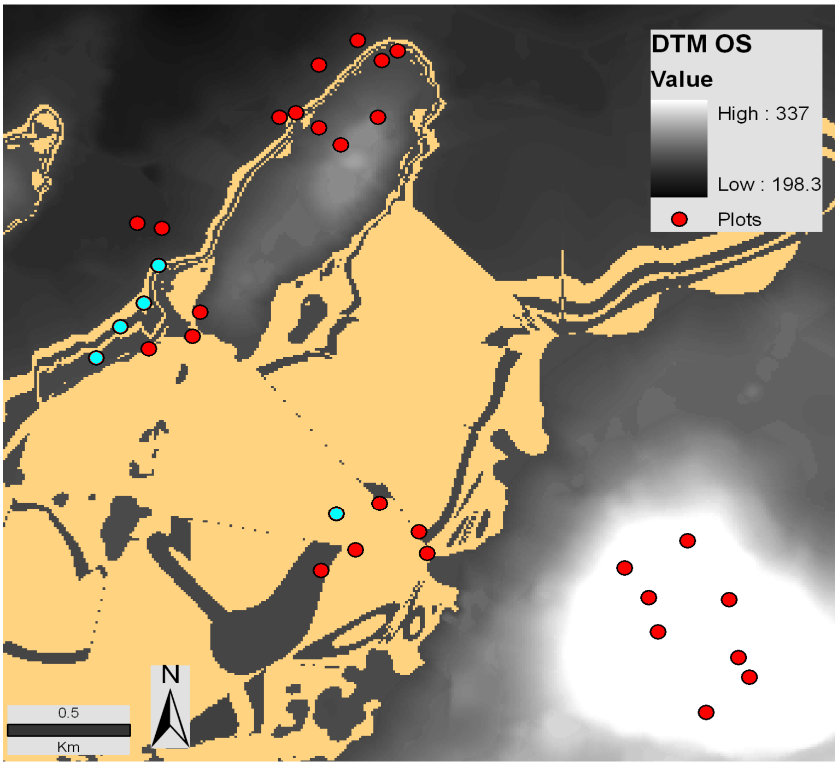


Figure 3.5 OS DTM, Abernethy Forest, Scotland. Irregularities where observed in this image: The same elevation (229m) was observed for the whole area highlighted in yellow. Circles represent plots where field work was carried out. Those points where the difference between both DTMs is > +/-5 are highlighted in blue.

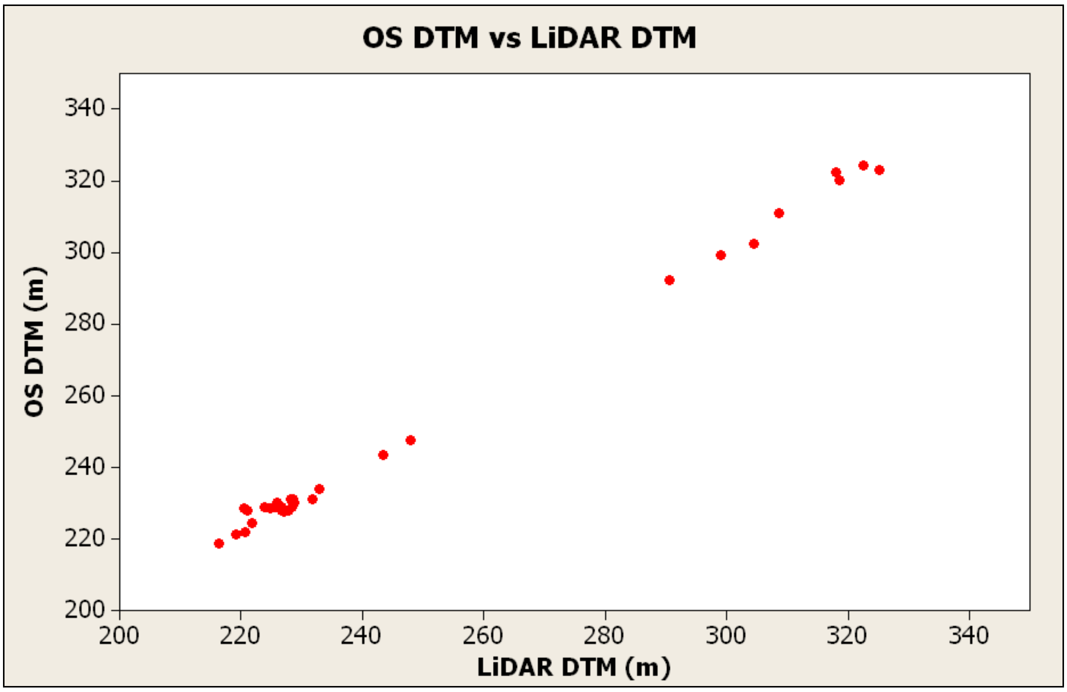


Figure 3.6: Scatter plot showing the correlation between values extracted from both the LiDAR and Ordnance Survey DTMs (*r* = 0.998, *n*=32, *P* < 0.001), Abernethy Forest, Scotland

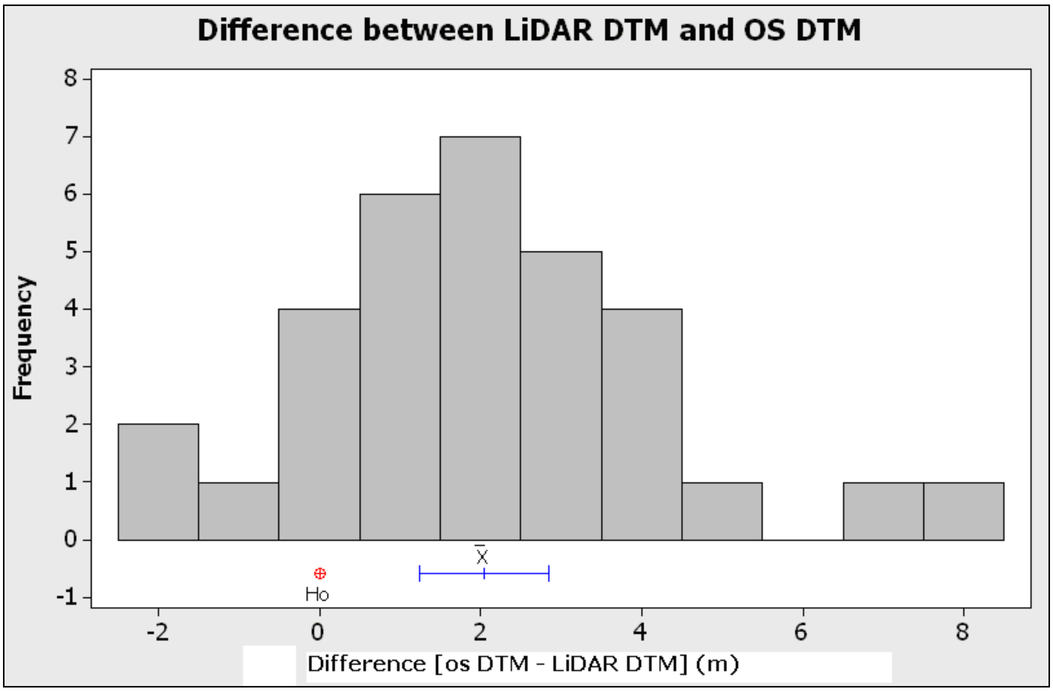


Figure 3.7: Histogram showing distribution of difference between OS DTM and LiDAR DTM. Mean difference is 2, and it is significantly different from 0 (*t-test*, *P*<0.001). Blue lines represent 95% confidence interval of the mean. Abernethy Forest, Scotland.

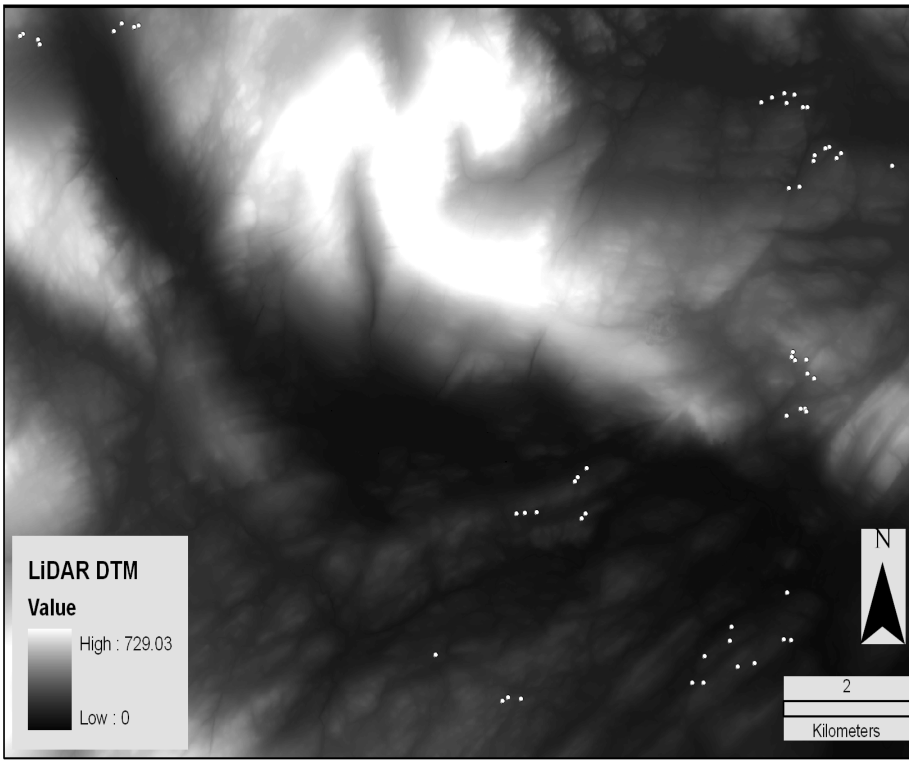


Figure 3.8: Digital terrain model (DTM) derived from LiDAR data and plots (white dots) surveyed during the field work, Aberfoyle Forest, Scotland.

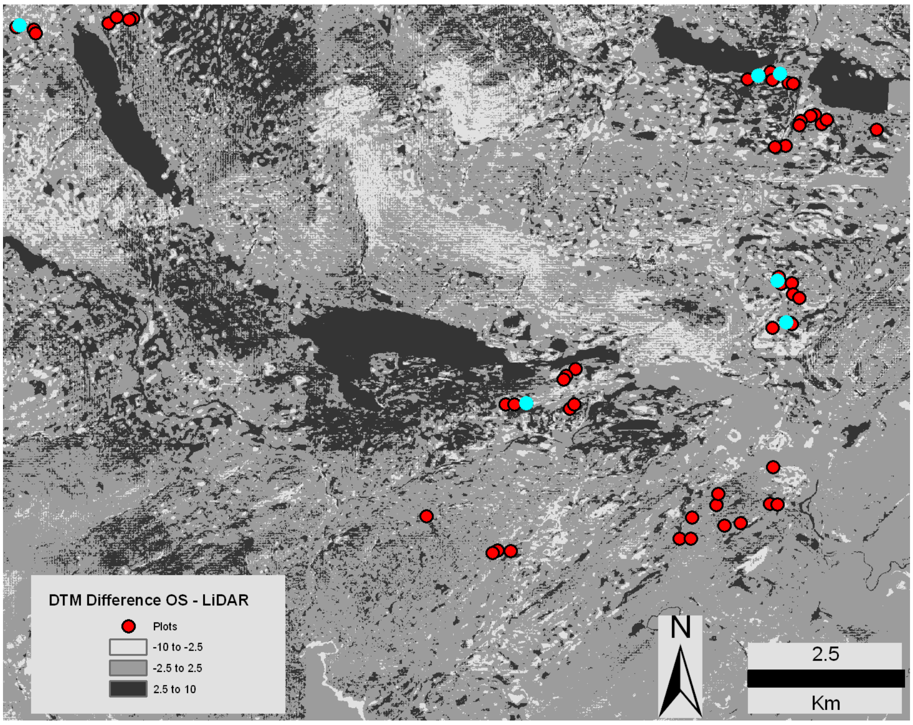


Figure 3.9: Map showing the result of the difference between the OS and LiDAR DTMs at Abernethy Forest, Scotland. Circles represent central points of the plots where field work was carried, points where the difference between both DTMs is > +/-5 are highlighted in blue.

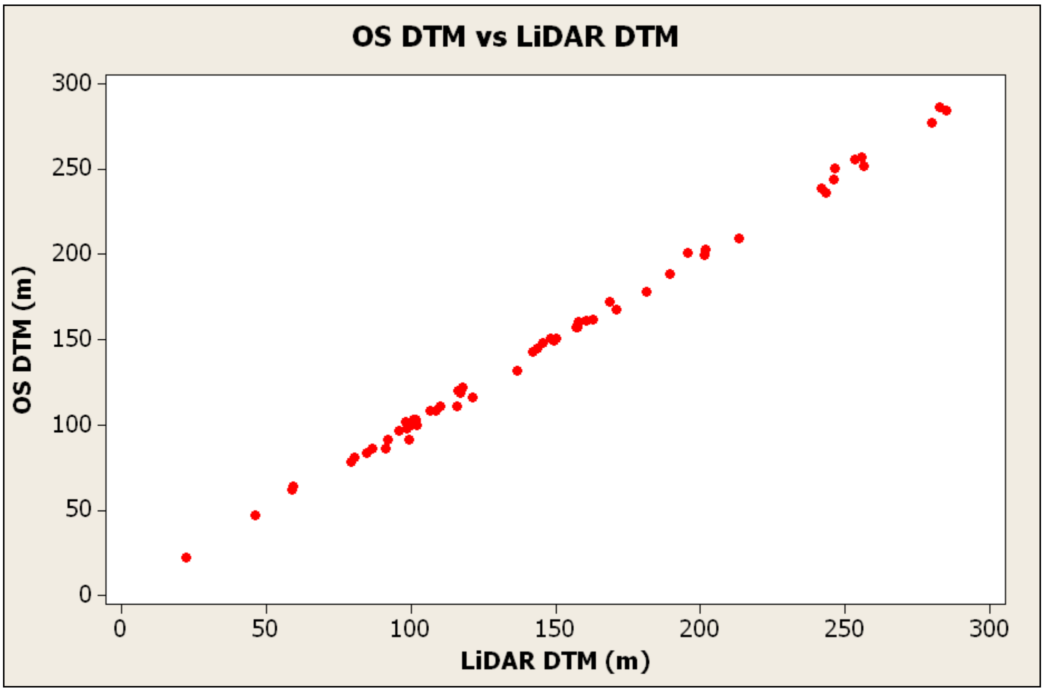


Figure 3.10: Scatter plot showing correlation between values in meters extracted from both LiDAR and Ordnance Survey DTMs (r = 0.999, n=56, P < 0.001), Aberfoyle Forest, Scotland

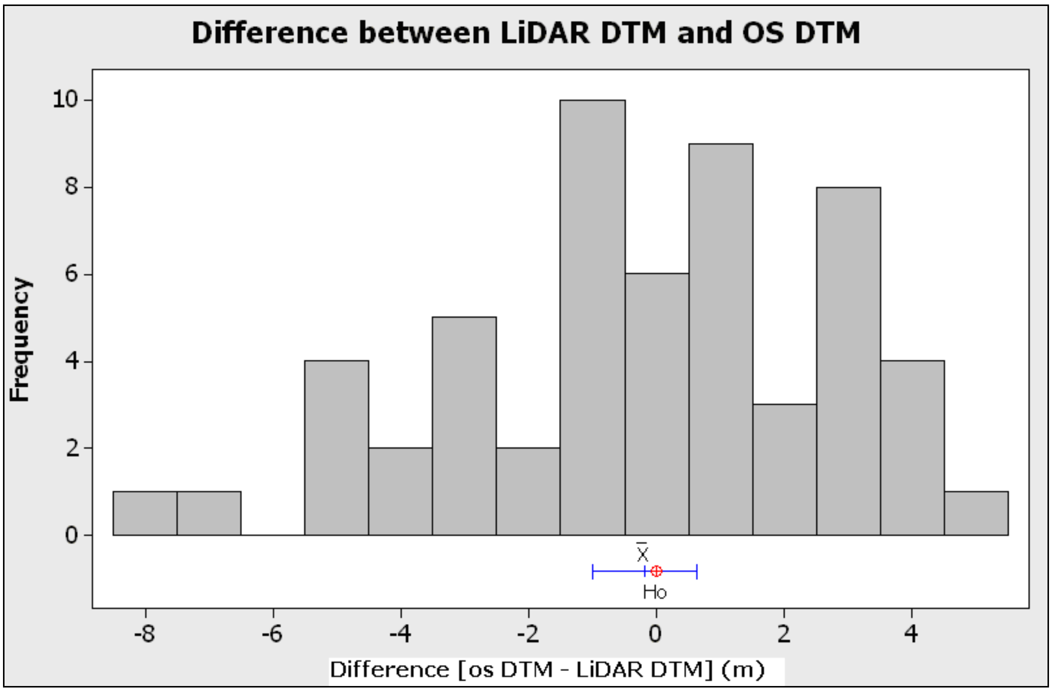


Figure 3.11: Histogram showing distribution of difference between OS DTM and LiDAR DTM. Mean difference is -0.19 and it is not significantly different from 0 (*t-test*, *P*<0.646). Blue lines represent 95% confidence interval of the mean. Aberfoyle Forest, Scotland.

3.3.2 Canopy Cover

Correlation between mean canopy cover (LiDAR) and mean canopy closure (field) was assessed at both Abernethy Forest and Aberfoyle.

Abernethy Forest

Mean LiDAR canopy cover and mean field canopy closure were not normally distributed and therefore correlation was assessed using Spearman's rank correlation coefficient (r_s). Results show that both variables are strongly correlated (r_s = 0.65 (n=32, P[3] < 0.001).

Aberfoyle Forest

As opposed to Abernethy Forest, where only Scots pine plots were surveyed, two tree species were surveyed at Aberfoyle: Scots pine and sitka spruce (*Picea sitchensis*). Correlation between LiDAR canopy cover and field canopy closure was tested first for all plots together (i.e. Scots pine + sitka spruce) and was found to be weaker than at Abernethy (r_s =0.53, P< 0.00, n=56). Sitka spruce and Scots pine crown shapes are considerably different and this could have an effect on the relationship between canopy cover and canopy closure. Thus, correlations were also assessed for each tree species separately.

Sitka spruce: Correlation between mean LiDAR canopy cover and mean field canopy closure was assessed using Spearman's rank correlation coefficient. Results show that correlation is weak when only sitka spruce plots are considered (r_s=0.40, P< 0.015, n=36).

Scots Pine: Correlation was assessed also for Scots pine plots only. Results show that mean field canopy closure and mean LiDAR canopy cover for Scots pine are strongly correlated (Spearman's rank correlation coefficient = of 0.0.73' P< 0.001, n=20)

---

[3] P-value of the Spearman rank correlation is the p-value from the correlation of ranks

Abernethy Forest and Aberfoyle: Scots pine.

Correlation between mean LiDAR canopy cover and mean field canopy closure was assessed for all Scots pine plots (i.e. Abernethy Forest and Aberfoyle Forest). Both variables were non-normally distributed and heteroscedastic and were log transformed first, with no success. Thus, correlation was assessed using Spearman's rank correlation coefficient. Results show that a strong correlation exists between mean field canopy closure and mean LiDAR canopy cover when all Scots pine plots are assessed together (Spearman's rank correlation coefficient = 0.71, n=52, P< 0.001).

3.3.3 Number of trees

The number of detected "tree tops" (i.e. local maxima) within each plot was compared with the number of trees observed in the field in order to assess the accuracy of each approach, namely *canopy height model* and *cloud of points*..

3.3.3.1 Canopy height model approach

Three different search window sizes were tested in order to find the one which best fits average crown size: 4m, 3m and 2m radius. In a first visual examination it was clear that the 4m-radius search window was too large and that a number of trees were not being detected, therefore it was not even considered for further analysis and validation was carried out only for the 3m and 2m radius search windows.

Abernethy Forest

Out of 526 trees counted in the field, 315 (59.9%) were correctly detected using the 3m radius window and 366 (69.6%) using the 2m radius window. Errors of omission and commission were also assessed: percentage of trees that were wrongly detected was 9.7% (51 trees) for the 2m radius, and 2.1% (11 trees) for the 3m radius. Percentage of omitted trees was 40.1 % (211 trees) for the 2m radius, and 42.2% (222 trees) for the 3m radius. All these figures are summarized in Table 3.5 (see *Discussion*).

Aberfoyle

When both tree species (sitka spruce and Scots pine) were considered together, 424 out of 1214 trees (39.6%) were correctly detected using the 2m radius search windows. Performance of the local maxima approach varies with tree species: for sitka spruce, total number of trees identified using 2m search window was 272 out of 890 trees counted in the field (30.6%) while 632 trees were missed (71.0%) including 14 trees that were wrongly identified (2.2%). For Scots pine, 143 out of 324 trees were correctly detected (44.1 %), 190 trees were omitted (58.7%) and 9 trees were wrongly identified (2.8%). When a search window of 3m is used, only 17.5 % of total number of trees was identified (212 out of 1214 trees); 14.7% of sitka spruce trees (131 out of 890) were identified while 759 trees (85.3%) were missed; and 25% of Scots pine trees (81 out of 324) were identified while 75% (243 trees) were missed.

3.3.3.2 Cloud of points approach

Applying local maxima algorithm to the cloud of points is time consuming, and therefore, only two window sizes were tested: 3m and 2m radius.

Abernethy Forest

Out of 526 trees counted in the field, 296 (56.3%) were correctly detected using the 3m radius window and 374 (71.1%) using the 2m radius window. Errors of omission and commission were also assessed: percentage of local maxima that were wrongly identified as trees is 5.5 % (29) for the 2m radius, and 1.1% (6) for the 3m radius. Percentage of omitted trees was 34.4 % (181) for the 2m radius, and 44.8 % (236) for the 3m radius.

Aberfoyle

Again, algorithm performance was tested for both tree species together and also for each species separately. When both tree species (sitka spruce and Scots pine) are considered together, 422 out of 1214 trees (34.8%) were identified using the 2m radius search windows. For sitka spruce only, total number of trees identified was 269 out of the 890 trees counted in the field (30.2%) while 632 trees were missed (71.0%) and 11 trees were wrongly identified (1.2%). For Scots pine, 153 out of 324 trees were identified (47.2%) and 171 trees were omitted (52.8%). There were no trees wrongly identified.

Results for the 3m radius search window are as follow: 19.9 % of total trees counted in the field was identified (242 out of 1214 trees); 17% of sitka spruce trees (151 out of 890) were identified while 739 trees (83%) were missed; and 28.1 % of Scots pine trees (91 out of 324) were identified while 71.9% (233 trees) were missed.

Table 3.5 (Discussio*n*) and Figures 3.12 and 3.13 summarise the results presented above.

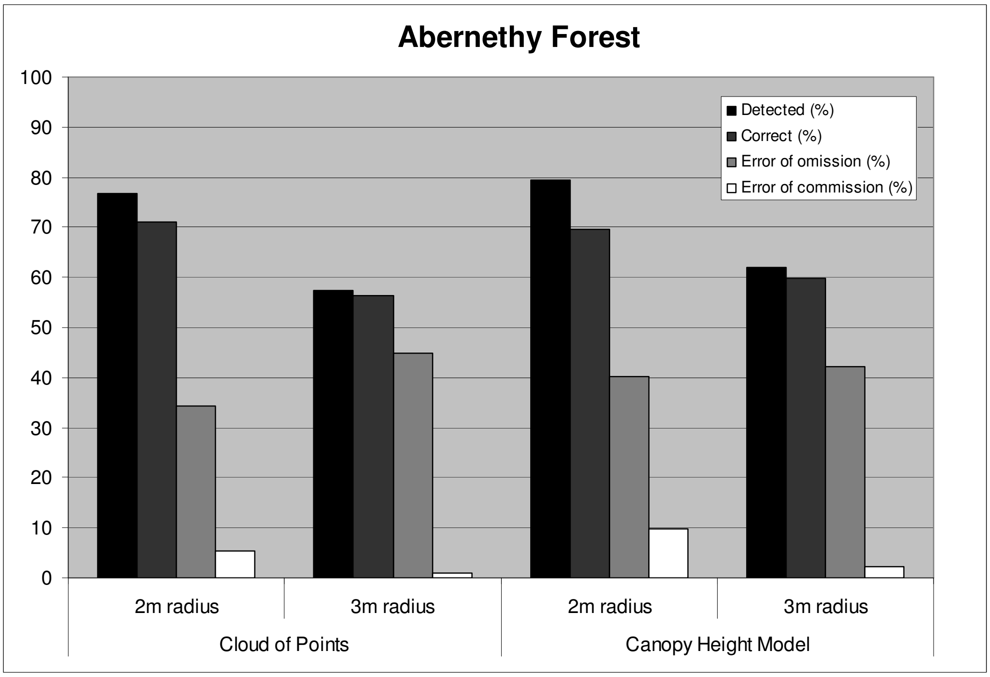


Figure 3.12: Bar chart showing percentage of correctly detected trees when applying local maxima algorithm to cloud of points (left) and canopy height model (right), and using 2m-radius and 3m-radius search windows. Data for Scots pine only, Abernethy Forest, Scotland.

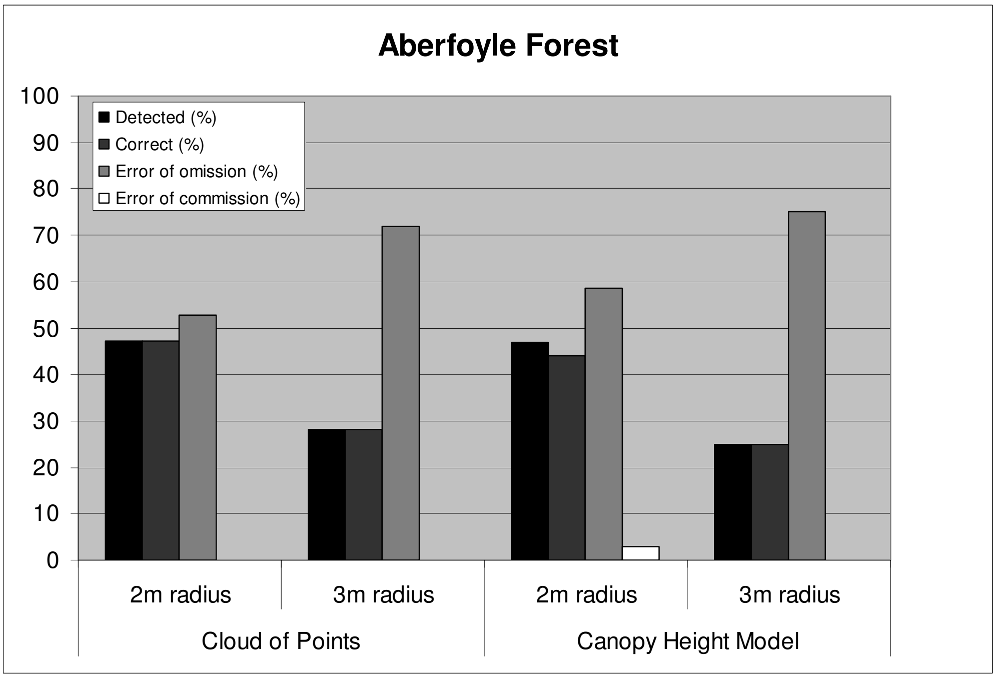


Figure 3.13: Bar chart showing percentage of correctly detected trees when applying local maxima algorithm to cloud of points (left) and canopy height model (right), and using 2m-radius and 3m-radius search windows. Data for Scots pine only Aberfoyle Forest, Scotland.

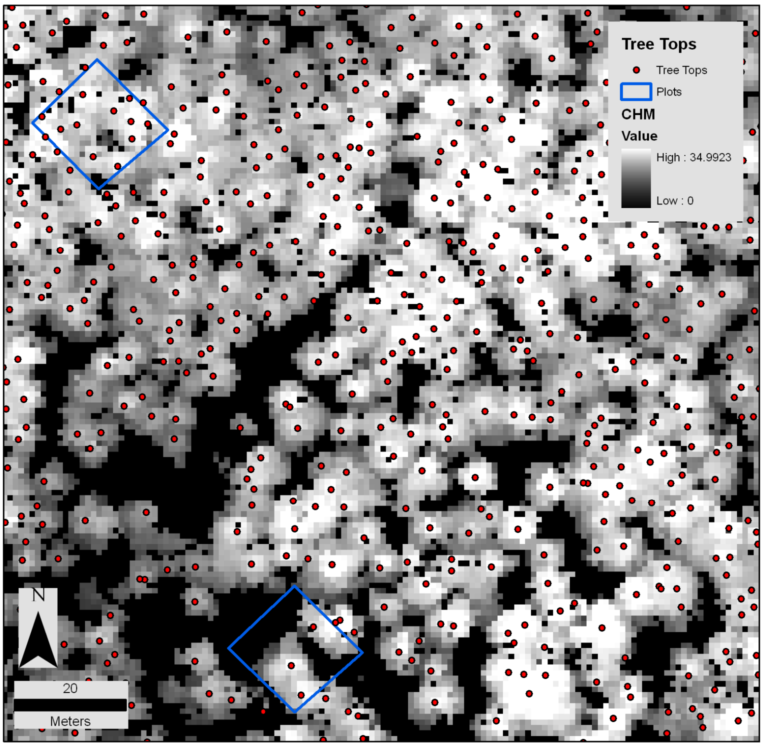


Figure 3.14: Results of the application of the local maxima algorithm to the cloud of points using a circular search window of 2 m-radius. Red dots and blue rectangles represent tree tops and plots respectively. Abernethy Forest, Scotland

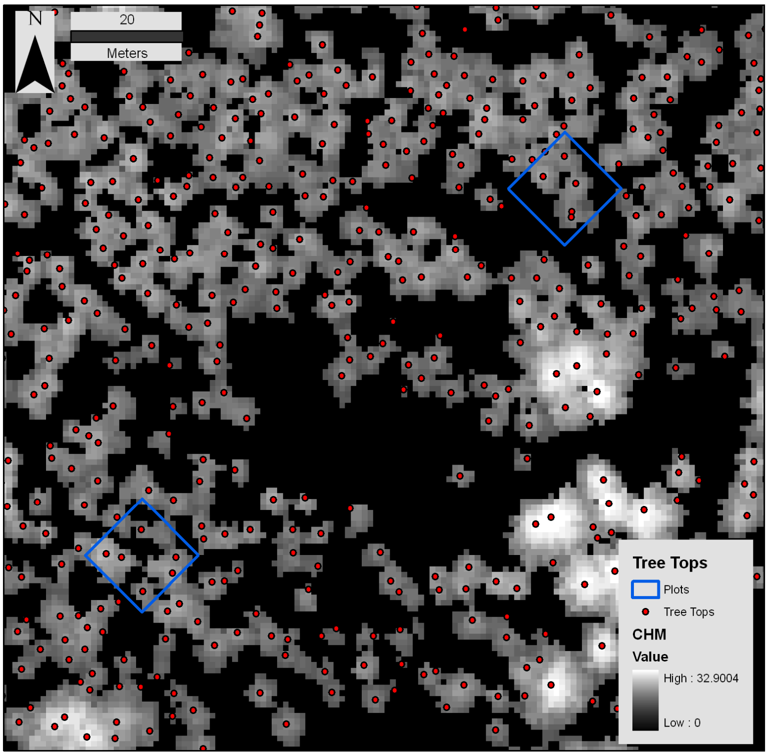


Figure 3.15: Results of the application of the local maxima algorithm to the cloud of points using a circular search window of 2 m-radius. Red dots and blue rectangles represent tree tops and plots respectively. Aberfoyle Forest, Scotland

3.3.4 LiDAR 90th and 95th percentiles and mean tree height

Mean tree height at the plot level was compared to 90th and 95th percentile LiDAR height and results are presented below:

Abernethy Forest

Both LiDAR 90th and 95th percentile height produced strong correlations with field mean tree height (*r*=0.91 and r=0.92 respectively, *n*= 32, *P*< 0.001). RMSE was 2.7m and 2.6m respectively and mean difference 2.2m and 2.0m.

Linear regression was also investigated. Results show that both LiDAR 90th and 95th percentile height are significant predictors and explains 84% and 83% respectively of variation in mean tree heights at the plot level (*n*=32, *P*< 0.001; Figures 3.16 & 3.17).

Aberfoyle Forest

Correlation between field mean tree height and LiDAR 90th and 95th percentile respectively was also assessed for Aberfoyle. Both LiDAR 90th and 95th percentile height produced strong correlations with field mean tree height (*r*=0.91 and r=0.94 respectively, n=56, *P*< 0.001. RMSE was 4.4m and 2.6m respectively and mean difference 3.3m and 1.3m.

Linear regression was also investigated. Results show that both LiDAR 90th and 95th percentile height are significant predictors and explains 82.4% and 88.3% respectively of variation in mean tree heights at the plot level (*n*=56, *P*< 0.001; Figures 3.18 & 3.19)

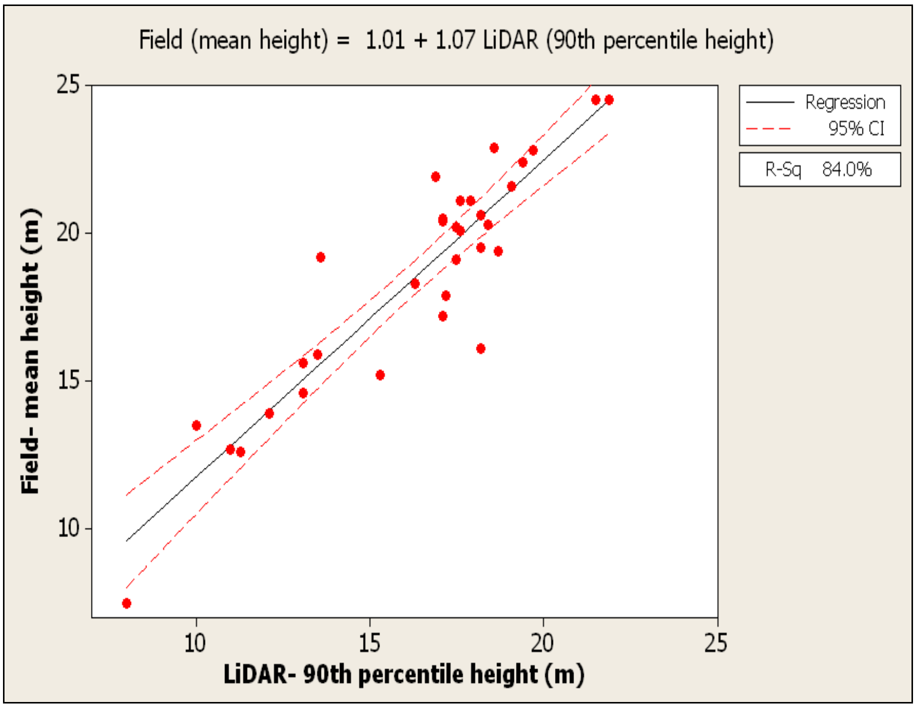


Figure 3.16: Linear regression between LiDAR 90th percentile and field mean tree height. LiDAR 90th percentile explains 84% of variance in field mean tree height at the plot level (P< 0.00, n=32) Abernethy Forest, Scotland

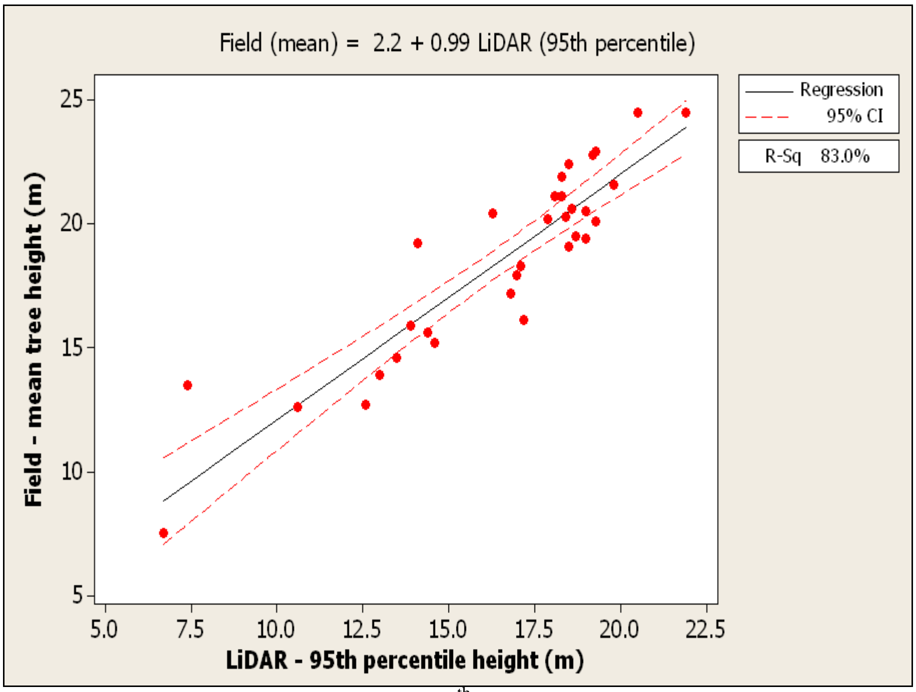


Figure 3.17: Linear regression between LiDAR 95th percentile and field mean tree height. LiDAR 95th percentile explains 83% of variance in field mean tree height at the plot level (P < 0.00, n=32) Abernethy Forest, Scotland

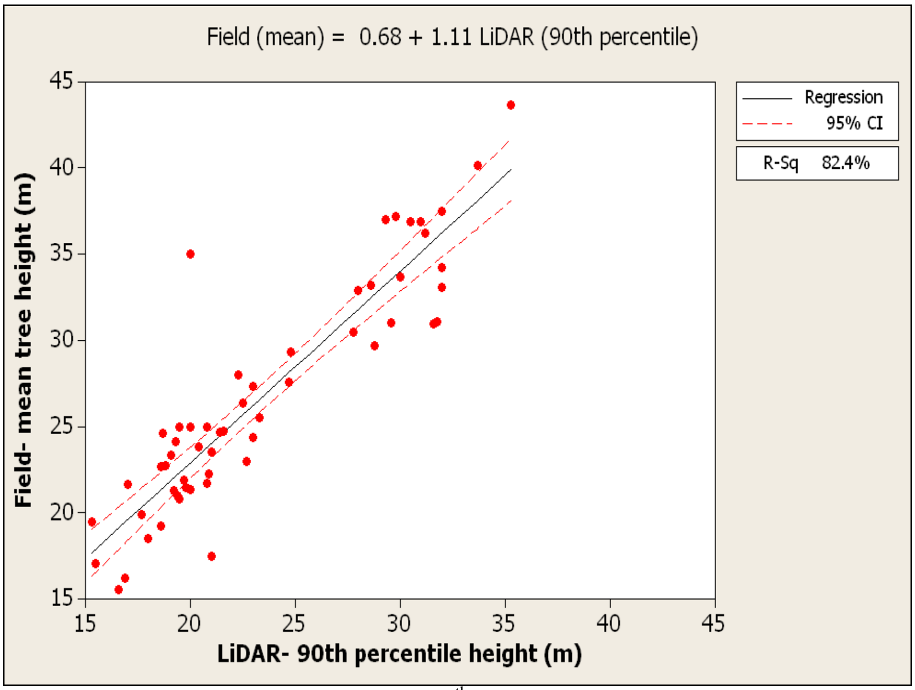


Figure 3.18: Linear regression between LiDAR 90th percentile and field mean tree height. LiDAR 90th percentile explains 82.4% of variance in field mean tree height at the plot level (P<0.00, n=56) Aberfoyle Forest, Scotland

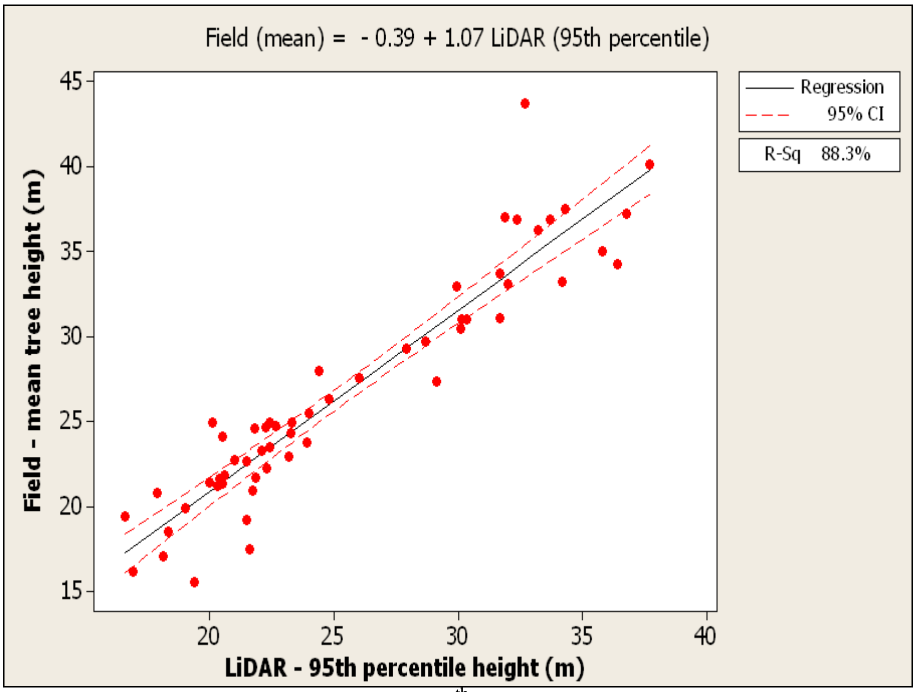


Figure 3.19: Linear regression between LiDAR 95th percentile and field mean tree height. LiDAR 95th percentile explains 88.3% of variance in field mean tree height at the plot level (P< 0.00, n=56). Aberfoyle Forest, Scotland

3.4 Discussion

3.4.1 Digital Terrain Model

LiDAR DTMs at Abernethy and Aberfoyle were compared to OS DTMs to assess whether gross systematic errors could be detected and, if possible, whether this error could be attributed to LiDAR or OS DTM.

In the case of Abernethy Forest, mean difference between the two DTMs was 2.0 m, and was found to be significantly different from zero suggesting the presence of systematic error. A large "flat" area (i.e. no variation in elevation) was detected in the OS DTM (Figure 3.5) and all outliers (i.e. points where the difference between both DTMs was higher than +/-5m) fall within that area, suggesting that these outliers are due to poorer quality of the OS DTM.

Despite the irregularities detected in the OS DTM, the strong correlation between both DTMs (r= 0.998) suggest that height variations are well represented. Furthermore, mean difference (2.0m) matches results from previous studies: Gaulton (2008) assessed the accuracy of LiDAR DTM (created within FUSION) in forested areas of the UK. A number of reference points distributed over five different woodlands located in Wales and Scotland were used. In four of these sites, elevation was measured in the field using a total station; for the fifth site, LiDAR derived DTM was compared to OS DTM as no accurate field measurements of elevation were available. Mean difference in meters between LiDAR and field measured elevations was 0.06, 0.58, -0.94, -1.80, and -2.08 for the fifth site. This last value (i.e.-2.08m) corresponds to the difference between LiDAR and OS DTM (Gaulton, 2008).

In the case of Aberfoyle Forest, mean difference between LiDAR and OS DTM (-0.19m) was much lower than for Abernethy and was not significantly different from zero. Furthermore, the strong correlation between both DTMs (r= 0.999) indicates that variations in height are well represented. No obvious explanation was found for the presence of outliers (i.e. differences between OS and LiDAR DTM larger than +/-5m). Since the results of the assessment were highly satisfactory (i.e. low mean difference and high correlation) these outliers were not further investigated.

3.4.2 Canopy Cover

The discussion focuses on Scots pine results only as this is the key tree species for this research.

Although canopy cover and canopy closure have been frequently used as synonymous, both are different measures of canopy density and mean canopy closure over a given area might not be correlated to mean canopy cover over the same area (Jennings *et al.*, 1999). Canopy closure has been traditionally associated with ecological applications such as habitat assessment and monitoring (Paletto and Tosi, 2009). Moreover, previous studies that have investigated habitat preferences of arboreal squirrel have found a positive relationship between canopy closure and squirrels presence (Smith and Mannan, 1994; Nelson *et al.*, 2005). On the other hand, remotely sensed data allow for a simple and direct estimation of canopy cover. However, due to the narrow angle of view (sensor scan angle), if canopy closure is to be estimated using LiDAR remote sensed, a more complex approach which includes in situ data and regression models needs to be developed (Korhonen *et al.*, 2011).

To determine the extent to which LiDAR canopy cover could be used as a surrogate for canopy closure measured in the field to assess habitat suitability for red squirrels in this project, the correlation between mean canopy cover and mean canopy closure at the plot level was assessed. In general it was observed that canopy closure values were higher than canopy cover values, the reason for this being that canopy closure measured with the spherical densiometer, which has a wider angle of view, reflects trees that are not only in vertical direction (Korhonen *et al.*, 2011)

When the correlation between both variables was assessed, the main conclusions were: Correlation between canopy closure and canopy cover is strong and Spearman correlation coefficients (r_s) are similar when a) all Scots pine plots at Abernethy Forest are considered (r_s =0.65, n=32, P< 0.00); b) when only Scots pine plots at Aberfoyle Forest are considered (r_s =0.75, n=20, P< 0.00) and c) when all Scots pine plots -from both study areas- are considered (r_s =0.71, n=52, P< 0.00). Correlation decreased when only sitka spruce plots at Aberfoyle are considered for the analysis (r_s =0.41, n=36, P< 0.015). These results support previous research carried out by Cook *et al.* (1995) who suggest that relationship between canopy cover and canopy closure is species dependant.

The difference between mean canopy cover and mean canopy closure was calculated for each plot. Plots with differences >30% were analysed individually:

Abernethy Forest: Plots 10, 12 13 and 14 at Abernethy Forest were all located in a semi-natural stand, and tree densities in these plots were relatively low, ranging from 5 to 12 trees. The large difference at these plots could therefore be explained by the fact that the difference between canopy cover and canopy closure increases as canopy density decreases (Cook *et al.*, 1995). In the case of plot number 2 (diff = 49.8%, Table B.3, Appendix B) it was located within a stand where felling activities were being carried out at the time the stand was being surveyed. Therefore, it is possible that trees in this particular plot have been felled between the time when the plot was surveyed and that when LiDAR data was acquired.

Aberfoyle Forest: 3 plots out of 20 (if only Scots pine plots are considered) present a difference larger than 30% (39, 43 & 45, Table B.4, Appendix B). In all cases, LiDAR canopy cover is lower than field canopy closure and the 3 plots are located near the boundaries of the forest. Plots locations in the field were recorded using a GPS with accuracy of +/- 1m to 5m. Thus, a miss-match between LiDAR and field plots can occur – which would lead to LiDAR canopy cover being, for example, underestimated if part of the plot was located outside the boundary of the forest due to an error in geolocation.

It is important to highlight here that field canopy closure measurements show low variability: mean percentage canopy closure ranges from 61% to 93%, while mean percentage canopy cover (LiDAR) ranges from 11.7% to 95.7 %. Spherical densiometers have been criticised for their poor resolution and weaker sensitivity to relatively large variations in canopy closure (Jennings *et al.* 1999, Cook *et al*, 1995). For example, a study carried out by Cook *et. al*, (1995) showed that moosehorn estimates from 50% to 95% corresponded to densiometer estimates from 80% to 95%. Nonetheless, spherical densiometers are still widely used as they provide a more objective approach to visual assessments (Jennings *et al.* 1999).

Despite spherical densiometer limitations, correlation between LiDAR mean canopy cover and field mean canopy closure at the plot level is strong (r_s=0.71) when only Scots pine is considered. This matches results from a previous study carried out by Rosette *et. al.* (2009) which reports strong correlation between canopy cover derived from airborne LiDAR and canopy closure measured in the field using hemispherical photography (*r*=0.77). Results obtained in this study support the use of LiDAR canopy cover as a surrogate of field canopy closure to assess forest stand characteristics and therefore red squirrels habitat quality.

3.4.3 Individual tree delineation

The local maxima algorithm was applied to both the canopy height model (CHM) and the cloud of points. From the results obtained – summarised in Table 3.5- it can be concluded that the best performance is reached when applying the local maxima algorithm to the cloud of points with a circular search windows of 2m-radius (Figures 3.14 & 3.15). A combination of a) higher percentage of trees correctly detected (71.1% at Abernethy, 47.2 at Aberfoyle); b) lower percentage of omitted trees (34.4% at Abernethy, 52.8% at Aberfoyle) and c) low percentage of local maxima wrongly identified as tree tops (5.5% at Abernethy, 0% at Aberfoyle) was achieved.

Accuracy of individual tree identification using local maxima approach ranges from 75% to 128% (Gaulton, 2008; García *et al.*, 2007; Table 3.6). Therefore, the overall percentage of trees correctly identified at Abernethy (71.1%) is not far from the range of values that were found in the literature.

Table 3.5: Percentage of number of trees corrected detected applying local maxima technique to cloud of points and to canopy height modes, using 2m-radius and 3m-radius search windows.

Abernethy Forest	Cloud of Points		Canopy Height Model	
Windows search size →	2m radius	3m radius	2m radius	3m radius
Detected trees (%)	403 (76.6)	302 (57.4)	417 (79.3)	326 (62)
Correct (%)	374(71.1)	296 (56.3)	366 (69.6)	315 (59.9)
Error of omission (%)	181 (34.4)	236 (44.8)	211(40.1)	222(42.2)
Error of commission (%)	29 (5.5)	6 (1.1)	51 (9.7)	11(2.1)
Aberfoyle Forest	Cloud of Points		Canopy Height Model	
Windows search size →	2m radius	3m radius	2m radius	3m radius
Detected trees (%)	153 (47.2)	91 (28.1)	152 (46.9)	81(25)
Correct (%)	153 (47.2)	91 (28.1)	143(44.1)	81(25)
Error of omission (%)	171 (52.8)	233 (71.9)	190 (53.7)	243 (75)
Error of commission %)	0 (0)	0 (0)	9 (2.8)	0 (0)

Error of commission and omission can be caused by search-window size being too small or too large respectively. Overlapping crowns in dense stands also cause error of omission (Popescu *et. al.*, 2003). In this study, lower accuracies at the plot level were achieved in plots with high tree densities, which suggest that errors of omission are more likely due to overlapping crowns. These findings support previous research by Vauhkonen *et al.* (2012) who found that the number of trees successfully detected under different forest types was strongly dependent on tree density and spatial distribution of trees (i.e. clustering).

Using a smaller window size (i.e. 1m) would probably increase the number of trees correctly detected in young Scots pine stands but would also presumably increase the error of commission (i.e. wrongly detected trees) in mature stands. In Aberfoyle, all sampled Scots pine stands were composed of mature trees, while in Abernethy, only 1 out of 4 stands was composed of young trees. On the other hand, only a small percentage of local maxima (5.7 % at Abernethy, 0% at Aberfoyle) were wrongly identified as trees, which is likely due to more than one local maxima allocated to the same crown. This suggests that only in a few cases the search window was larger than the tree crowns, and therefore, the 2m-radius window size was considered to be a good balance.

The use of a variable-size search window -where the window-size would be a function of the tree height- could potentially increase the number of trees accurately detected. This approach used in combination with local maxima produced an accuracy of 89.3% (García *et al*, 2007; Table 3.6). One limitation of this technique is that accurate allometric relationships between tree height and crown size are needed.

Furthermore, it is not clear whether –in the study mentioned above- the accuracy increased due to the variable-size search window or to the higher pulse densities (3-4 pulses/m^2).

LiDAR data resolution (i.e. point's density) has a strong influence on individual trees delineation and high densities are needed for effective and robust individual trees detection (Lee *et al*, 2010; Gaulton, 2008; Gaulton & Malthus, 2010; Vauhkonen *et al.*, 2012). Higher proportions of total number of trees have been detected using laser resolution higher than 5 pulses/m^2 (Holmgren, 2004) Table 3.6 shows a summary of accuracy achieved in previous studies and LiDAR data resolution (pulses/m^2) used. The number of trees correctly detected seems to depend more on the data resolution than on the approach itself. This explains the low percentage of correctly detected trees in Aberfoyle (47.2 %, 1 pulses/m^2) in comparison to Abernethy (71, 1%; 2 pulses/m^2). Gaulton and Malthus (2010) report accuracies of 78% when using LiDAR data densities of 1 pulse/m^2 in spruce plantations in Aberfoyle. However, the current study suggests that at least data densities of 2 pulses/m^2 are needed to achieve relatively good results (71.1%) in pine stands.

Finally, as validation was not performed based on individual tree locations but on number of trees per plot, errors in geolocation could have also contributed to errors in number of detected trees.

Table 3.6: Summary of accuracy achieved and LiDAR data resolution (pulses/m^2) used for delineating trees in previous studies

Detected trees (%)	**LiDAR pulses/m^2**	**Approach**	**Reference**
75-79	1-2	Local maxima	Gaulton, 2008; Doo-Ahn Kwak *et al*, 2007
80	2	GIS morphological tools (contours around crowns)	Koukoulas *et al.*; 2005
77.9	3-4	Watershed	Garcia, *et. al.*,2007
89.3	3-4	Local maxima (variable windows size)	Garcia, *et. al.*,2007
83 (dominant trees); 39.5 (total trees)	10	Local maxima	Maltamo *et. al.*, 2004
84	11	Local maxima	Gaulton , 2008
95	12 to 18	Local maxima	Lee *et al*, 2010
128	3-4	Local maxima + crown segmentation	Garcia, *et. al.*,2007

3.4.4 LiDAR 90th and 95th percentiles as estimators of mean tree height

Based on previous research (see *Introduction*) the relationship between mean field tree height and 90th and 95th percentiles of LiDAR height was investigated.

Both correlation and linear regression were explored to see which of these two LiDAR metrics would best match mean tree height at the plot level. Previous studies (for example, Hopkinson *et al*, 2008; Holmgren, 2004) investigated the relationship between LiDAR metrics and field tree height for heterogeneous forest without distinction of tree species. Thus, for Aberfoyle, all plots (i.e. sitka spruce and Scot pine) were assessed together.

Results are summarised in Table 3.7. In both study areas, strong correlations exist between both LiDAR 90th and 95th, and mean field height at the plot level. Furthermore, 90th and 95th percentiles explain a high percentage of variation of mean tree height. In both cases, correlation and regression coefficients as well as root mean square error suggest a better performance of 95th percentile as estimator of mean tree height. These results do not match results from a previous study carried out by Hopkinson *et al* (2008) where correlation with mean field tree height was slightly stronger for LiDAR 90th percentile (r=0.80, n=38) than for 95th percentile (0.79, n=38).

Table 3.7: Correlation and regression between LiDAR 90th and 95th percentiles and mean tree height at the plot level, Abernethy and Aberfoyle Forests, Scotland.

	90th percentile Vs. mean tree height		**95th percentile Vs. mean tree height**	
	Correlation	**Regression**	**Correlation**	**Regression**
Abernethy n=32	r=0.91 p-value<0.000 RMSE= 2.7	R^2 = 84% p-value<0.000	r=0.92 p-value<0.000 RMSE= 2.6	R^2 = 83% p-value<0.000
Aberfoyle n=56	r=0.91 p-value<0.000 RMSE= 4.4	R^2 =82.4% p-value<0.000	r=0.94 p-value<0.000 RMSE= 2.6	R^2 =88.3% p-value<0.000

Doce *et al* (2008) suggested that the effectiveness of LiDAR percentiles of height as estimators of stand canopy heights is species dependent. In this study, correlation parameters were very similar for Abernethy Forest - where all plots consist of Scots pine only, and Aberfoyle – where 20 plots (out of 56) are Scots Pine and the rest are sitka spruce. This would suggest that, at least for these study areas, tree species composition does not affect the performance of the approach. However, if the approach is intended to be used in different forest types (i.e. different species or mixed stands) it should be tested in each case.

CHAPTER 4

GLM implementation using LiDAR derived explanatory variables

The importance of forest structural parameters for red squirrels habitat mapping was addressed in Chapter 2. A General Linear Model (GLM) was used to relate the number of cones stripped by squirrels to *mean canopy closure*, *mean tree height* and *total number of trees* at the plot level. Chapter 3 introduced LiDAR remote sensing as a possible tool to extrapolate the analysis to the whole study areas. Methodologies to derive *canopy cover* (as a surrogate for field canopy closure), *number of trees* and *tree height* were described and results of accuracy assessment presented and discussed. The main aim of this Chapter is to implement the GLM using LiDAR derived explanatory variables in both study areas and to assess LiDAR-based model performance. The latter was achieved by performing a correlation between LiDAR-predicted and field-predicted number of cones stripped by squirrels. Moderate to high Spearman rank correlation coefficients (0.59 for Abernethy and 0.54 for Aberfoyle) suggest that LiDAR performs relatively well over the extent of the study areas. Finally, based on the GLM and using LiDAR data, habitat suitability maps were generated. Results suggest that when forest structure is considered, only 27% of the total forest area at Abernethy and 37% at Aberfoyle are suitable for red squirrel. Implications for management are discussed.

4.1 Introduction

Forest structure is an important factor explaining wildlife distribution and species habitat preferences (Clawges *et. al.* 2008). Several statistical models that relate the presence or abundance of specific animal species (i.e. birds) to variations in vegetation structure have been developed. However, since vegetation structural data collection at broad scale is both prohibitively expensive and time consuming, these models and studies have often been focussed on small areas (Bradbury *et. al.*, 2005; Clawges *et. al.* 2008; Martinuzzi *et.al.* 2009).

Passive (i.e. optical) remote sensing has been widely used to assess aspects of forested habitats over large areas but has not been able to successfully characterize and describe vertical forest structure (Lefsky *et. al.*, 2002; Bradbury *et al*, 2005; Turner *et al,* 2003). Active remote sensing, in particular LiDAR, can be used to directly measure structural characteristics of forest stands such as canopy cover, canopy height and height variability (Patenaude *et al.* 2004, Bradbury *et al.*, 2005; Clawges *et. al.* 2008; Martinuzzi *et al*. 2009).

Several researchers have used LiDAR remote sensing to assess habitat quality for different species with different degrees of success. Clawges *et al.* (2008) used LiDAR data to investigate the relationship between remote sensing derived vegetation indices, diversity and density of birds in South Dakota (USA). They calculated three LiDAR derived vegetation indices: *shrub density*, which is calculated using all returns between 0.5m and 2m; *foliage height diversity* which is the proportion of returns at different levels ranging from 0 to 20m; and *total vegetation volume* which is the total number of LiDAR returns above 2m. Their main findings show that, out of the 43 bird species surveyed, the relative densities of two species (dark-eyed juncos *Junco hyemalis* and warbling vireos *Vireo gilvus*) were strongly correlated with LiDAR *shrub density* (r= 0.63, P<0.01, n=51 and r=0.59, P<0.01, n=51 respectively), while total bird species density was significantly but not strongly correlated with LiDAR total vegetation volume (r= 0.33, P< 0.017, n=51).

LiDAR remote sensing has also been used to assess habitat quality for great tits (*Parus major*) and blue tits (*Parus caeruleus)* in Monks Wood, UK. Hill *et al.* (2004) found that great tits average nestling body mass increased with mean vegetation height estimated from LiDAR data; while blue tits average nestling body mass decreased with LiDAR derived mean vegetation height. Average nestling body mass is a measure of breeding success which results from the combination of food abundance and adults foraging efficiency, and therefore reflects habitat quality.

Goetz *et al.* (2010) investigated the applicability of LiDAR remote sensing to habitat quality prediction for black-throated blue warbler (*Setophaga caerulescens*) in Hubbard Brook Experimental Forest, USA. *Canopy height*, *height of median return*, *canopy complexity* (computed taking into account number and amplitude of peaks in a waveform), and *vertical distribution ratio* (related to the distance between the *canopy height* and the *height of the median return*: the shorter the distance, the lower the *vertical distribution ratio*) were derived from LiDAR data. LANDAT ETM data was also used to generate an image of *seasonal NDVI change* (difference between leaf-on and leaf-off NDVI). A decision tree method was used to model the distribution and abundance of the bird species and results showed that the variables derived from remote sensing accounted for 47% of variation in birds' data: *seasonal NDVI difference*, *canopy height* and *vertical complexity* were the most significant predictors.

Lesak *et al*. (2011) used step regression to assess the relationship between a number of LiDAR metrics and songbird species richness in Baraboo Hills, USA. LiDAR-derived variables used for this study were *mean* and *coefficient of variation of return height*, *number of non-ground returns*, *proportion of returns* within different height intervals, and 10% *quantiles of height* (i.e. 10, 20, 30...100). All variables were computed for the same 15m-radius plots where bird surveys were carried out. Several models were run and the best performance was achieved by a combination of *50th, 60th* and *100th height percentile*, and the *proportion of returns* within a 10 m layer in the middle (i.e. between ground elevation and maximum tree height). This model explained 21.6% of variability in songbird species richness.

LiDAR remote sensing has also been used to improve habitat modelling for Capercaillie (*Tetrao urogallus;* Alps, Switzerland) by incorporating vegetation vertical structure. Graf *et al.* (2009) used r*elative fraction of tree canopy*, *mean and standard deviation of canopy height*, and *density of tree canopy edges* (defined as contour length at 10, 20m and 30 m height) derived from LiDAR data at a spatial resolution of 125m (i.e. cell size = 125m). A general linear model (GLM) was used to predict presence/absence of the species, with the above mentioned LiDAR metrics as the explanatory variables. Model predicted presence of the species in 36% of the study area and absence in the rest, where presence and absence of the species were assumed to represent suitable and unsuitable habitat respectively.

Although mostly used to assess habitat for birds, LiDAR data have also been used to improve habitat modelling for mammals. For example, Nelson *et al.* (2005) used tree height and canopy cover to assess habitat quality for the endangered Delmarva fox squirrel (*Sciurus niger;* DFS) in the Delmarva Peninsula, USA. LiDAR flight lines were split into segments of 40m and *average canopy height* and *average canopy cover* were calculated for each segment. Knowing that the squirrel prefers tall trees and dense canopies, those areas with mean tree height > 20m and mean canopy cover

> 80% were selected. Out of the 32 identified sites, 25 (78%) were actually suitable habitat for the species.

With respect to the red squirrel in the UK - the focus of this research- suitable habitat or habitat quality has been mainly related to tree species composition and food availability (e.g. Gurnell 1983, 1987; Lurz *et al.* 2000). While the relationship between red squirrel habitat use and forest structural factors, such as canopy connectivity, tree densities and height heterogeneity has been suggested (e.g. Gurnell *et al.* 2002) it has not yet been quantified. In order to better understand and quantify this relationship, in this study data on forest structure and red squirrel food remains were collected during two field seasons carried out in a semi-natural Scots pine (*Pinus sylvestris*) forest (Abernethy) and a Scots pine plantation (Aberfoyle). A general linear model (GLM) was then used to relate key stand structural variables to squirrel feeding behaviour and thus patch selection. Results showed that *mean canopy closure, total number of trees* and *mean tree height* (at the plot level) were significant predictors and explained 43% of the variability in the number of cones stripped by squirrels ($P < 0.013$, 0.031 and 0.058 respectively, n=52). Details on data collection and analysis are presented in Chapter 3 and in Flaherty *et al.* (2012).

These results highlight the importance of considering structural characteristics of forest stands in the forest design for red squirrels. However, evaluating and monitoring vegetation structure at the forest level is expensive and time consuming. Hence, for management purposes these results advocate the need for methods to extract and utilise structural data (notably canopy closure and total number of trees) to derive habitat suitability information over large forest areas. LiDAR remote sensing can be used to retrieve the three variables found to significantly influence red squirrel feeding behaviour (namely canopy cover, tree height and number of trees). The aim of this Chapter is to estimate and map habitat suitability over the whole study area using LiDAR derived variables and the GLM presented in Chapter 3. For a review of techniques used to retrieve these forest structural variables as well as validation performed by comparing LiDAR derived products to data collected in the field, please consult Chapter 3. To achieve the aims of this Chapter, the following objectives will be addressed:

1. To ensure that only the error resulting from LiDAR is accounted for (excluding that inherent from the original GLM), results from a leave-one-out cross validation approach will be presented. This enables field-based predictions of the number of cones stripped by squirrels to be generated. These predictions, rather than the raw field number of stripped cones, are used to validate LiDAR predictions.
2. To assess the number of cones stripped by squirrels at wider scales, the GLM will be implemented using LiDAR data
3. The accuracy of the LiDAR predicted number of stripped cones will then be assessed, and finally,
4. Habitat suitability maps for both study areas and based on LiDAR data and the GLM will be produced.

In the next section a brief overview of the study sites is presented along with the methodology adopted to achieve the objectives listed above.

4.2 Methodology

4.2.1 Study Areas

Fieldwork was carried out at Abernethy Forest in October 2009 and at Aberfoyle in May 2010.

Abernethy Forest (57° 15' N, 3° 40' W) is owned and managed by the Royal Society for the Protection of Birds (RSPB) and lies between 200 m and 500 m altitude with a total area of 28 km^2 (Summers and Proctor, 1999). Two thirds of the forest (19 km^2) is native forest and one third is plantation. The dominant tree species is Scots pine.

Aberfoyle (56° 10" N, 4° 22" W) is managed by the Forestry Commission Scotland. The forest is part of the Loch Lomond and Trossachs National Park, located in the west of Scotland, approximately 25 km North-West of Glasgow. Total forest area estimated from Forestry Commission stock maps is slightly less than 12000 ha. Tree species present in the forest are predominantly conifers and include Scots pine, sitka spruce (*Picea sitchensis*), lodge pole pine (*Pinus contorta*) and Norway spruce (*Picea abies*). A number of semi-natural stands consisting of oak (*Quercus petraea*), birch (*Betula* spp.), alder (*Alnus glutinosa*) and ash (*Fraxinus excelsior*) are also present. Scots pine covers 943.5 ha of the total forest area (McInerney *et. al.*, 2010). Both forests are home to the native red squirrel. Further details on both study areas are provided in Chapter 2.

4.2.2 Field-based GLM validation

GLM development

A general linear model (GLM) was developed to relate key stand structural variables to squirrel feeding behaviour. The resulting GLM is presented below:

$$\boldsymbol{SC = -6.5 + (0.083)\, CC + (0.018)\, NT + (0.083)\, TH}$$

Where SC is *total number of stripped cones*, CC is *mean canopy closure*, NT is *total number of trees* and TH is *mean tree height* (See Chapter 2 for more details).

GLMs are used when variables are not normally distributed and variance is not constant (Crawley, 2007). GLMs use a link function to relate predicted values to linear predictors. In the case of Poisson error structure, which is commonly used for count data, the default link function is *log (e).* In order to obtain values on the scale of the original dependent variables, predictions from the model need to be back-transformed (antilog) before results can be interpreted (Crawley, 2007).

GLM Validation

Cross validation is used to assess model performance. The approach relies on making new predictions using data not used in the development of the model. *Hold-out* is the simplest way to perform cross-validation. It consists of splitting the data into two datasets: one for model fit (training dataset) and one for model validation (testing dataset). A key disadvantage of this approach is that evaluation depends heavily on which data points are used for training and which ones are used for testing. Moreover, data might not be enough to keep part of it for testing. A more exhaustive version of this method is referred to as *leave-one-out* (LOO) cross-validation (Arlot & Celisse, 2010). In this case, the predictive power of the model is assessed as follows:

(a) Considering *n* observations, observation *i* is left out and the model is fit using the rest of the data.
(b) The model is then run and a prediction is made for the omitted observation
(c) The error is computed ($e_i = \textit{observed } y_i - \textit{predicted } y_i$).
(d) This procedure is repeated for each individual observation. As a result, the model is run *n* times.
(e) Model performance is ultimately assessed by exploring the correlation between observed data (i.e. data collected in the field) and the values predicted by the model for each data point.
(f) Average or mean square error is then also computed to evaluate the overall performance of the model (Arlot & Celisse, 2010).

This approach provides an efficient use of the available data, as only one observation is omitted at each step. One key criticism of the approach is that it can be very time consuming to implement.

In this study, LOO cross-validation was performed to assess field-based model performance. The model was expected to provide relative rather than absolute abundance of stripped cones per plot (Pearce and Ferrier, 2001). In this context this means that plots with higher numbers of stripped cones would be more suitable than those with lower numbers of stripped cones. For this reason, and also because variables were not normally distributed, all correlations were assessed using a Spearman rank correlation coefficient.

The values predicted by LOO cross-validation (field-predicted stripped cones) were also used to assess LiDAR performance. This is explained in more detail in the following sections.

4.2.3 Implementation of GLM using LiDAR

The field measured variables used in the GLM to predict number of cones stripped by squirrels were replaced by LiDAR derived variables. This enables an assessment of habitat quality for the whole study areas.

4.2.3.1 LiDAR data acquisition and pre-processing

LiDAR data characteristics are summarised in Table 4.1.

Table 4.1: Details of the LiDAR data available for the study. Scotland, UK

	Abernethy	**Aberfoyle**
Date	27th November 2009	8th May 2008
Resolution (pulses/m^2)	2 pulses/m^2	1 pulse/m^2
Data provided	First, second, and last return- intensity	First and last return – intensity
Scan angle	+/- 18°	+/- 20°
Average flight altitude	1760 m	1310 m

LiDAR data were first processed to generate a digital terrain model (DTM), a digital surface model (DSM) and a canopy height model (CHM). Canopy cover, the number of trees and tree heights were derived for both study areas. An accuracy assessment was performed by comparing LiDAR derived metrics to field measurements at the plot level. The following LiDAR variables, namely *mean canopy cover*, *95th percentile of height* and *total number of trees* were compared to field derived mean canopy closure, mean tree height and total number of trees respectively. Detailed descriptions of LiDAR data processing and of the accuracy assessment are provided in Chapter 3. Table 4.2 provides a summary of the validation results.

Table 4.2: Summary of the accuracy assessment (Spearman Correlation coefficient, r_s) between field and LiDAR data (at the plot level). Both study sites are considered separately (see Chapter 3 for details)

	Abernethy Forest	**Aberfoyle**
LiDAR Mean Canopy Cover Vs Field Mean Canopy Closure	$r_s = 0.65$ $n = 32$ $P < 0.00$	$r_s = 0.73$ $n = 20$ $P < 0.00$
LiDAR Number of trees Vs Field Number of Trees	71.1% of trees correctly detected	47,2 % of trees correctly detected
LiDAR 95th percentile height Vs Field mean tree height	$r = 0.92$ $P < 0.001$ $n = 32$	$r = 0.94$ $P < 0.001$ $n = 56$

4.2.3.2 Raster file generation

For the GLM to be implemented using LiDAR data, three raster files were created: *Lidar Canopy Cover* (hereafter "*LCC*"), *95th percentile of height (Lidar Tree Height,* hereafter "*LTH*") and *Lidar Number of Trees* (hereafter "*LNT*"). For the field-based GLM, mean values at the plot level were used. To ensure comparability, pixel size for the LiDAR derived raster files was the same as field plot size (i.e. 14m x 14m).

LiDAR Canopy cover

LCC was computed as the proportion of vegetation returns above a threshold or *height-break* for a given cell grid, where

LCC = number of returns > height-break / total number of returns (McGaughey, 2009).

The value used as threshold was the height at which measurements were made in the field (breast height =1.3 m). The output pixel size was 14m. To compute and extract LCC, the FUSION software was used (details provided in Chapter 3).

LiDAR Tree Height

The *GridMetrics* functionality available in FUSION enables the computation of a series of descriptive statistics for all returns within each cell in the output grid. The program was used to compute the *95th percentile* height value for each of the 14m x 14m cells. The 95th percentile was used as a surrogate for mean tree height following my detailed review and validation (Chapter 3). *GridMetrics* computes percentiles as follows:

$(n-1)\,p = i + f$

Where i is the integer part of $(n-1)\,p$; f is the fractional part of $(n-1)\,p$, n=number of observations (in this case, height values per cell) and p is percentile value divided by 100

If $f=0$, Percentile Value = x_{i+1}

If $f>0$, Percentile Value = $x_{i+1}+f\,(x_{i+2} - x_{i+1})$ (McGaughey, 2009).

LiDAR Number of trees

Original LiDAR files containing first-return cloud of points (noise removed, see Chapter 3 for details) were split into smaller more manageable tiles and the local maxima algorithm was applied to all tiles (using MATLAB 7.12.0). The local maxima technique identifies the highest return within a moving window by comparing them to their near neighbours (also described in Chapter 3). To avoid false detections on the edges of the tiles, overlapping areas (between tiles) were kept.

Once the local maxima had been performed those overlapping areas were removed. The algorithm produces ASCII files containing *X, Y* coordinates and *heigh*t of the identified trees. These files were converted into vector (point) files using ArcGIS 9.3. A polygon (*fishnet*) composed of 14m x 14m cells was created, LiDAR detected trees falling within each cell were counted and recorded and a raster file was created using the “count” field as pixel value. The output file is a raster where each 14m x 14m pixel value represents the number of trees within each square of the fishnet. All tiles were finally merged together to create one raster file for the whole study area.

Calibrated Number of trees

Unlike the LCC and LTH, the LiDAR number of trees (LNT) was the LiDAR derived variable with the poorest performance, in particular for Aberfoyle, where only 47.2 % of the trees were correctly detected. This poor result for Aberfoyle is probably due to the low spatial resolution of LiDAR data (i.e. 1 pulse/m^2 as opposed to 2 pulses/m^2 for Abernethy).

LiDAR spatial resolution can range from an average of 1 pulse/m^2 or less (i.e. 0.3 or 0.5) to more than 12 pulses/m^2 .Acquiring lower densities LiDAR data allows for higher flying altitudes and therefore reduces acquisition costs (Evans *et al*, 2009). However, higher pulse densities allow for more accurate detection and mapping of objects on the earth surface, and as discussed in Chapter 3, it also allows for more accurate detection of individual trees (Lee *et al*, 2010; Gaulton, 2008).

Given this poor result for Aberfoyle, and acknowledging that the aim of this study is fundamentally to generate red squirrel habitat suitability maps using only LiDAR data, I calibrated the *LNT* using field data (i.e. field counted number of trees) and a linear regression. While this may appear as a circular argument-as I am using field data to calibrate LiDAR- the reasoning for doing so is to assess the effects on the habitat suitability maps of the low spatial resolution of the Aberfoyle LiDAR data, and to determine if higher density LiDAR data is necessary to improve the accuracy of the LiDAR predicted number of cones and therefore, of the LiDAR based habitat suitability maps.

To achieve this aim, the following objectives will be addressed:

- To assess whether the accuracy of the LNT improves when the correction is applied

- To implement the GLM using the LNT as originally derived from LiDAR (GLM 1) and the calibrated LNT (GLM 2).
- To assess the accuracy of both GLM 1 and GLM 2 using LOO cross-validation and RMSE (as explained in section 4.2.2)

Calibration regression

There is evidence that a relationship between number of trees and tree height might exist, although it depends on other factors such as tree species and yield (Zeide, 1995). With the purpose of improving the calibration regression, I tested whether this relationship existed in Aberfoyle by incorporating LiDAR 95th height percentile (LTH) into the equation. I found that LTH was also a significant predictor of LiDAR number of trees and that LTH and FNT together explained 57% of the variation in LiDAR number of trees ($P < 0.001$, $n=20$)

The calibration regression is presented below:

$$\boldsymbol{LNT = 31.2 - 1.37\, LMH + 1.08\, FNT}$$

Where LNT is the LiDAR number of trees, LMH is the LiDAR mean height and FNT is the field number of trees,

This regression was used to calibrate the Aberfoyle LNT and two different habitat suitability maps were generated (GLM 1 and GLM 2). The LiDAR number of trees per plot after applying the calibration was compared to the number of trees counted in the field to assess the performance of the regression.

In the case of Abernethy, the number of trees correctly detected (71.1 %) was considered to be within the expected range of accuracy as found in the literature (Gaulton, 2008; Doo-Ahn Kwak *et al.*, 2007; Garcia, *et al.*, 2007) and no correction was applied.

4.2.3.3 GLM implementation

For Abernethy Forest, the whole LiDAR image was used for the analysis. For Aberfoyle (based on forest stock maps, Forestry Commission Aberfoyle, 2010) only forested areas corresponding to Scots pine stands were selected. For both study areas, the LiDAR derived explanatory variables were stored as raster files. As regression models should only be used to generate predictions within the limits of the range of the available data (Rees, 1995), the values outside the range of field measurements were masked out and excluded from the raster files. As a result, only the pixel values between 54% and 95% for LCC, 3 and 74 for LNT and 10m and 26m for LTH were kept.

The GLM was applied using the raster layers. The resulting maps were then back-transformed (antilog) by calculating base *e* exponential function of cells in the raster (ArcGIS 9.3). The final results present the number of cones stripped by squirrels per pixel, when field measured explanatory variables are replaced by LiDAR data.

Finally, in order to assess LiDAR performance, the values at the plot level were extracted and compared with values predicted using field data (i.e. using the same LOO cross-validation as that described above).

4.2.3.4 Habitat suitability maps

The model was not expected to provide absolute numbers of cones stripped by squirrels but a relative measure of habitat use. By this, I mean that the more stripped cones found, the more suitable the habitat relative to the other measured plots. To reflect and emphasise this relative, rather than absolute measure, I initially classified the LiDAR-based GLM maps into 2 basic levels of suitability: namely unsuitable (LSC = 0) and suitable (LSC >= 1). To allow for further discrimination, suitable areas were further classified into two levels of suitability. To inform this sub-discrimination, frequency histograms of LiDAR maps where generated. This was completed to explore whether natural breaks in number of stripped cones could be observed, thereby indicating natural thresholds between low, medium and high use (Figure 4.1). As no breaks were observed, experts on red squirrels were consulted instead (Lurz, *pers. com*, 2012) to provide advice on the level of cones necessary for consideration as medium suitability in the UK. No information was available on the high suitability; hence only one category for medium to high was created. Our final categorisation therefore includes three categories as follow: Unsuitable (LSC=0), Low suitability (LSC < 10) and finally Medium to High suitability (LSC >=10).

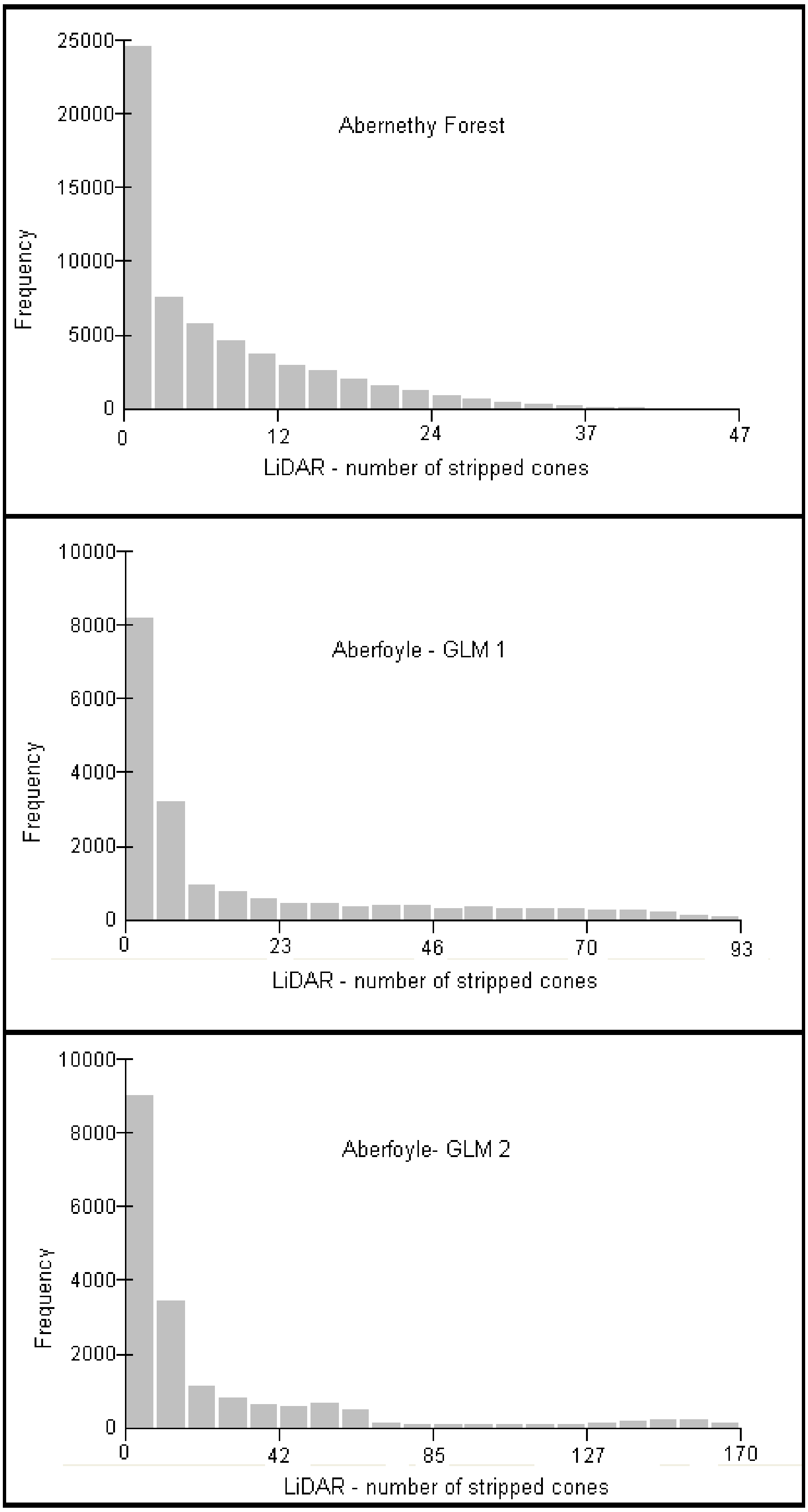


Figure 4.1: Frequency histograms of LiDAR maps for Abernethy, Aberfoyle GLM 1 and Aberfoyle GLM 2. No natural breaks were observed and thresholds for classification into different levels of habitat suitability were based on expert knowledge.

4.3 Results

4.3.1 Field-based GLM validation

A Spearman rank correlation between the field-collected and the field-predicted (LOO cross-validation) cones stripped by squirrels was assessed for all data together (i.e. Abernethy plus Aberfoyle). Results show a moderate performance of the field-based model (r_s =0.40; P <0.004, n=52, RMSE = 20, Figure 4.2, Table C.3, Appendix C).

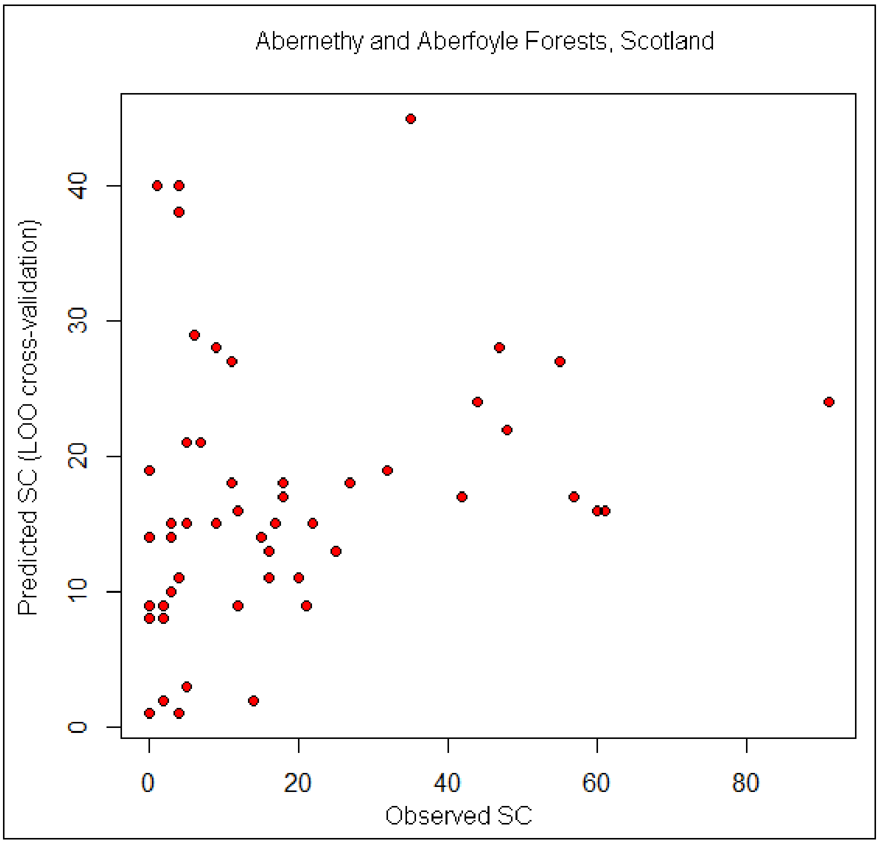


Figure 4.2: The correlation between the field-collected (Observed SC) and the field-predicted (Predicted SC) number of stripped cones for all data together (i.e. Abernethy plus Aberfoyle). Results show a moderate performance of the field-based model (r_s =0.40; P <0.004, n=52, RMSE = 20,

4.3.2 Implementation of GLM using LiDAR

The field-predicted number of stripped cones was also compared to the LiDAR-predicted number of stripped cones. LiDAR data acquired at Aberfoyle and Abernethy had different characteristics (in particular pulse density) which has an influence in the accuracy of LiDAR derived metrics. Thus, correlations between field-predicted and LiDAR-predicted number of stripped cones were assessed for each study area separately (Figures 4.3, 4.4 & 4.5; Tables C.1 and C.2, Appendix C). Root mean squared error (RMSE) was also computed for all the model comparisons to assess models' performance. Results are summarised in Table 4.6.

Table 4.6: Spearman rank correlation between field predicted and LiDAR predicted number of stripped cones for both study areas, Abernethy Forest and Aberfoyle, Scotland.

Study Area	**Correlation between field predicted stripped cones & LiDAR predicted stripped cones**
Abernethy	$r_s = 0.59$ $P < 0.00$ $n = 32$ RMSE=12.3
Aberfoyle GLM 1 (un-calibrated number of trees)	$r_s = 0.54$ $P < 0.014$ $n = 20$ RMSE=11.9
Aberfoyle GLM 2 (calibrated number of trees)	$r_s = 0.60$ $P < 0.005$ $n = 20$ RMSE=29.8

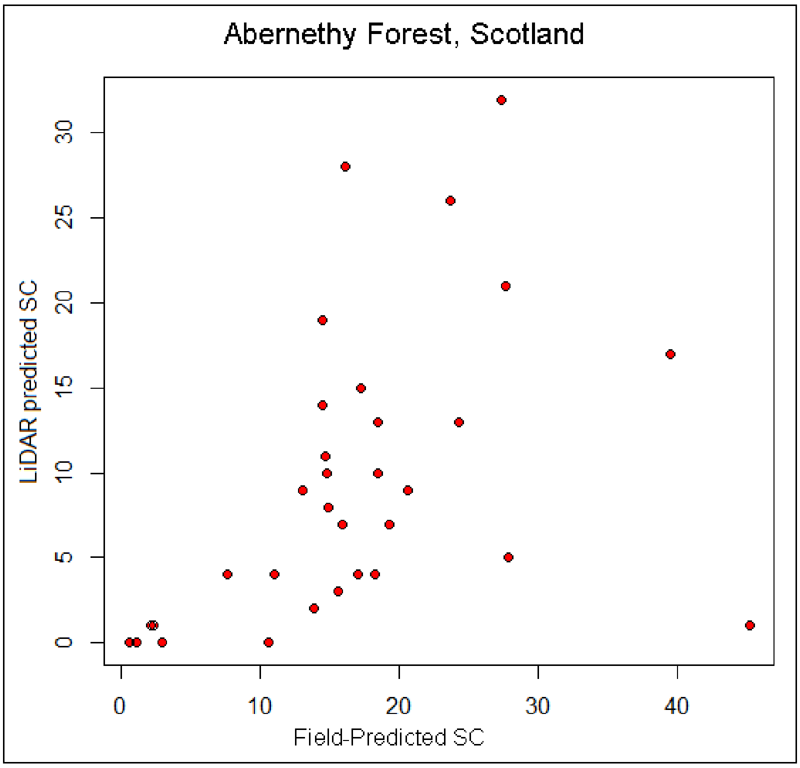


Figure 4.3: The correlation between the field-predicted stripped cones (Field-Predicted SC) and LiDAR predicted SC. Results show a moderate to strong performance of the LiDAR based model for LiDAR data collected at Abernethy Forest. Spearman rank correlation coefficient = 0.59, n=32, RMSE=12.3.

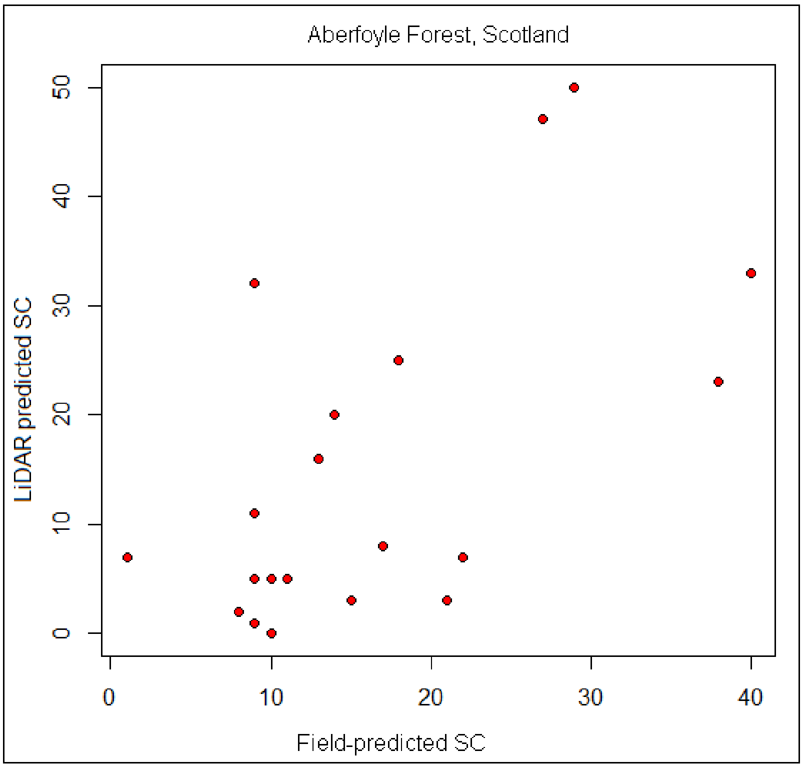


Figure 4.4 Correlation between field-predicted and LiDAR-predicted number of stripped cones using the un-calibrated LNT (GLM 1) Spearman rank correlation coefficient = 0.54, n=20, RMSE= 12.2. Aberfoyle Forest, Scotland

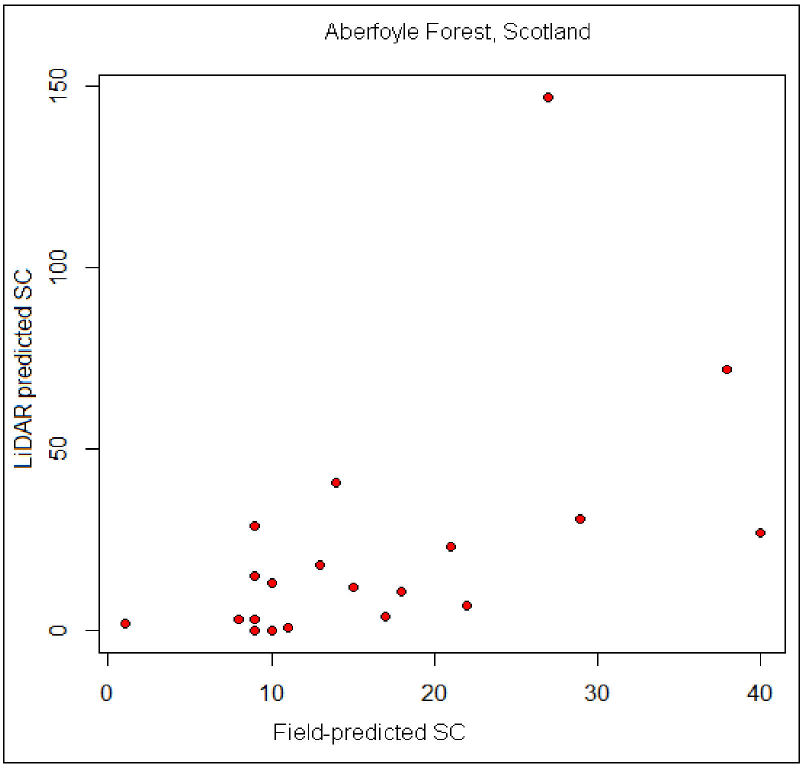


Figure 4.5: Correlation between field-predicted and LiDAR predicted number of stripped cones (SC) using the calibrated LNT(GLM 2) Spearman rank correlation coefficient = 0.60, n=20, RMSE=29.8 Aberfoyle Forest, Scotland

4.3.2.1 Calibration of Aberfoyle number of trees

Considering all plots, a total of 354 trees were detected (109%). Out of 324 trees counted in the field, 243 (75%) were correctly detected, 81 (25%) were omitted, and 108 (33%) were wrongly detected. Accuracy assessments for Abernethy and Aberfoyle (un-calibrated) are presented in Chapter 3.

4.3.2.2 Habitat suitability maps

LiDAR-predicted number of cones stripped by squirrels (i.e. GLM map pixel values) ranged from 0 to 48 at Abernethy, 0 to 93 at Aberfoyle GLM 1 and 0 to 170 for GLM 2. LiDAR-based GLM maps were classified into three habitat suitability levels: Unsuitable, Low suitability and Medium-to-High suitability.

Sizes of the areas falling within the different categories were calculated for all the maps: at Abernethy, 30% of the area was classified as Unsuitable and 70% as Suitable, of which 43% as Low and 27% as Medium-to-High suitability. For Aberfoyle GLM 1, 26% was classified as Unsuitable and 74% as Suitable; of which 37% as Low and 37% as Medium-to-High suitability. For GLM 2, 24% was classified as Unsuitable and 76% as Suitable, of which 29% as Low and 47% as Medium-to-High suitability.

The size of the areas for both Aberfoyle GLM 1 and GLM 2 were compared to assess the effects of the correction in number of trees. Results show a significant difference in the size of the areas (*Chi-squared test*, *$p<0.016$*) with an increase in the size of the Suitable and Medium-to-high suitability areas as well as a decrease in the Unsuitable and Low suitability areas when the number of trees is corrected at Aberfoyle (GLM 2). These results are presented in Table 4.7 and Figures 4.6, 4.7, 4.8a & 4.8b.

Table 4.7: Total areas (ha) within each habitat suitability category for both Abernethy and Aberfoyle forests- Aberfoyle results for both GLM 1 and GLM 2.

	Abernethy	**Aberfoyle**	
Suitability Level	**area (ha) GLM**	**area (ha) GLM 1**	**area (ha) GLM 2**
Unsuitable	352.5 (30%)	93.8 (26%)	87.9 (24%)
Low	492.4 (43%)	132.1 (37%)	101.6 (29%)
Medium to high	319.6 (27%)	133.5 (37%)	169.9 (47%)

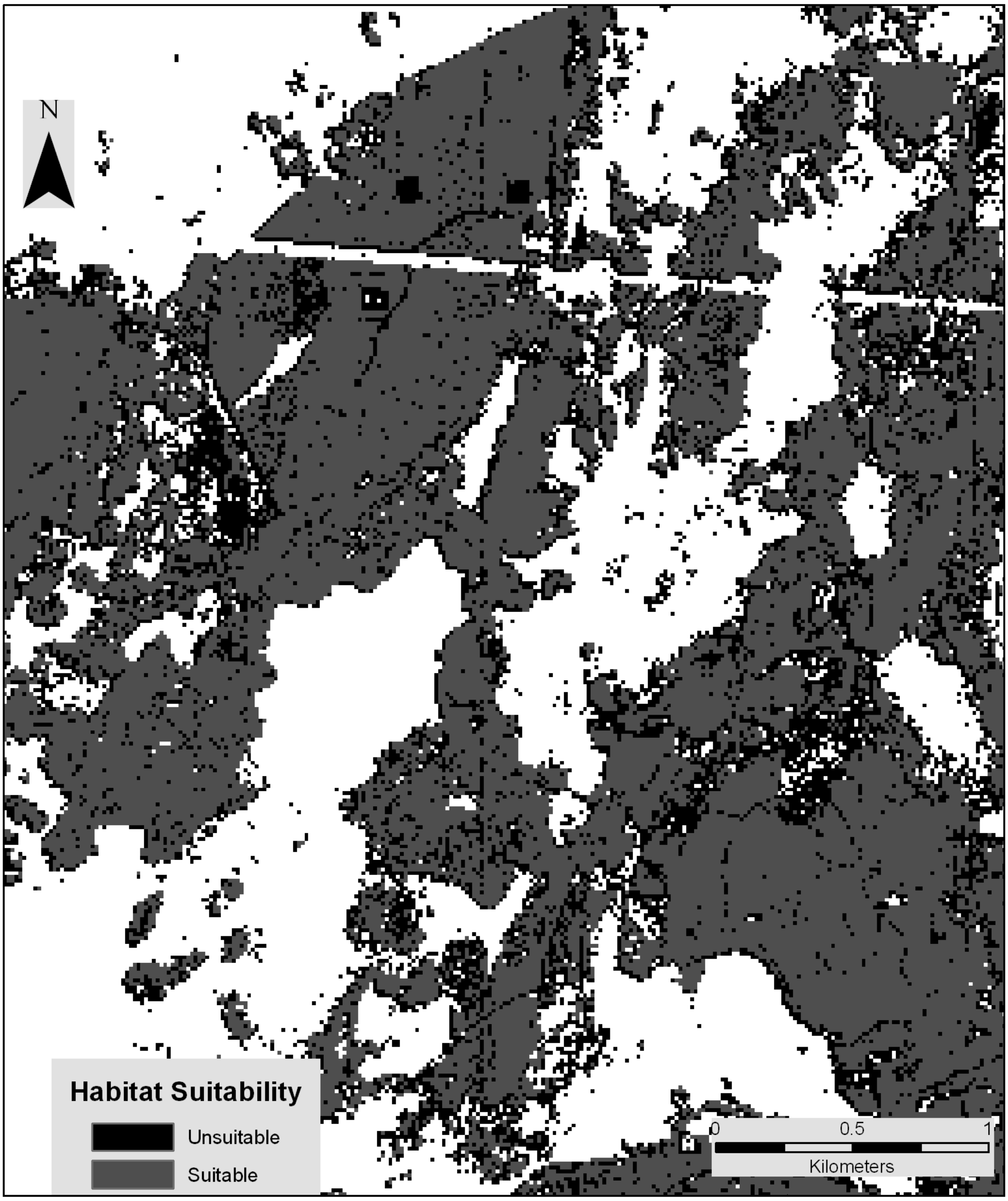


Figure 4.6: LiDAR derived habitat suitability map, Abernethy Forest, Scotland. Habitat suitability was classified into 2 categories: Unsuitable and Suitable. Non-data areas (i.e. non forest and areas outside the range of values observed in the field) are shown in white.

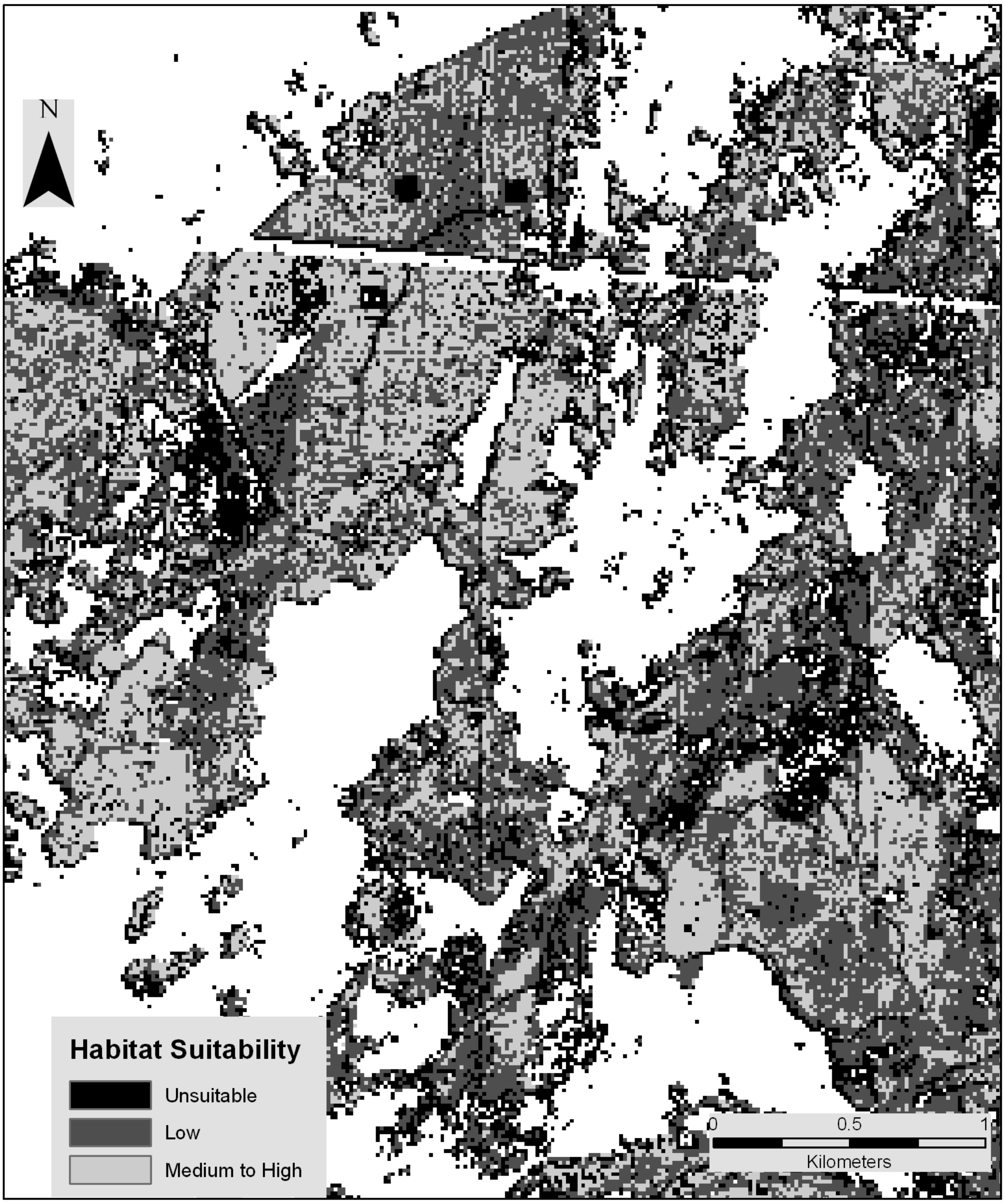


Figure 4.7: LiDAR derived habitat suitability map, Abernethy Forest, Scotland. Habitat suitability was classified into 3 categories: Unsuitable, Low suitability and Medium-to-high suitability. Non-data areas (i.e. non forest and areas outside the range of values observed in the field) are shown in white.

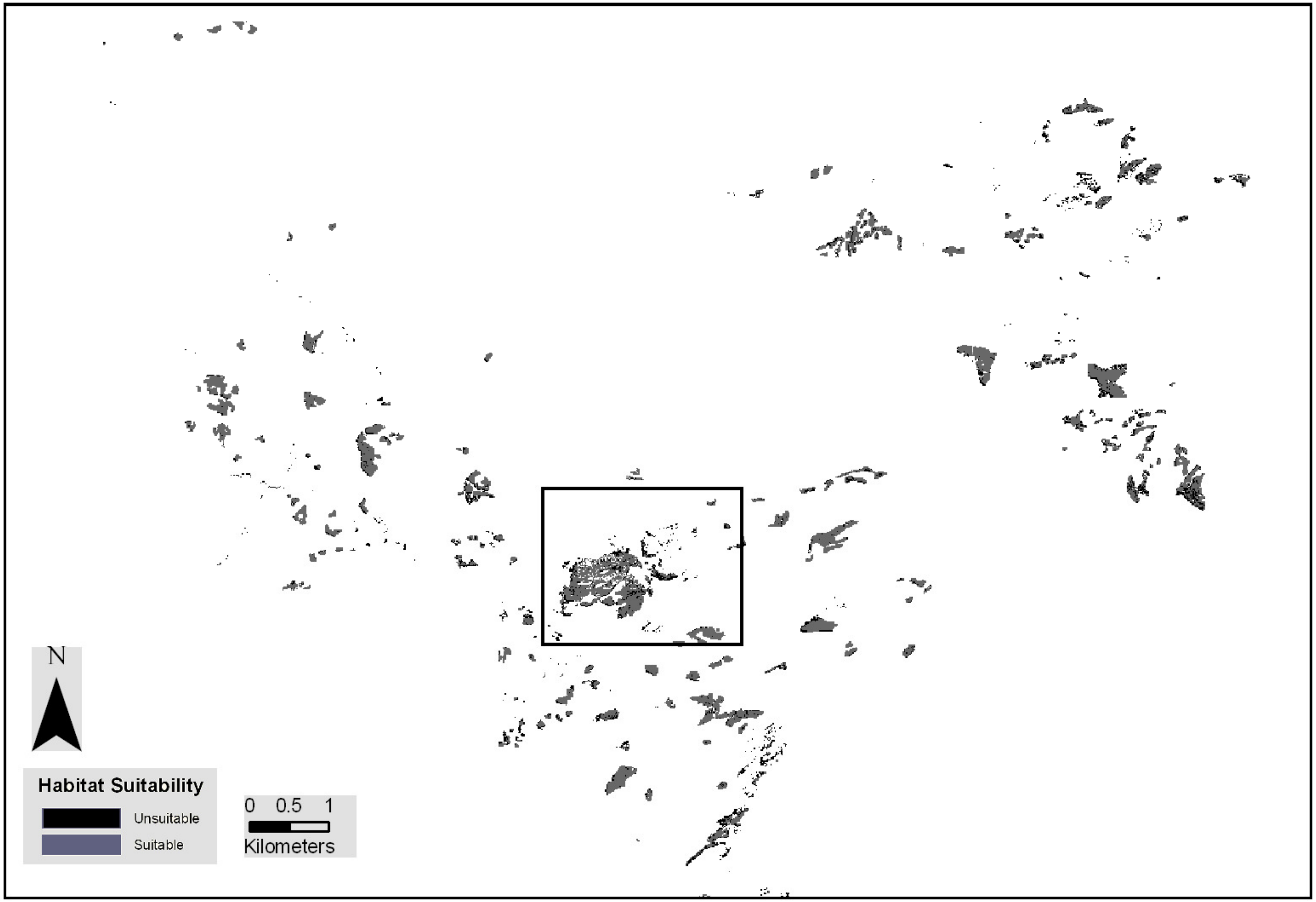


Figure 4.8a: LiDAR derived habitat suitability map (GLM 1), Aberfoyle, Scotland. Scots pine stands are widely spread in Aberfoyle and therefore is difficult to show differences between different models/classifications schemes. The whole study area is shown in this figure. The largest stand (black rectangle) has been zoomed –in to show in detail habitat suitability classification in Figure 4.8b.

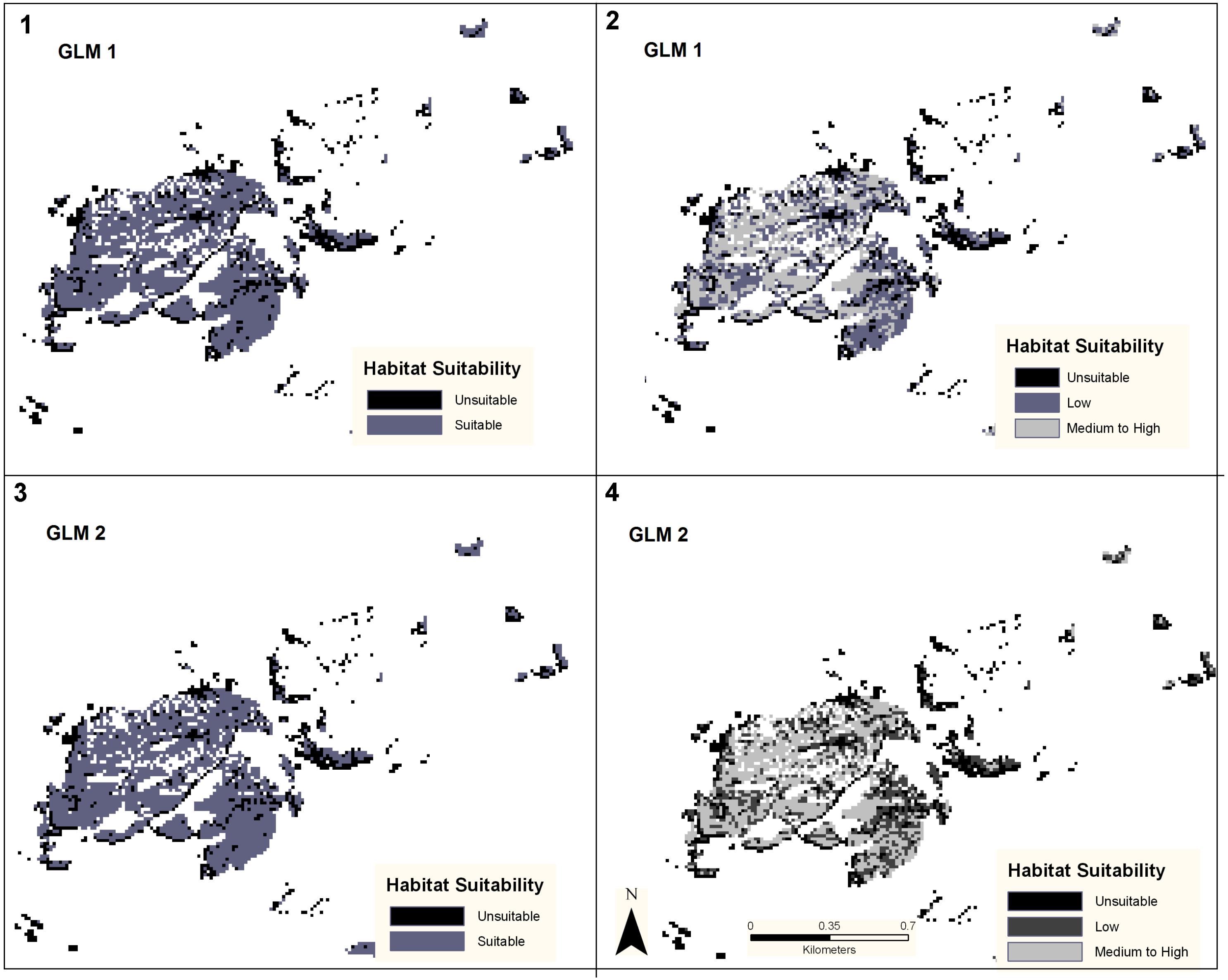


Figure 4.8b: Largest Scots pine stand in Aberfoyle Forest. The different models/classifications schemes are show as follow: 1) GLM-1/2 classes, 2) GLM-1/3 classes, 3) GLM-2/2 classes; 4) GLM-2/3 classes. No-data areas (i.e. non Scots pine stands, no-forest and areas outside the range of values observed in the field) are shown in white.

4.4 Discussion

4.4.1 Field-based GLM

The first objective of this chapter was to validate the field-based GLM developed in early stages of this project (see Chapter 2). The results from the LOO cross-validation of the field-based model show moderate model performance for both study areas together (Spearman's rank correlation coefficient = 0.40, *P<0.004, n=52*).

The GLM explains 43% of the variance in cones stripped by squirrels. This percentage of variability explained by three variables only clearly indicates that canopy closure, tree height and number of trees -all significant predictors of the number of cones stripped by squirrels- are important factors that shape squirrels feeding behaviour at the sub-stand level.

It is important to highlight that the functionality of the GLM in the context of the species management in the UK is to provide a better understanding and a quantification of the relationship between red squirrel habitat use and forest structural factors. The current study considers 3 forest structure variables. Other variables not included in the analysis might also influence the species habitat preferences at the plot level. Previous studies illustrate the fact that animal-habitat relationships are complex and involve different factors. For instance, Hill *et. al.* (2004) found that the relationship between Great tits chick mass and canopy height is affected by temperature variations in spring time; while others have highlighted the importance of understory vegetation for habitat selection by birds (Carrascal and Telleria 1988; Goetz, *et al.* 2010; Lesak *et al.* 2011) and small mammals such as fat dormouse (Milazzo *et al.*, 2003) and Delmarva fox squirrel (Nelson *et. al.*, 2005). In the case of the red squirrel, factors not considered in this study, such as the presence of food other than seeds (i.e. fungi) or potential mating partners would also influence individuals' habitat use (Gurnell, 1987). A more detailed description of red squirrel habitat preferences is provided in Chapter 1.

Furthermore, the current study is based on 2 years of fieldwork and further research is needed to test the robustness of the predictions and to better understand habitat use by red squirrel in more complex scenarios, such as food shortage or competition for food when high densities of squirrels occur (Gurnell, 1987).

4.4.2 LiDAR-based GLM

The objectives 3 and 4 were addressed and the GLM was implemented using LiDAR derived explanatory variables. LiDAR-based model performance was also assessed: strong correlations ($r_{s} = 0.59$ for Abernethy, $r_{s} = 0.54$ and $r_{s} = 0.60$ for Aberfoyle GLM 1 and GLM 2 respectively, Table 4.6) were observed when LiDAR-predicted stripped cones are compared to field-predicted stripped cones (i.e. LOO cross-validation), suggesting that LiDAR derived explanatory variables perform reasonably well over the extent of the study areas. Discrepancy between LiDAR-based and field-based model predictions could stem from inaccuracy in LiDAR metrics, more specifically the number of trees. Delineating individual trees using LiDAR is a challenging task and has been the focus of a great deal of forestry research (i.e. forest inventories) over recent years (see for example Maltamo *et al*, 2004; Koukoulas and Blackburn, 2005; Popescu *et al*, 2003). This study provides a novel approach by exploring the potential of LiDAR derived number of trees and other LiDAR metrics as an input to estimate and map habitat suitability for red squirrel.

The aim of this study is to assess the usefulness of LiDAR data to remotely map and monitor habitat quality for red squirrels, and therefore only LiDAR data should be used. However, in the case of Aberfoyle, the performance of the number of trees derived from LiDAR was particularly low (47.1% of correctly delineated trees) and field data (i.e. number of trees counted in the field) was used to calibrate this parameter with the purpose of assessing the effects of this limitation. Results show that the number of trees influences both the distribution and the range of values resulting from the implementation of the LiDAR-based model. The correlation between field-based and LiDAR-based model predictions increases when the correction is applied to the number of trees ($r_s = 0.54$ for GLM 1 and 0.60 for GLM 2, n=20). However, the error also increases (RMSE = 11.9 for GLM 1 and 29.8 for GLM 2). This suggests that when the number of trees is corrected using the calibration equation, LiDAR-based model predictions represent better spatial variations in field-based model predictions but the difference between absolute values is greater. The correction applied improved the percentage of correctly detected trees (from 47.7% to 75%) and decreased the number of omitted trees (from 52.8% to 25%), but it also considerably increased the number of wrongly detected trees (from 0% to 33%). In addition to this, the correction relies on field data being collected to develop a calibration equation. The low performance of the number of trees derived from LiDAR at Aberfoyle can be attributed to a lower data resolution (i.e. 1 pulse/m^2 as opposed to an average of 2 pulses/ m^2 for Abernethy, see Chapter 3). Thus, the above results highlight the need for using LiDAR data of sufficient resolution for red squirrel habitat assessment and management.

The difference between canopy cover and canopy closure could be also influencing LiDAR-based model performance. Canopy closure is the most significant predictor of number of cones stripped by squirrels. Although canopy closure measured in the field and LiDAR derived canopy cover are strongly correlated (r_s=0.70), these are different methods for measuring canopy density. Moreover, while canopy closure measured in the field fluctuates from 54% to 95%, LiDAR canopy cover ranges from 10% to 96%, showing considerably more variability (see Chapter 3). This can be explained by the fact that canopy closure was measured in the field using spherical densiometer, an instrument that is widely used for providing a robust and more objective approach to visual assessments, while also being criticised for their poor resolution and weak sensitivity to variations (Jennings *et al*. 1999). Further research could explore, for example, the relationship between the species preferences and LiDAR canopy cover.

In terms of management for species conservation the main advantage of using LiDAR data is that it allows for an assessment of animal-habitat relationships in three dimensions and over the entire landscape (Vierling *et al*, 2008). In this way, the use of LiDAR remote sensing improves habitat assessment by incorporating vegetation structure and allowing further differentiation of areas where habitat quality is not homogeneous.

In the particular case of the red squirrel in the UK, the main advantage has been the representation of habitat heterogeneity which had not been previously considered. Assessment of suitable areas at the sub-stand level is currently based mostly on tree species composition and age. The results of this study suggest that this approach could be overestimating the area of the forest suitable for red squirrel. The last objective of this chapter was to classify the results of the GLM implementation using LiDAR data into habitat suitability levels. The results of this classification suggest that only a proportion of the forests (27% at Abernethy, 37% at Aberfoyle considering only un-calibrated number of trees, Table 4.7) could be suitable for red squirrels while the rest could be of little or no use for the species due to a combination of low canopy cover, low tree density and immature trees (i.e. trees too young to produce seeds, Figures 4.6, 4.7, 4.8a & 4.8b). The use of LiDAR not only allows for identification of suitable areas but also areas where current conditions are not optimal and management is required. This study presents a methodology that can be used to assess current conditions as well as to monitor changes over time. Furthermore, this methodology is also applicable to other species.

In this study, LiDAR metrics were used to replace field measurements. Whilst results are still relatively crude, they illustrate the potential of this approach to map habitat suitability for endangered species. Future research is needed to fully explore the potential of LiDAR metrics as possible predictors of the species habitat preferences. For instance, knowing that the number of trees influences red squirrel habitat use and assuming that understory vegetation could also be a significant predictor, LiDAR metrics such as the proportion of first returns above a given threshold (to represent tree density) and below a given threshold (to represent understory vegetation density) could be assessed by directly exploring the relationship between the squirrels presence and/or abundance and the LiDAR derived variables.

CHAPTER 5

Using LiDAR derived habitat suitability data to model red squirrel population viability

---

The previous Chapters have explored i) the impact of forest structure on red squirrel habitat use; ii) the methodology to retrieve forest structural parameters (that relate to red squirrel habitat suitability) from LiDAR; and iii) the use of LiDAR derived forest structure variables to extrapolate the analysis and create habitat suitability maps for both study areas.

This Chapter illustrates one of the potential applications of the LiDAR derived habitat suitability data to red squirrel habitat management. A population viability analysis was carried out for Abernethy Forest, one of the 18 proposed strongholds. Two scenarios were modelled: *Basic*, where carrying capacity is estimated for the whole mature forest (information extracted from digital forest maps) and *LiDAR,* where carrying capacity is estimated based on the suitable patches identified on the LiDAR habitat suitability maps. One catastrophe is modelled to account for the effects of poor cone crops (i.e. poor food provision) on squirrels.

Results suggest a steady decline in red squirrel population for both scenarios, and a higher probability of extinction for the *LiDAR* scenario (58% and 74% for the *Basic* and *LiDAR* scenarios respectively). These results highlight both the need for considering forest structure when managing strongholds and the usefulness of LiDAR as a tool to assist that management.

5.1 Introduction

Protecting endangered species involves the management of their habitat to ensure it will support species populations over time (Brito & Grelle, 2006). Habitat quality is one of the most important factors to take into account when managing landscape for endangered species survival. When population viability is assessed, variations in habitat quality can be translated into variations in carrying capacity[4] (Shaffer, 1981). However, due to a lack of empirical data, habitat quality is sometimes assumed to be homogeneous along entire landscapes which leads to, for example, overestimation of carrying capacity. This has in occasions proved to lead to overly optimistic population viability predictions (Brook *et al.*, 1997). Over recent years, remote sensing has become an important tool to assess species habitat requirements and habitat quality over broad areas (McClain *et. al.*, 2000).

In the case of the red squirrel in the UK, assessment of habitat quality has been so far mainly based on forest stock maps, which allow for tree species and age classes assessment at the stand level. For instance, in order to model population viability of a given red squirrel population, carrying capacity would be estimated by multiplying the size of the stand by the squirrel's density (i.e. number of squirrels per ha) that the tree species present in the stand can support (Lurz, 2011). Variations in carrying capacity can then be simulated by, for example, modelling annual available seed energy, variations in life history parameters (e.g. reduced fecundity in poor seed years) and direct reductions in carrying capacity (e.g. to simulate felling in compartments; Lurz *et al.* 2003). Partly due to a lack of information on habitat quality and cost-efficient data collection methods, habitat quality at the sub-stand level has so far not been considered in these estimations.

The relationship between red squirrel habitat quality and forest structural factors at the sub-stand level was explored as part of this thesis (Chapter 2). By using LiDAR remote sensing, the analysis was extrapolated to the whole study area and habitat suitability maps were generated (see Chapter 4 for further details). These LiDAR derived maps allow for further differentiation of habitat quality for red squirrels, and therefore, for a more refined estimation of carrying capacity. In this way, carrying capacity offers a suitable way to use LiDAR derived habitat suitability data to assist red squirrel conservation.

The aim of this Chapter is to assess the potential of LiDAR derived habitat suitability data to model red squirrel population viability.

To achieve this aim, the following objectives will be addressed:

---

[4] Carrying capacity can be defined as *the population size that the resource of the environment can maintain without a tendency to either increase or decrease* (Begon *et al*., 1996). For a model definition of carrying capacity see section 5.1.5.

- Population viability analysis (PVA) model will be validated using an independent set of data to assess model performance
- Sensitivity analysis will be carried out to assess the model sensitivity to changes in carrying capacity
- Carrying capacity will be estimated for two different habitat types: All-forest, where all the available mature forest will be considered; and High-to-Medium suitability, where based on the LiDAR habitat suitability maps, only High-to-Medium suitability patches will be considered.
- Two scenarios will be modelled: *Basic* (All-forest carrying capacity) and *LiDAR* (High-to-Medium suitability carrying capacity). All parameters will be kept the same except carrying capacity. For each scenario, both catastrophe and no-catastrophe sub-scenarios will be also modelled.
- Results of both scenarios (i.e. final population and probability of extinction at the end of the period) will be compared and discussed

5.1.1 Population Viability Analysis

Wild populations of endangered species face specific threats such as loss of habitat or competition with invasive species. One of the main aims of conservation biology is to identify those threats and to apply –when possible- corrective procedures (Brook *et al.*, 1997; Doak *et al.*, 2009). Given a set of data on environmental conditions and species characteristics, population viability analysis (PVA) is a process that assists the evaluation of the probability of a given species to become extinct over a specified period of time (Boyce, 1992; Begon *et al.*, 1996; Doak *et al.*, 2009).

A basic concept related to PVA is the minimal viable population (MVP). This is often defined as the minimum number of individuals of a given species necessary to ensure the survival of that population (Boyce, 1992). For endangered species, the classical experimental approach to identify MVP is usually not practical, as there is not enough time –and enough individuals- to monitor populations of different sizes for years. Hence, PVA provides a tool to estimate MVP (Boyce, 1992; Begon *et al.*, 1996).

It should be emphasised however that although PVA is a tool that provides a quantification of risk of extinction of endangered species (Brook *et al.*, 1997), attempting to predict an exact number for MVP or the number of years in which a population will become extinct may be unrealistic. Instead, PVA should be used to achieve a better understanding of which factors could lead to extinction, to assess the impact of changes in those factors on the populations, and to compare and rank management options (Boyce, 1992; Doak *et al*., 2009; Burgman *et al*., 2012). More in depth reviews of PVA can be found in Begon *et al*.(1996); Boyce (1992) and Doak *et al*., 2009.

Although other approaches such as a) use of available data on the rare species to find patterns and b) subjective assessment based on expert knowledge (see Begon *et al*., 1996, Harper, 1996, pp934; Burgman *et al*., 2012) have been explored, population viability models are one of the most widely used approaches to assess current and future threats and to compare the effectiveness of different management strategies (Boyce, 1992; Brook *et. al*., 1997; Doak *et al*., 2009; Burgman *et al*., 2012). The application and degree of success of PVA models depend on the ecology of the species, the availability of data and the expertise of the modellers.

5.1.2 Modelling population viability

In general, the target of PVA is populations of endangered species namely, small populations, particularly affected by deterministic and stochastic processes (Lacy, 1993; Doak *et al*., 2009; Burgman *et al*., 2012).

Deterministic forces such as habitat destruction or predation can lead to population decline (Lacy, 1993). However, even if those deterministic threats are identified and dealt with, stochastic forces can still lead a population to extinction (Shaffer, 1981). Stochastic processes have been grouped into four categories: *demographic, environmental, genetic stochasticity and catastrophic events* (a detailed explanation of each can be found in Shaffer, 1981 and Lacy, 1993; Doak *et al*., 2009).

One of the main problems that researchers have faced when trying to model endangered species population viability is the lack of accurate and adequate empirical data that would allow the use of theoretical approaches to predict the dynamics of those populations (Lacy, 1993; Doak *et al*., 2009; Burgman *et al*., 2012). This has lead researchers to look into Monte Carlo computer simulation techniques as an alternative to model population viability. The Monte Carlo method deals with the behaviour or outcome of random processes by using random numbers and probability distribution functions. Detailed descriptions of the method can be found in Metropolis & Ulam (1949) and Metropolis (1987). Based on this method, a wide range of computer models have been developed and used to simulate the effects of both determinist and stochastic events on small populations (Lacy, 1993). The model outputs most commonly used to show how threatened a population is and to assess different management options are: *expected growth rate*, *future population size* and *extinction risk* (Doak *et al*., 2009).

The selection of an appropriate model will depend on the ecology of the species being studied and the availability of ecological, demographical and environmental data (Boyce, 1992). In most cases, the best option is to use existing generic software that have been already used and tested (Brook *et. al*., 1997). One of the most important rules is to keep the PVA model simple, fitting the ecological data that is available for the species (Doak *et al*., 2009).

Finally, the interpretation of the results is also a key element of the PVA process, and model limitations need to be acknowledged and understood in order to avoid overconfidence (by resource managers) on model predictions (Burgman *et al*., 2012).

5.1.3 Sensitivity analysis

Sensitivity analysis is usually performed to assess how sensitive a model is to variations in a given input variable or parameter (Hamby, 1994). This can be helpful both to interpret the model results and to identify which parameters have an effect on the model predictions. This can also assist and inform future research and data collection (i.e. which life-history parameters need to be further investigated) (Burgman and Possingham, 2000).

The simplest way of assessing model sensitivity is by testing one parameter while the rest remain constant. This is called *one-at-a-time* or *local sensitivity analysis,* while *global sensitivity analysis* involves varying all input parameters simultaneously (Smith & Smith, 2007). Generally, a set of values is assigned to the input parameter(s) being evaluated, the model is run and changes in results are recorded and compared to changes in model inputs (Smith & Smith, 2007).

The simplest expression of model sensitivity is the visual representation (for example Figure 5.7) of input values against model results (Smith & Smith, 2007). Furthermore, the correlation between the parameter inputs and the model outputs can be used as a way to express the model sensitivity in a quantitative way. Although this is the simplest approach, other methods to express model sensitivity are available and a detailed review can be found in Hamby (1994) and Smith & Smith (2007).

In this study, different levels of habitat quality will be modelled by simulating different scenarios with different carrying capacity values. Therefore, it is important to know how sensitive the model is to variations in carrying capacity. The approach used to test model sensitivity to carrying capacity is described in the Methodology section

5.1.4 Background

Population viability analysis has been widely used as a tool to design and manage protected areas for endangered species (Brito *et. al.*, 2008). This section provides a review of case studies where PVA has been carried out for different endangered species, emphasising the use of the package VORTEX, as this is one of the most widely used PVA packages (Guo *et. al.*, 2002; Miller and Lacy, 2005; Brito *et. al.*, 2008), and the one used for this study. Some literature examples using other packages are also provided as well as a brief comparison between packages.

5.1.4.1 Case studies

PVA models in general allow for a range of scenarios to be modelled and parameters to be considered and therefore can be used to assess different types of management strategies.

For instance, VORTEX has been used to analyse cost-efficient management strategies: Duca *et. al.* (2009) used VORTEX to assess the most cost-efficient conservation approach for the white-banded tanager (*Neothraupis fasciata*) in the Cerrado area, Brazil. The white-banded tanager is an endemic bird species whose suitable habitat (woodland savannah) is being converted into agriculture. Five different scenarios were modelled: The *Basic scenario* represented the current situation as a no-management scenario. This scenario was used as the baseline to compare with the other scenarios: The *Habitat destruction scenario,* where carrying capacity was reduced by 50%, 25% and 12.5% to represent reduction of the size of suitable habitat; the *Mortality scenario* where juvenile mortality was 74% higher and sub-adult (1-2 year) mortality was 8% lower than the basic scenario; the *Drought scenario,* where drought was added as a catastrophe, and survival and reproduction were both reduced by 25%; and finally, the *Clutch size scenario* where the number of female progeny (number of eggs) was reduced from 3 to 2. Life-cycle information was taken from a 3-year field study on the white-banded tanager and from previous studies on a similar bird species. In all scenarios, quasi-extinction was achieved when the population became smaller than 100 individuals. The results suggested that probability of extinction was very low for the *Basic scenario* (3.8%); while higher quasi-extinction probabilities were observed for the *Habitat destruction, Drought* and *Clutch size* scenarios. The effects of three different management strategies (*Revegetation*, *Fire management* and *Nest protection*) on the quasi-extinction probability were assessed: *Revegetation* was assumed to increase the carrying capacity by increasing the amount of suitable habitat; *Fire management* avoids the negative effects of fires (to clear land for agriculture) in reproduction, and *Nest protection* increases female breeding by protecting nests from predators. Their findings suggested that *Nest protection* was the most effective management strategy, followed by *Fire management*. As *Nest protection* was six times more expensive than *Fire management*, it was concluded that the later was the most cost-effective strategy to reduce the risk of white tanager becoming extinct.

VORTEX has also been used to assess the need for management in current reserve areas for endangered species. Brito *et. al.* (2008) used VORTEX to assess the effectiveness of the Atlantic forest protected area network as habitat for the Northern muriqui (*Brachyletes hypoxanthus*). The Northern muriqui is endemic to Brazil. There are 42 protected areas in the Atlantic forest where this primate can be found. The Atlantic forest is one of the 34 world's Biodiversity Hotspots and is still highly threatened by fragmentation, fire (to clear land for agriculture), hunting and introduction of invasive species. It is also home to 70% of Brazil's population and an important industrial and silvicultural centre. As a consequence, habitat fragmentation has reduced in size and isolated the protected areas that are home to the Northern muriqui. VORTEX was used to investigate whether those 42 reserves were still sufficient to host viable populations of the species. Each of the protected areas was modelled as an isolated population (i.e. no dispersal among populations); carrying capacity was estimated based on information extracted from literature and initial population size was set as half of the carrying capacity. Based on previous research on the species, they modelled inbreeding depression and genetic drift for populations smaller than 700 individuals. They found that only 5 out of 42 (12%) of the protected areas would potentially hold demographic and genetically viable populations and that management was necessary in the rest of the protected areas.

In addition to the usual threats wildlife populations face (i.e. habitat destruction, over-hunting), endangered species populations face demographic and genetics risks when they become small and isolated. All those problems can result in populations becoming even smaller, which increases the difficulty for individuals to find a mate and reproduce. This in turn leads to more inbreeding and the loss of genetic variations. Mortality rates and susceptibility to diseases increase for individuals with lower levels of genetic variation. This ultimately leads to the extinction of the population (Guo *et. al*., 2002). This is potentially the case for the Giant panda in Xiangling Mountains, China, where the species' populations are small (less than 40 individuals in total), isolated by the mountains and threatened by habitat destruction. Guo *et. al.* (2002) used VORTEX to assess panda's population viability and to propose management strategies for this species conservation in Yele Nature Reserve. Five different scenarios were modelled: *no-inbreeding, no-catastrophe*, *inbreeding without catastrophe*, *catastrophe without inbreeding,* and *inbreeding and catastrophe*. Life-cycle parameters were taken from literature and previous research. As Giant pandas feed on bamboo, maximum carrying capacity was calculated by multiplying the maximum number of individuals that bamboo forest can host by the area of the reserve covered by bamboo. The initial population was known to be 11 Giant pandas. Only one population was modelled as physical characteristics of the reserve make it impossible for pandas to disperse. As bamboo constitutes the main part of the giant panda's diet, blossoming of bamboo is a catastrophe for pandas as bamboo die soon after they appear. Only one species of bamboo is present in the study area and it blossoms once every 60 years. Thus, a catastrophic event was included in two of the scenarios -1.6 % probability of blossoming occurring over a 100-year period- which would decrease panda's survival and reproduction by 16%. This information was taken from a combination of expert knowledge and previous research. Guo *et. al.* (2002) findings suggested that the Giant panda population in Yele Nature Reserve is likely to become extinct and very susceptible to inbreeding depression and bamboo blossoming. They proposed i) additional bamboo species to be planted in the area to provide pandas with an alternative source of food and avoid the negative effects of blossoming on the species' reproduction and survival rates and ii) to introduce individuals from other populations or from zoos to increase gene flow and reduce the possibility of inbreeding.

VORTEX has also been successfully used for squirrels in the UK. Reintroduction is a strategy commonly used to increase the chance of recovery of endangered species. However, for this strategy to be successful, it is necessary to know how many individuals are needed to establish a successful population (Wood *et. al.*, 2007). Wood *et. al.* (2007) evaluated a theoretical approach to tree squirrel reintroduction using VORTEX to assess the size of initial populations. Ecological parameters necessary to run the model were gathered from previous research on 6 different squirrel species. Catastrophic events were not included because the aim was to assess the potential of reintroduction in spite of extreme variations in environmental conditions. Inbreeding depression was not modelled as there was not observed effects of inbreeding depression on Eurasian red squirrels for fragmented populations of less than 30 individuals (Wauters, 1997). In red squirrels, density dependent reproduction effects have been observed at high density of females in highly fragmented habitats (Wauters *et al.*, 2004). To obtain optimum results, reintroduction of endangered species should be carried out only when the selected area meets the species habitat requirement. Therefore, density dependent reproduction was not modelled. Based on life-history published data, three values for litter size, percentage of female breeding, adult mortality and juvenile mortality were determined in order to model three different reproductive scenarios: *pessimistic, average, optimistic*. To model the effects of variations in habitat quality, and based on previous studies, Wood *et al.* (2007) generated a set of low and high standard deviation values for those parameters and each breeding scenario was ran at *low* and *high habitat variability*.

Model outputs suggested that for the *low habitat variability* scenario a number of 10 to 15 initial animals (depending on squirrel species and breeding scenarios) was sufficient to maintain a viable population for 100 years, while for the *high habitat variability* scenario, more than 35 squirrels in the initial population were needed in the most optimistic breeding scenario.

To compare their model outputs with empirical data, Wood *et. al.* (2007) investigated 25 cases of squirrel introduction that occurred in different locations around the world at least 50 years before they carried out this study. The results showed that 21 (84%)

of the introduced populations still persisted, and more than 10 initial individuals were needed in 13 of those 21 successfully introduced squirrel populations.

Being a spatially-explicit PVA package, RAMAS/GIS provides the opportunity to combine landscape data (i.e. habitat suitability) with demographic/ecological to spatially assess population viability of endangered species. For instance, Haines *et al.* (2006) used RAMAS/GIS to assess management strategies for the endangered ocelot (*Leopardus pardalis*) in Cameron County, USA.

Previous research suggested that the ocelot prefers areas with canopy cover (at the shrub level) > 75%. This was corroborated with the use of data from collar-tracking of 40 ocelots for a period of 10 years (1995 to 2005). Based on these habitat preferences, habitat suitability data was incorporated to the model as a land-cover map derived from remotely sensed data (i.e. LANDSAT ETM+) where those areas with canopy cover > 75% were identified by performing a supervised classification. Based on the ocelot habitat use (i.e. collar-tracking survey) and the species foraging distance, all pixels with canopy cover > 75% that were within 1km of each other were considered part of the same habitat patch. Carrying capacity for each patch was calculated based on ocelot breeding ranges size. Finally, a stage-matrix was produced consisting of life-history data (gathered from published literature and previous research) for a) females and b) males at 4 different stages: *Age 0, Age 1, Age 2* and *Age 3+*. Combining the habitat suitability data and the stage-matrix, three different scenarios were modelled: *translocation* (where one female ocelot would be translocated into the Cameron population every other year for 40 years); *reduced road mortality* (assuming that building culverts would reduce mortality by a 50%) and *habitat restoration* (assuming that increasing habitat of a certain soil type -which was found to be highly correlated with canopy cover- would increase carrying capacity by 50%). Population was projected 50 years into the future. Results of the PVA suggested that reducing road mortality was the most efficient management strategy to benefit ocelot population in the short-term, while habitat restoration would provide more benefits for the species conservation in the long-term (i.e. approx 40 years).

The case studies presented above represent a number of possible applications of PVA models for conservation management. However, these case studies also highlight some of the limitations and criticisms of PVA models applications, such as:

- No validation of the model was performed in any of the case studies summarized above with exception of Wood *et al.* (2007) who compared model outputs to real-life cases of squirrel introductions
- No sensitivity analysis was carried out in two out of the five studies (i.e. Guo *et al.*, 2002 and Wood *et al.*, 2007).
- Only two out of the three studies (Guo *et al*, 2002 and Haines *et al*, 2006) used ecological data to run the model that was site and species specific. The rest of the studies used generic data gathered from published work on similar species.
- Although in all five studies the authors acknowledged the uncertainty inherent to PBA models which was increased by the use of generic ecological data in some cases (e.g. Wood *et al.*, 2007; Brito *et al.* 2008; Duca *et al.*, 2009) they failed to critique the lack of validation of model results and sensitivity analyses in their studies
- Finally, all these studies propose management options but only one (Haynes *et al.,* 2006) provides a brief assessment of the feasibility of those management strategies and some advice on how to implement them (i.e. potential locations of culverts to reduce road mortality of the species considered)

Validation of modelling by comparing results with empirical data, sensitivity analyses and the use of site/species specific ecological data to feed the model are necessary to assess the utility of the model and to improve and increase the model value and its reliability (Lurz *et al.*, 2008b).

Despite these weaknesses, PVA is a valuable and sometimes the only tool to, for example, estimate the likelihood and extend of species spread following introductions, assess the risk of extinction of endangered species and to compare the potential outcomes of different management options (Gerber & González-Suárez, 2010).

5.1.4.2 Comparison between PVA packages

A number of PVA packages are available and have been used to assist the management of endangered species. In addition to VORTEX (described later in this Chapter), some of the other most commonly used packages are INMAT, developed mainly to assess short term effects of inbreeding depression; GAPPS, originally developed for grizzly bears, and now commonly used for large mammals; and RAMAS, which can handle very large populations, for example fish (Brook *et. al.*, 1997). It is beyond the scope of this thesis to critically review these packages. However, previous research has compared predictions of these PVA packages with the aim to assess whether predictions made using the same set of data were similar. For instance, Mills *et al.* (1996) compared the performance of GAPPS, INMAT, VORTEX and RAMAS/AGE to assess the different viability predictions using a grizzly bear (*Ursus arctos horribilis*) dataset; and Brook *et. al* (1997 & 1999) compared the predictions of five different PVA packages (GAPPS, INMAT, RAMAS/age, RAMAS Metapop and VORTEX) using historical data of two endangered species: Lord Howe Island woodhen (*Tricholimnas sylvestris,* 1996) and whooping crane (*Grus Americana,*1999). A summary of their main findings and conclusions is provided below:

- No model seemed to perform better when compared to real data. Projections differ from one package to another. However, these differences did not seem to be package dependent but instead seemed to depend strongly on species and scenarios (i.e. input parameters) modelled.
- Even projections made by two different versions of the same package (i.e. VORTEX 5.1 & 8.1) differed from each other.
- Complex scenarios (and potentially more realistic) produced greater differences among projections of different packages than simple scenarios (i.e. those where complex processes such as inbreeding depression or density dependent reproduction are not modelled)
- Adding density dependence produced greater divergence between model predictions.
- The selection of a PVA package will greatly depend on the species being modelled and on the available data to feed the model
- It is advisable to use models that have already been used and tested in the past

One of the aims of this project is to provide a methodology to assess habitat quality for red squirrel based on the use of operational tools. In this sense, VORTEX meets this aim as it is free and of easy access (can be downloaded from internet and installed), it has been widely used and tested, it is relatively easy to use by non-expert modellers (tutorials and examples are available), it produces results that are as accurate as those of other PVA packages and it has already been successfully used to model red squirrels population survival in the UK (Wood *et al.* 2007). Furthermore, VORTEX allows for modelling the effects of habitat modification on populations by manipulating habitat suitability and how many individuals a forest can support (i.e. simulating scenarios with differing carrying capacity values).

5.1.5 VORTEX

VORTEX is a PVA individual-based computer model that uses life cycle information for sexually reproducing diploid organisms to model the effects of deterministic forces (i.e. habitat modification) and demographic, environmental and genetic stochastic events on each animal in a given population (Lacy, 1993). Originally developed by the Department of Conservation Science, Chicago Zoological Society (Illinois, USA) to model mammalian and avian populations with low fecundity, VORTEX is one of the most used computer simulation packages (Brito & Grelle, 2008). It is distributed without cost for conservation and research purposes, relatively easy to use by non-experienced modellers, and offers some extra abilities such as the modelling of meta-population dynamics and genetic effects (Miller & Lacy, 2005). It also allows for the analysis of the effects of habitat modification on populations by manipulating carrying capacity values, where carrying capacity is defined in the VORTEX model as *the upper limit for the size of the simulated population within a given habitat* (Miller & Lacy, 2005).

A number of studies carried out using VORTEX was reviewed in previous sections (see section 5.1.4) and a summary of input data required to run the model is provided in the following section (for a detailed description of model outputs refer to Miller & Lacy, 2005, Chapter 4, pp 78-80).

5.1.5.1 Input parameters

Input data is divided into 13 different sections, summarised in Table 5.1. VORTEX accepts most of the input values the user provides, as long as the values are biologically possible and within the limits set by the program (details on range of values accepted by VORTEX are provided in Miller & Lacy, 2005, Chapter 2, pp 7).

Table 5.1: Summary of VORTEX sections and input parameters (Miller & Lacy, 2005)

Section Number	**Parameters**	**Description**
Section 1	*Scenario name* , *Number of iterations, Number of years, Extinction Definition, Number of Populations*	Scenario settings
Section 2	*Inbreeding depression, EV(*Environmental variation) *Concordance of Reproduction & Survival, Number of Types of Catastrophes*	Species Description
Section 3	*Population Labels and State Variables, Individual State (IS) Parameters*	Labels and State Variables
Section 4	*Age Range – Youngest and Oldest, Dispersing Sex(es), Percent Survival of Dispersers, Dispersal Rates*	Dispersal Among Populations
Section 5	*Monogamous, Polygamous, Long-term Monogamy, or Long-term Polygamy, Age of First Reproduction for Females (and Males), Maximum Age of Reproduction, Maximum Number of Progeny per Year, Sex Ratio at Birth (in % of males),Density Dependent Reproduction*	Reproductive System
Section 6	*% Adult Females Breeding, EV in % Breeding,* *Specify the distribution of number of offspring per female per year, Use Normal distribution approximation* or *Specify exact distribution*	Reproductive Rates
Section 7	*Mortality rates of Females and Males as %:*	Mortality
Section 8	*Global/Local, Frequency %, Severity (proportion of normal values):*	Catastrophes
Section 9	*% Males in Breeding Pool, % Males Successfully Siring, Mean # of Mates/Successful Sire*	Mate Monopolization
Section 10	*Stable Age Distribution* or *Specified Age Distribution*	Initial Population Size
Section 11	*Carrying Capacity (K), Trend in K?*	Carrying Capacity
Section 12	*First Year of Harvest* and *Last Year of Harvest, Interval between Harvests, Optional Criterion for Harvest, Female (Male) Ages being Harvested*	Harvest
Section 13	*First (Last) Year of Supplementation, Interval Between Supplementations, Optional Criterion for Supplementing, Female (Male) Ages being Supplemented*	Supplementation
Section 14 (optional)	(applicable primarily to populations that are captive)	Genetic Management

5.2 Methodology

5.2.1 Model validation

As no model can accurately predict the complexity of nature and as some degree of uncertainty is unavoidable, it is advisable to field-test the selected model before making any decision based on model predictions (Brook *et al.*, 1997).

As part of an ongoing project (Squirrel monitoring Kielder Forest District, P. Lurz pers. Comm., 2009), the red squirrel population at Kidland Forest, Northumberland, UK has been annually surveyed since 2001. Available data include field estimated red squirrel density and forest carrying capacity per year. These data were used to assess VORTEX performance by comparing the model outputs with the field-based red squirrel population size estimated at Kidland Forest.

5.2.1.1 Kidland Forest

Kidland Forest (55° 25’ N; 2° 10’ W; Figure 5.1) is located in the Northumberland National Park, north of England and is part of the Kielder Forest District. Being a conifer dominated forest; Kidland Forest is one of the 17 reserves within the Red Alert North England’s Red Squirrel Conservation Project (http://www.saveoursquirrels.org.uk). Sitka spruce (*Picea sitchensis*) is the dominant tree species in the area. There are also small plantations of Japanese larch (*Larix kaempferi*), Scots pine (*Pinus sylvestris*), lodgepole pine (*Pinus contorta*), Douglas fir (*Pseudotsuga menziessi*) and Norway spruce (*Picea abies*) as well as small areas of small-seeded broadleaves (Lurz *et. al.*, 2008a). As part of an ongoing project, annual surveys to assess red squirrel presence and density in Kidland Forest have been carried out since 2001. The aim of these surveys is to estimate and monitor red squirrel population and carrying capacity in relation to ongoing timber harvesting operations (Lurz & Lloyd, 2001). The presence of red squirrel has been assessed using cone transects across the forest to estimate food consumed by squirrels (see Gurnell *et. al.*, 2009 for a complete and detailed description of squirrel survey techniques). The total number of animals is then calculated based on food consumed. The observed number of uneaten cones has also been recorded to obtain an estimate of annual cone crops.

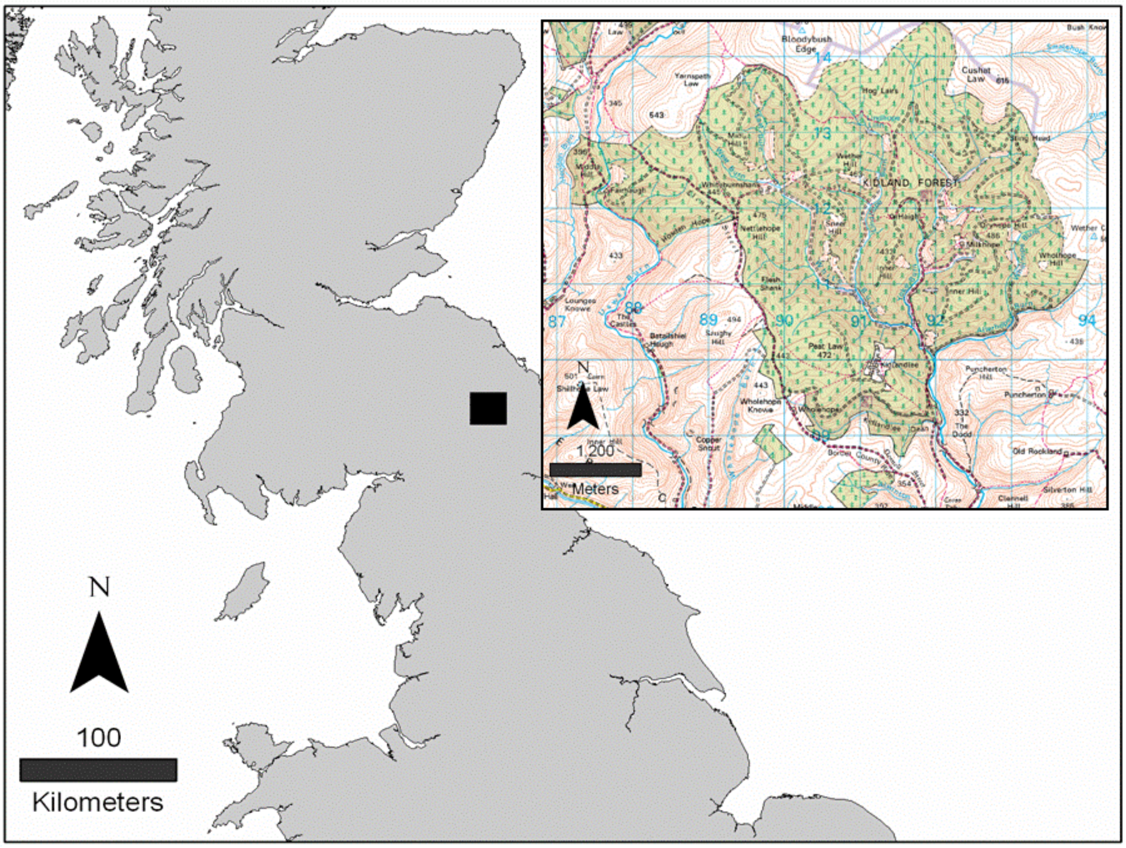


Figure 5.1: Kidland Forest in Northumberland National Park, England, UK Source: EDINA Digimap.

5.2.1.2 Model Input data

Life-history data used to run the model were gathered from the literature and expert knowledge. A summary is provided in Table 5.2.

Table 5.2: Red squirrels ecological parameters used to run the model

Parameter	Value	Source
Reproductive system	Polygynous mating	Gurnell, 1987
Age of 1st offspring for males and females	1	Lurz *et. al.*, 2005
Number of broods per year	2	Lurz *et. al.*, 2005
Maximum number of progeny per brood	6	Lurz *et. al.*, 2005
Adult Females Breeding (SD) (maximum)	70% (30%)	Lurz *et. al.*, 2005
Distribution of brood per year	60% and 40%	Lurz *et. al.*, 2005
Number of offspring per female per year (SD)	4 (2)	Lurz *et. al.*, 2005
Mortality rates of Females and Males from age 0 to 1 (SD)	75% (10%)	Lurz *et. al.*, 2005
Mortality rates of adult Females and Males (from age 1 to 5) (SD)	50% (20%)	Lurz *et. al.*, 2005

Assumptions made to run the simulation are:

- *Extinction* is defined as only one individual remaining.

- *Inbreeding depression* occurs when species populations are too small (Wauters *et al.*, 2004) and was not modelled in this case.
- Good years for reproduction are also good years for survival (*environmental variation*[5] *concordance (EV) of reproduction and survival*)
- Squirrels reproduce until they die (no old-age cut off with respect to breeding)
- *Sex ratio at birth* is 50% (Lampio, 1965; Gurnell, 1987)
- *Density dependent reproduction:* Density dependent processes are related to the presence of high number of individuals of the same sex. Density dependence in the reproductive rate of red squirrels depends on i) high densities of females (resulting in reduced rate of reproduction at higher female's concentration) and ii) high density of females in highly fragmented habitats (Wauters *et. al.*, 2004; Wood *et. al.*, 2007). None of those conditions were observed in Kidland Forest; thus *density dependent reproduction* was not modelled.
- *Normal distribution approximation* was used to model distribution of number of offspring per female per year
- *Future change in carrying capacity* was not modelled but it was considered when initial carrying capacity and SD in carrying capacity due to environmental variation were estimated.

Catastrophe: Although tree squirrels feed on more than 30 different kinds of food, most squirrel species feed mostly on tree seeds, which make squirrel populations highly vulnerable to variations in tree seeds production (Koprowski, 1991). It has been registered that increases in squirrel population are connected to high seed fall and that mast crops (i.e. abundant seed crops) have a positive effect on red squirrel densities (Wood *et. al.*, 2007). On the other hand, trees need time to recover from mast crops and the year after a good cone crop occurs, a poor cone crop is expected (Summers & Proctor, 2005). The consequent food shortage has a negative impact on the reproductive success and survivorship of squirrels (Koprowski, 1991). This is also true for Kidland Forest, as can be observed in Figure 5.2. In order to account for

---

[5] Environmental variation is defined in VORTEX as *the annual variation in the probability of reproduction and survival that arise from random variation in environmental conditions* (Miller & Lacy, 2005)

the effect of poor cone production on the squirrel population, one *catastrophe* was modeled.

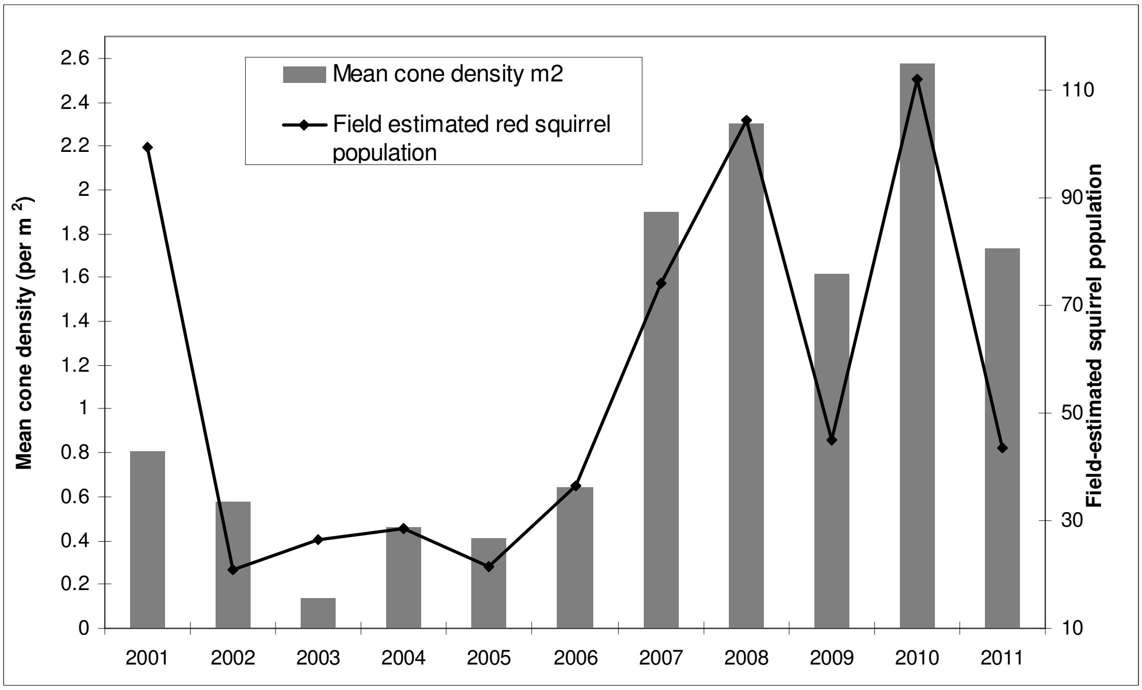


Figure 5.2: Mean annual cone density and field-estimated squirrel population for the period 2001-2011- Kidland Forest, UK (Lurz *et al*, 2011)

The *frequency* at which this *catastrophe* could occur within the given period of time was modeled based on good crop intervals for sitka spruce, the predominant tree species in Kidland Forest (Table 5.4). As found in the literature, sitka spruce mast years occur every 3 to 5 years (Lurz*,* 2002) or every 4 years (Broome *et al*, 2007). An average of 4 years was used to run the model.

VORTEX requires the *frequency* to be input as the probability of the catastrophe happening in any year of the given period. A cone crop failure could occur 2.5 times over the 11-year period and therefore the *frequency* was set at 23 (i.e. a 23 % probability of it occurring any given year).

.

Two parameters are required to model the *severity* of a *catastrophe*: *reproduction* and *survival*. In absence of specific information on how much crop failure affects squirrel's reproduction rate, but knowing that squirrel's densities in Kidland have fluctuated along with cone densities (see Figure 5.2), it was estimated that reproduction would be reduced by 15% (P. Lurz, pers. comm.). The *reproduction* factor was then set to 0.85 indicating that 85% of the females that would breed in a normal year (i.e. 70% +/- 30%, Table 5.2) would still breed in a bad seed crop year. With respect to survival rate, Koprowski (1991) investigated the effects of food shortage on grey and fox squirrels in Kansas, USA, and found that between 91% and 94% of adult squirrels would survive a bad seed crop year (i.e. further 10% would perish) . As no similar studies for red squirrels were found, Koprowski findings were used and 0.9 (90%) was used as a conservative *survival* factor.

Carrying capacity (K): The relationship between tree species and squirrels densities is empirical and based on previous research using squirrel-trapping data within the same forest district or in similar type of plantations (Table 5.4). The total area for each tree species was obtained from stock maps data for Kidland Forest provided by the Forestry Commission (Lurz, 2011; Table 5.4). Annual felling plans for the forest as well as other factors affecting forest size and/or quality (for example, trees damaged by climatic events) were also considered in each annual survey at Kidland Forest and therefore carrying capacity varied annually. The average of the annual carrying capacities (170) was used as the initial value, and the standard deviation (SD= +/- 17) was used as *SD in carrying capacity due to environmental variation*. SD also represents all other variations in K (i.e. due to seed crop).

Table 5.3: Squirrel densities in relation to habitat type for Kidland Forest (Lurz, 2009)

Tree species	Red squirrel density (ha^{-1})	Source
Sitka spruce	0.02-0.20	Lurz *et al*., 1998
Norway spruce	0.12-0.41	Lurz *et al*., 1998
Pine	0.16-0.43	Halliwell, 1997; Lurz *et al*., 1998
Larch	0.21	Garson & Lurz 1998
Other conifers (*)	0.03-0.80	Bobyr 1978; Lurz *et al*., 1995

(*) Douglas Fir (*Pseudotsuga menziesii*), Western Hemlock (*Tsuga heterophylla*), *Abies Sp.*

Table 5.4: Estimated areas of the main tree species able to support red squirrels at Kidland Forest in 2002 based on digitised stockmap data (Lurz & Lloyd, 2001)

Tree species	Area (ha)
Pine (Scot pine and Lodgepole pine)	107
Larch	34
Norway spruce	7
Sitka spruce	644
Fir	14

Initial population was set at 100 individuals, as that was the field-estimated number of red squirrels in Kidland Forest in 2001, when the first survey was carried out.

Population was projected 11 years into the future (i.e. from 2001 to 2011) and simulations were repeated 500 times (500 iterations).

5.2.2 Sensitivity analysis

Sensitivity analysis was carried out to assess how changes in carrying capacity (*K*) were reflected in model outputs (i.e. number of squirrels).

Eleven *K* values arbitrarily selected were used to run the model. The scenario used as baseline was the same scenario used for Kidland, and the model was run for 11 years. The model outputs were recorded and plotted against carrying capacity values and correlation was performed to visually and quantitatively assess model sensitivity.

5.2.3 Red squirrel population viability analysis at Abernethy Forest

Population viability analysis for red squirrels was carried out for Abernethy Forest only as LiDAR data for this study area was of better quality (i.e. point density and scan angle) and therefore habitat suitability maps were assumed to be more reliable (see Chapter 3 and 4 for more details). Furthermore, and as opposed to Aberfoyle Forest (the other study area) Abernethy is also one of the 18 proposed red squirrels strongholds in Scotland.

5.2.3.1 Abernethy Forest

Abernethy Forest (57° 15’ N, 3° 40’ W) is owned and managed by the Royal Society for the Protection of Birds (RSPB). Two thirds of the forest (19 km^2) is native forest and one third is plantation. The dominant tree species is Scots pine (*Pinus sylvestris* L). Detailed description of the forest and maps are provided in Chapter 2.

5.2.3.2 Model Input Data & Scenarios

In the case of Abernethy Forest, a gap area (see Figures 5.3 & 5.4) naturally divides the study area into two distinctive zones and therefore two populations were modelled. However, both populations are connected through patches of forest and the gap was not considered to be large enough to prevent or reduce dispersal. Therefore, *dispersal among populations* was modelled as 100%, as well as *survival of dispersers*. Previous studies have shown that both red squirrel sexes disperse in the

same proportion (Wauters *et. al.*, 2010) and therefore dispersal was modelled for both males and females.
The rest of life-history data used to run the model for Abernethy Forest were the same as used for Kidland Forest (see Table 5.3). Assumptions made are detailed in section 5.2.1.3.

Catastrophe: Shortage of food was modelled as a *catastrophe* at Abernethy Forest also. A study carried out by Summers & Proctors (2005) over an 11-year period showed that Scots pine at Abernethy Forest produce a mast cone crop followed by a poor cone crop every 3 years. Projections were made 20 years into the future, which means that a poor cone crop could occur 6.5 times over that period. Thus, *frequency* at which a cone crop failure may occur was set as 32 (i.e. a 32% probability of it occurring any given year).

Severity of the catastrophe: The reaction of seed-eaters (including red squirrels) to Scots pine cone crops patterns at Abernethy Forest was also investigated by Summers (2011). He reports little to no noticeable change in number of cones taken by squirrel in relation to cone production, suggesting little change in population size. Based on this study and assuming that a small decrease in red squirrels reproduction would still occur in a year with a poor cone production, a *reproduction* factor of 0.95 was used. As for Kidland Forest, Koprowski (1991) findings were used for Abernethy Forest also and 0.9 (90%) was used as *survival* rate.

Carrying capacity (K)
Two different scenarios were modelled based on two different carrying capacities: *Basic* and *LiDAR*.

Basic scenario: carrying capacity was calculated considering all the available mature (i.e. old enough to produce food) forest. Carrying capacity was estimated as the number of squirrels (per ha) that Scots pine support multiplied by the size of the area. The mature forest (*i.e.* trees mature enough to produce food) area was estimated based on available digital forest maps (ArcMap GIS; RSPB 2009, Figure 5.3).

LiDAR scenario: As part of this study, a GLM was developed that relates forest structural parameters (i.e. canopy cover, number of trees and tree height) to the number of cones stripped by squirrels (details provided in Chapter 2) . Using LiDAR data, the GLM was extrapolated to the whole study area, and habitat suitability maps were generated. These maps were classified into *Low suitability* (number of stripped cones < 10) and *Medium-to-High suitability* (number of stripped cones ≥10; see Chapter 4 for details). For the *LiDAR* scenario, those areas classified as *Low suitability* were discarded for being of little or no use for squirrels (i.e. low canopy cover, low tree density, trees not tall enough). Carrying capacity was then estimated considering only *Medium-to-High suitability* patches on the LiDAR habitat suitability maps (Figure 5.4).

Areas were calculated separately for each habitat type (i.e. All-forest and Medium-to-High suitability) and for each population (Table 5.5).

Table 5.5: Area size and carrying capacity estimated for each population and habitat type, Abernethy Forest, Scotland. Forest areas were extracted from digital stock maps provided by the RSPB (2009) and Medium-to-high suitability patches are based on LiDAR habitat suitability maps.

	Population 1		**Population 2**	
	All forest	**Medium to high**	**All forest**	**Medium to high**
Area (hectares)	395	162.6	366.5	104.6
Carrying capacity (number of squirrels)	328	135	304	87

Carrying capacity was then calculated (as described above) for each population. Based on previous studies, the density of red squirrels per hectare for Scots pine in Scotland is known to be between 0.33 and 0.83 in a poor and in a good cone crop year respectively (Tittensor 1970; Moller, 1986; see also review by Lurz *et al.* 1995). It was assumed that the first year of the period for which the model was run was a good crop year and the higher value (i.e. 0.83) was used to calculate carrying capacities.

Information on current red squirrel population size in Abernethy Forest is not available and therefore *Initial population* was set as full carrying capacity (values provided in Table 5.5) for both scenarios.

The two scenarios were then modelled in VORTEX keeping constant life-history parameters and assumptions and modifying only the carrying capacity. For both *Basic* and *LiDAR* scenarios, catastrophe and no-catastrophe sub-scenarios were also modelled.

In all cases, populations were projected 20 years into the future, and simulations were repeated 500 times (500 iterations).

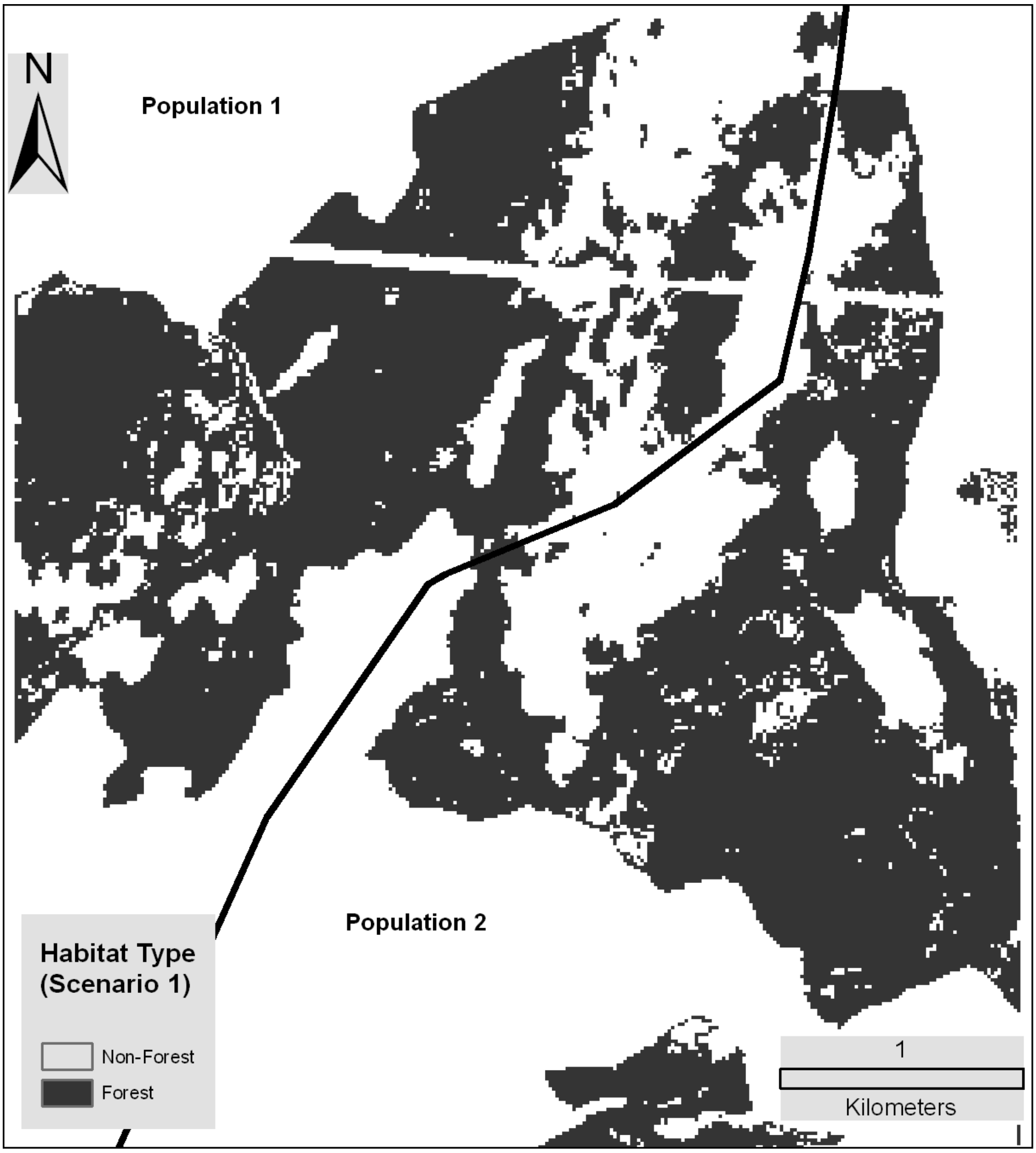


Figure 5.3: Habitat type for *Basic* scenario – Carrying capacity was calculated for all mature forest (i.e.forest old enough to produce food). The mature forest area was estimated based on available digital forest maps (ArcMap GIS; RSPB 2009). The black line separates Population 1 and Population 2. Abernethy Forest, Scotland.

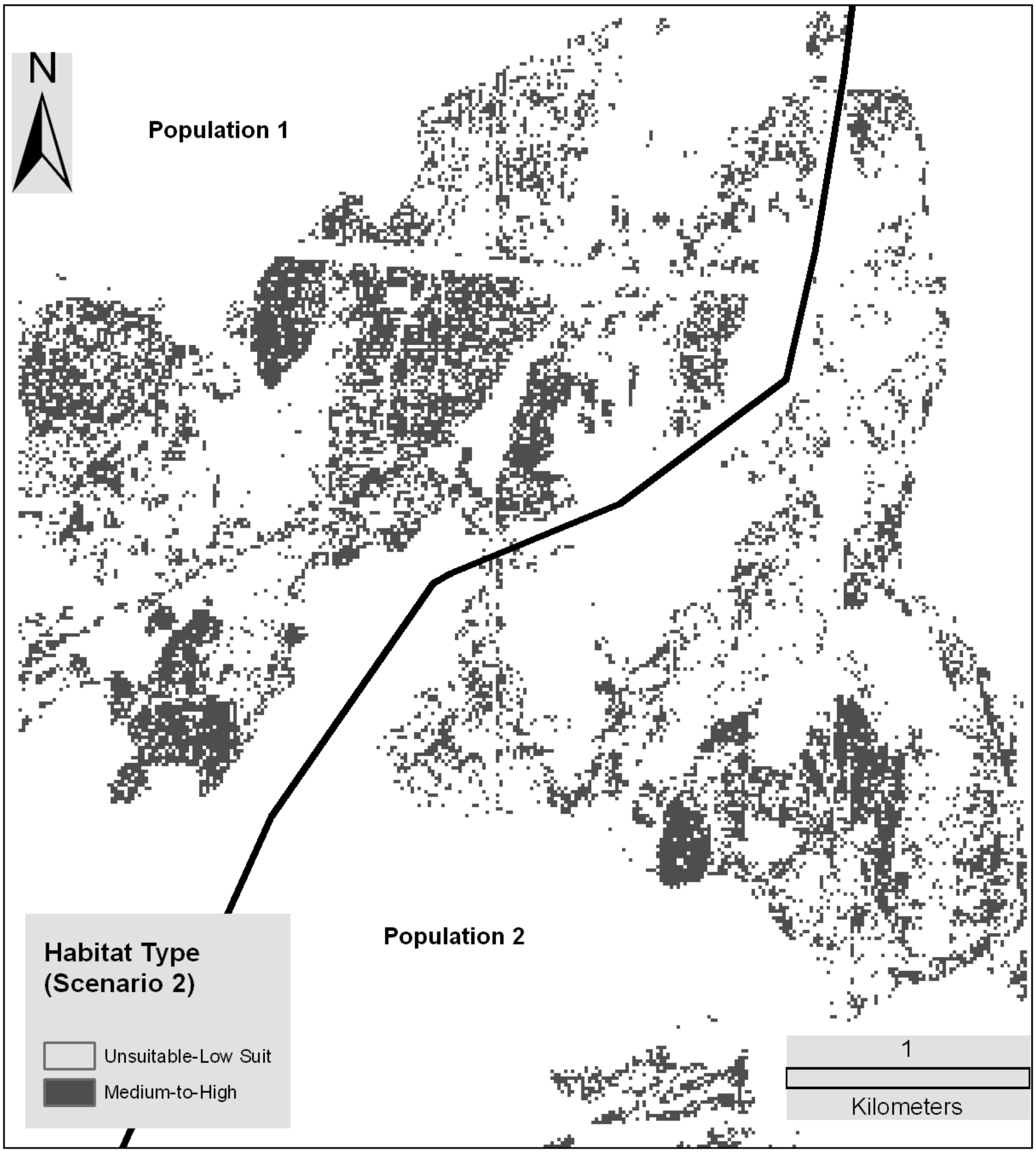


Figure 5.4: Habitat type for *LiDAR* scenario – based on LiDAR habitat suitability maps, Medium-to-High suitability patches were retained. The black line separates Population 1 and Population 2. Abernethy Forest, Scotland.

5.3 Results

5.3.1 Model Validation

Table 5.6 and Figure 5.5 show results of the model run for Kidland Forest. Annual observed population ranges from 21 to 105, and annual mean predicted population by VORTEX range from 72 to 110 individuals. Standard deviations of predictions are also given in Table 5.6.

The number of squirrels estimated based on field observations was expected to be within +/- 1SD of the VORTEX predicted populations. Whilst there was a mismatch for early predictions (see Discussion) this was true for 7 out of 11 years (Figure 5.5).

Table 5.6: Numbers of squirrels observed in the field (Observed), mean number of squirrels predicted by VORTEX (Projected) and standard deviation (SD)- Kidland Forest, UK

Population size	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011
Projected	110	104	101	97	90	87	84	80	76	74	72
Observed	100	21	26.5	28.5	21.5	36.5	74	104.5	45	112	44
SD (projected)	52.1	55.9	60.2	61.9	63.2	63.3	66.2	65.4	66	67.4	67.5

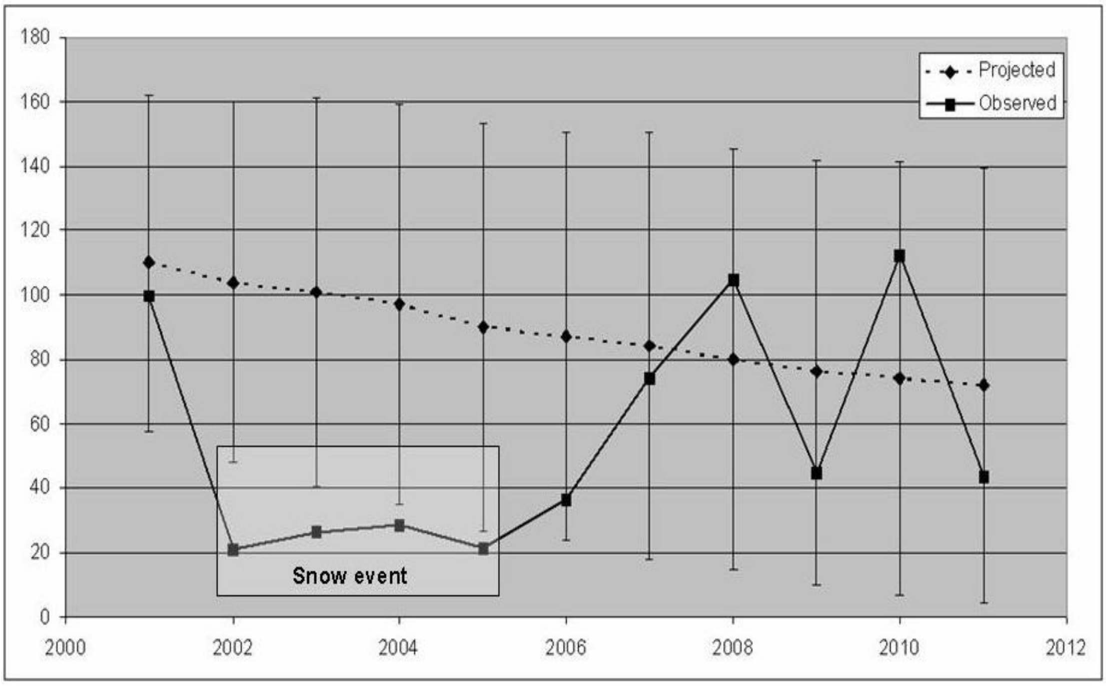


Figure 5.5: Plot of annual numbers of squirrels observed in the field (full line) and annual number of squirrels predicted by VORTEX (dotted line) - Kielder Forest, UK

5.3.2 Sensitivity analysis

A strong correlation was observed between the different carrying capacity values used as input for the model and the mean population size (i.e. number of squirrels) predicted by VORTEX at the end of the period considered ($r = 0.99$; $P< 0.001$, n=11, Figures 5.6 & 5.7, Table 5.7).

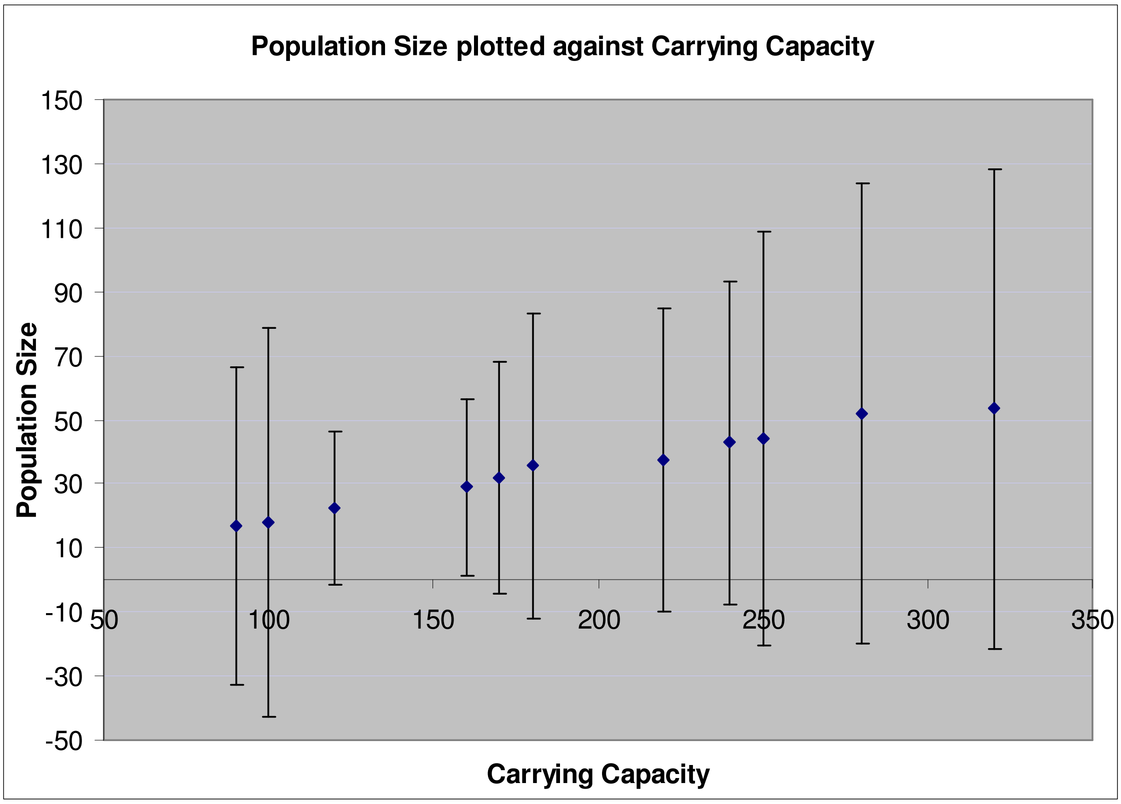


Figure 5.6: VORTEX sensitivity analysis. Scatter plot of Mean Population size plotted against Carrying Capacity. Error bars represent SD. Strong correlation is observed between carrying capacity and population size. ($r = 0.99$; $P< 0.001$, n=11)

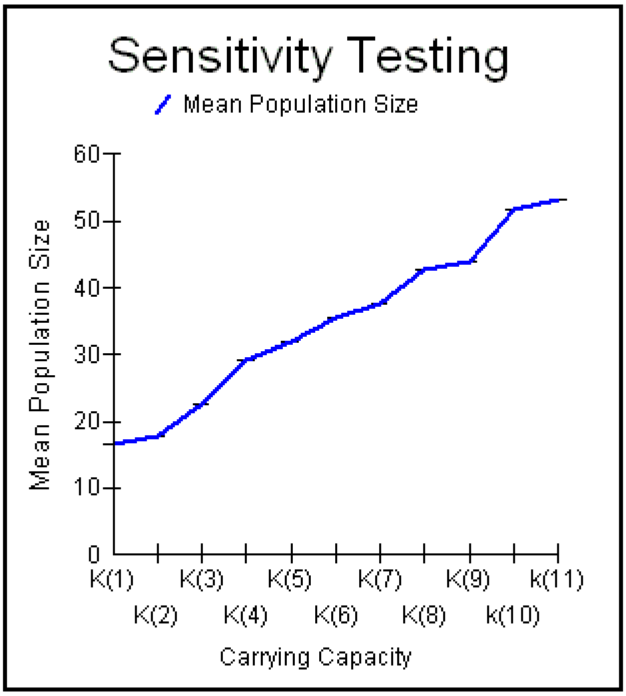


Figure 5.7: Graph produced by VORTEX sensitivity test showing variation of *Mean population size* with *Carrying capacity*. Values for K (1)….K(11) are given in Table 5.7

Table 5.7: Carrying capacity values used to perform the sensitivity analysis and mean annual population predicted by VORTEX, Abernethy Forest, Scotland.

K (VORTEX)	Carrying Capacity	Mean Population Size	SD
K(1)	90	17	49.6
K(2)	100	18	60.9
K(3)	120	22	24.1
K(4)	160	29	27.6
K(5)	170	32	36.2
K(6)	180	36	47.6
K(7)	220	38	47.3
K(8)	240	43	50.6
K(9)	250	44	64.5
K(10)	280	52	71.9
K(11)	320	53	75.0

5.3.3 Red squirrel population viability analysis at Abernethy Forest

In all scenarios and for both populations, mean population size showed a steady and constant decline over the 20-year period (Figures 5.8 & 5.9). However, the probability of extinction was much higher for the scenario based on LiDAR data, indicating that management decision based on an overestimate of habitat suitability (*Basic* scenario) can critically endanger local populations.

Basic scenario: For the *no-catastrophe* sub-scenario, mean population size decreased from 260 to 42 for Population 1 and from 254 to 42 for Population 2. When one catastrophe was modelled, mean population size decreased from 242 to 38 for Population 1 and from 238 to 37 for Population 2. Considering both populations together, probability of extinction at the end of the period was 53% and 58% for the *no-catastrophe* and *catastrophe* sub-scenarios respectively.

LiDAR scenario: When no catastrophe was modelled, mean population size decreased from 87 to 13 for Population 1 and from 78 to 11 for Population 2. For the *catastrophe* scenario, mean population size decreases from 87 to 11 for Population 1 and from 76 to 9 for Population 2. Considering both populations together, probability of extinction at the end of the period was 69% and 74% for the *no-catastrophe* and *catastrophe* scenarios respectively.

Mean annual populations and standard deviations projected by VORTEX are presented in Appendix D, Table D.1.

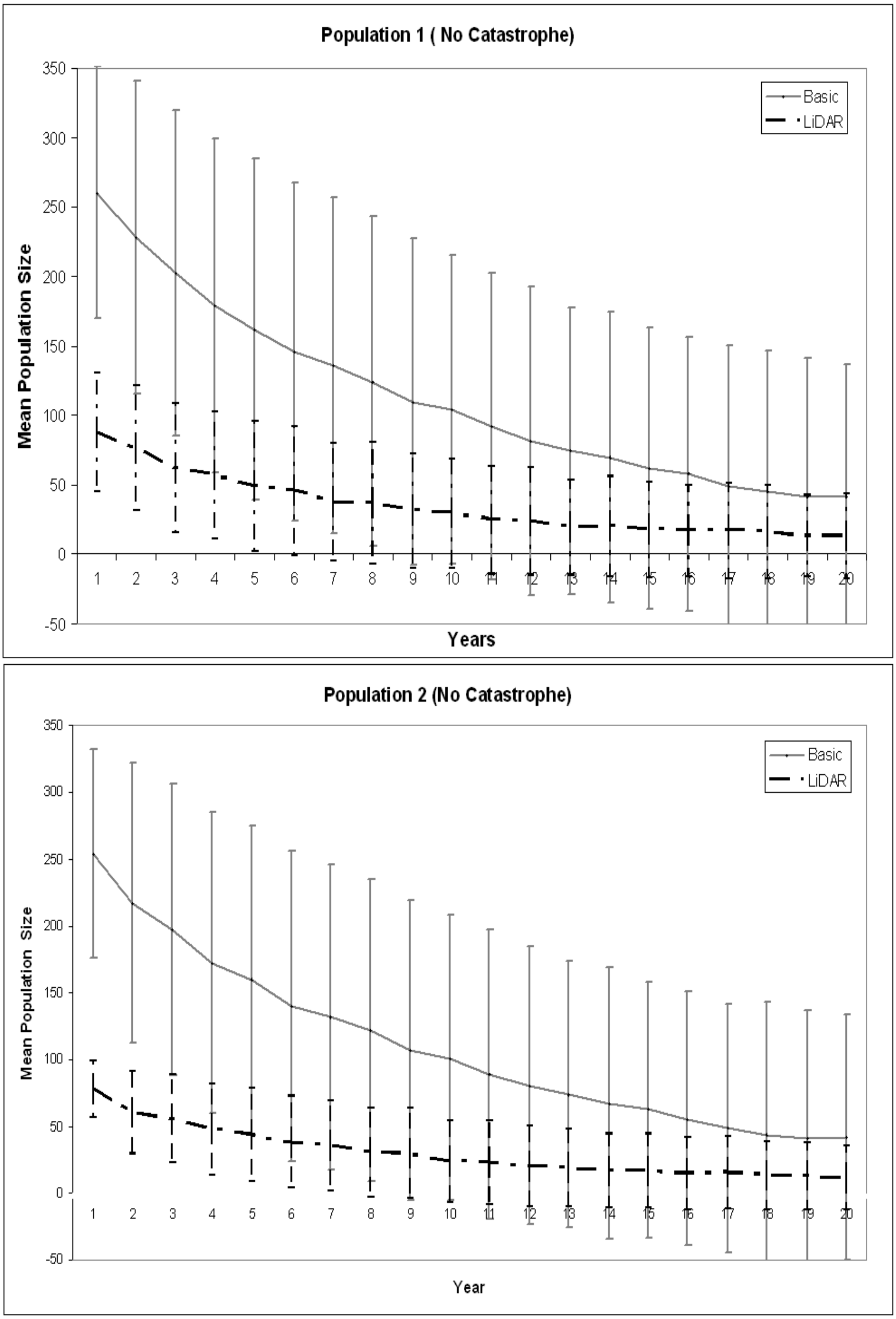
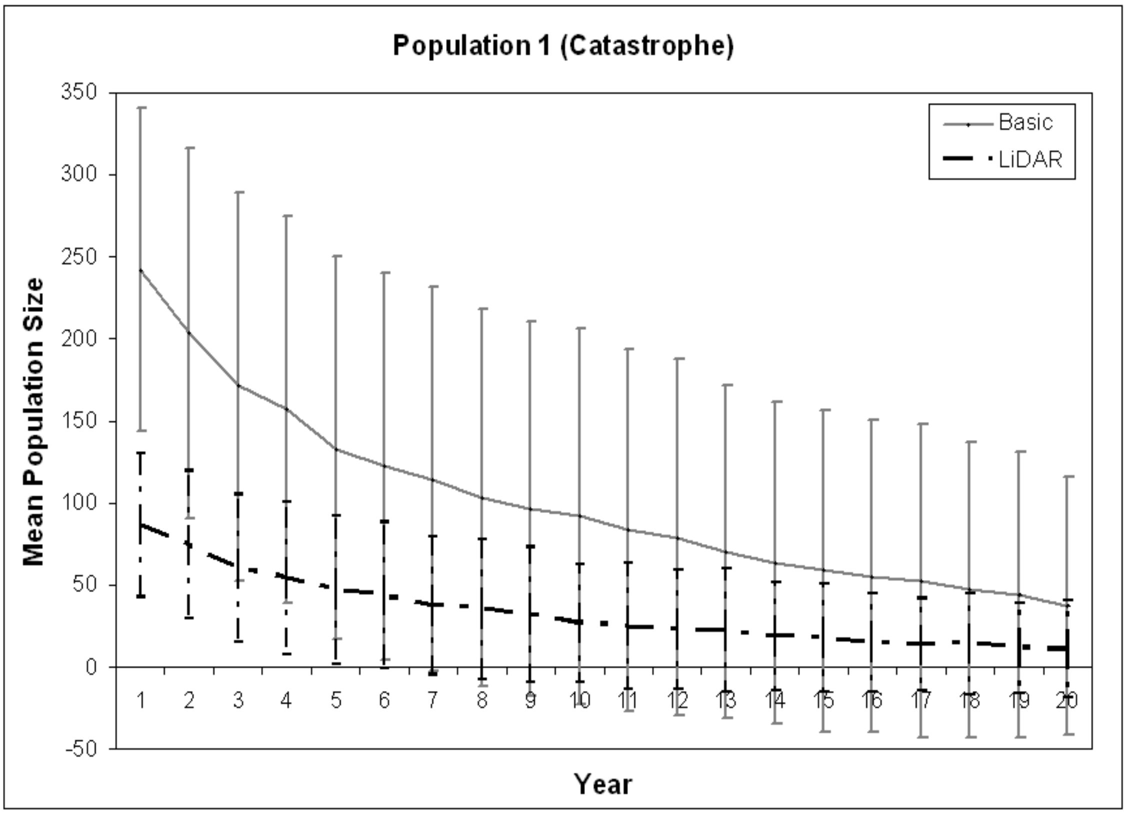


Figure 5.8: Annual population size for both Basic (full line) and LiDAR (dotted line) scenarios, for Population 1 (top) and Population 2 (bottom), when no-catastrophe is modelled. Error bars represent +/- SD. Abernethy Forest, Scotland.



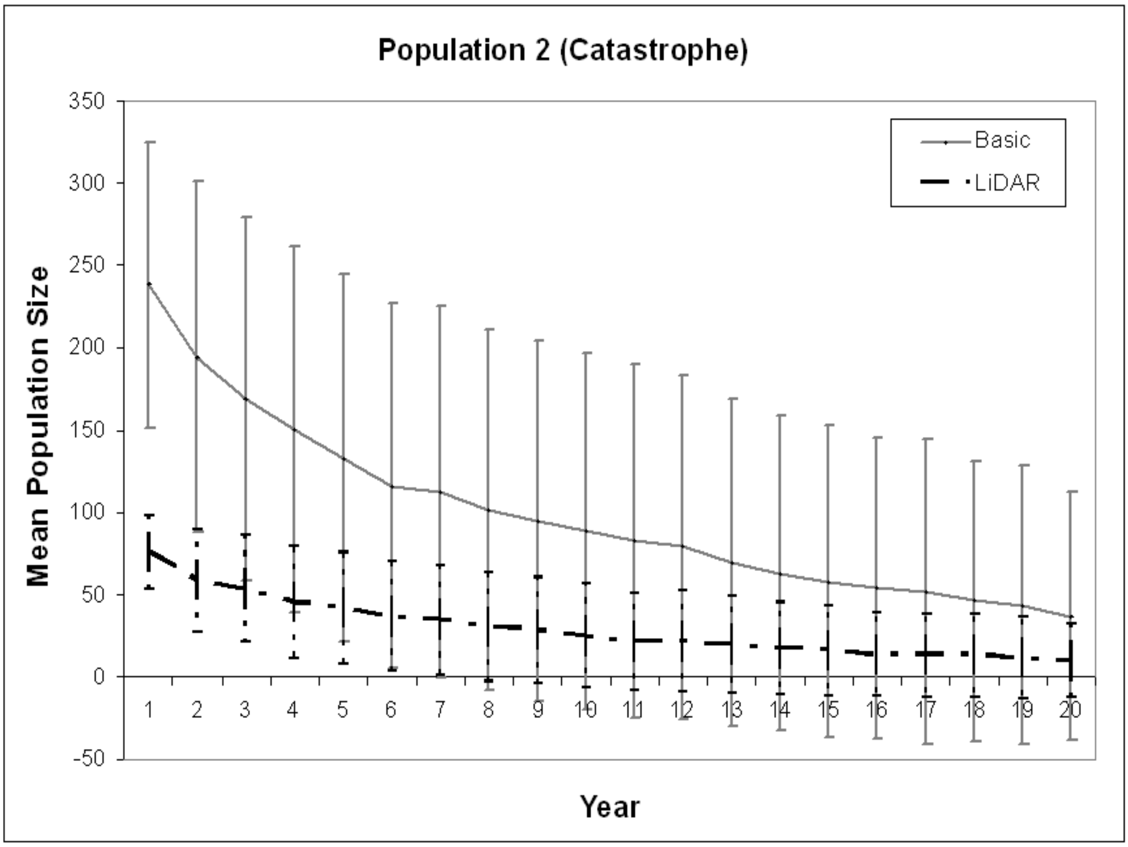


Figure 5.9: Annual population size for both Basic (full line) and LiDAR (dotted line) scenarios, for Population 1 (top) and Population 2 (bottom), when one catastrophe is modelled. Error bars represent +/- SD. Abernethy Forest, Scotland.

5.4 Discussion

5.4.1 Model validation

One key criticism of PVA models is the simplification of population dynamics Populations dynamics are complex and PVA provide only a relatively simple estimation (Lindenmayer *et al*., 1993). In the particular case of VORTEX, population dynamics are represented by the mean population size and variations (i.e. fluctuations) in population size are represented by the standard deviation (Miller & Lacy, 2005). Thus, VORTEX predictions were not expected to follow the natural cycles of population dynamics. Instead, field estimated annual populations were expected to be within the range of +/- the standard deviation of the annual mean population projected by VORTEX. This was the case for 7 out of 11 years. The field estimated population was considerably lower than that projected by VORTEX over the 2002 to 2005 period (see Table 5.6 and Figure 5.5, Results section). In 2002, most Scots pine plantations and some lodgepole pine plantations at Kidland Forest were severely damaged by snow, and lost part or all of their crowns. This had a high impact on the cone production and therefore on squirrel densities (Lurz, 2002). However, the magnitude of this event and the extent of the spatial damage at Kidland were not quantified during the survey. Hence, no data were available to accurately model this catastrophe. Model predictions therefore overestimate the observed data for the period 2002-2005. Once red squirrel population started to recover (in 2006), field estimated population fall well within the range of +/- SD of model predictions.

PVA at Kidland Forest also illustrates the potential effects of environmental stochasticity (i.e. snow event) on local populations. Furthermore, current model predictions seem to indicate a reduction in mean predicted squirrel population at Kidland Forest. Future field surveys will show if this is indeed the case, or a result of input ranges for life history parameters which do not completely capture long term population dynamics at Kidland Forest (see also 5.4.4).

5.4.2 Sensitivity analysis

Strong correlation (r=0.99, $P < 0.001$, n=11) between input values and model outputs show that VORTEX is highly sensitive to variations in carrying capacity. In this study, mainly variations in carrying capacity were modelled and the rest of the parameters were kept constant. Therefore, only VORTEX's sensitivity to carrying capacity was tested. However, other researchers have found the model to be sensitive to variations in a range of life-history parameters. For instance, Duca *et al* (2009) found that variations in percentage of female breeding and adult mortality of white-banded tanager in Brazil had an impact on probability of population persistence, while the latter was not particularly sensitive to the percentage of males in the breeding pool.

In addition, Brito & Grelle (2008) tested VORTEX's sensitivity to mortality rate, sex ratio, percentage of reproductive females and inbreeding depression for the Northern muriqui, Brazil. Their findings showed that inbreeding depression, percentage of female breeding and sex ratio influence population growth and final population size, while variations in mortality rate produce variations in final population size. These and the results from this Chapter suggest that VORTEX is in general fairly robust and sensitive to variations in a range of parameters.

5.4.3 Red squirrel population viability analysis at Abernethy Forest

In general, and considering both scenarios, VORTEX predicts a steady reduction in mean red squirrel population and a high probability of extinction (53%-58% for the *Basic* scenario and 69%-74% for the *LiDAR* scenario, Figures 5.8 & 5.9). These results match and support findings from a previous field study by Summers (2011) who reports a decrease of the number of Scots pine cones taken by squirrels in Abernethy Forest, and suggests a long-term decline in red squirrel population.

When carrying capacity is estimated using the LiDAR habitat suitability maps and one catastrophe is modelled, the mean population at the end of the period reaches very low numbers (11 for Population 1, 9 for Population 2) and a high probability of extinction (74%). The difference in probability of extinction between catastrophe and no-catastrophe scenarios is not large (55% and 53% respectively for the *Basic* scenario, 74% and 69% for the *LiDAR* scenario). This was expected as the percentage of females breeding was reduced by 5% only in a year when shortage of food occurs (i.e. 95% of total females breeding will still breed in a bad cone crop year). This conservative approach was based on research carried out by Summers (2011), who reported no noticeable changes in red squirrel population -over an 11-year period- in relation to food availability in Abernethy Forest. However, the reason for this apparent lack of reaction of red squirrel could be that the species population is already too small to react to peaks in food production. This could be indicating that initial populations used to run VORTEX in this study (Table 5.5) are overestimating the actual red squirrel population at Abernethy Forest, and the risk of extinction could be even higher.

It should be highlighted here that PVA models provide probabilities and not certainties (Brook *et al*, 1997; Boyce, 1992), as such, results should be cautiously interpreted: for instance, high standard deviations for mean annual population sizes (Table D.1, Appendix D) indicate a high uncertainty in predictions probably stemming from high standard deviations in input life-history data (i.e. % of females breeding, mortality rates, Table 5.2). Nevertheless, results of this study also suggest that red squirrels populations are highly sensitive to variations in carrying capacity. The high probability of extinction at the end of the 20-year period highlights the need for forest management for the species conservation in Abernethy Forest, not only in terms of habitat quality (i.e. increasing canopy cover and tree density) but also food availability. In systems where more than one tree species is present, squirrels would naturally switch to the tree species producing food (Andrén & Lemnell, 1992). This is not possible in Abernethy Forest which consists of Scots pine only. Data from Sweden show that in old-growth pine forests red squirrels may be naturally absent for 2 out of 10 years as a result of cone crop cycles and changes in food availability (Andrén & Lemnell, 1992). Data for Abernethy Forest (Summers, 2011) and this study illustrate the potential constraints and challenges of single species management in confined locations. Abernethy Forest is one of the oldest forests in Scotland and part of the Scots pine woodlands are remnants of ancient native pine forests (Summers, 2011). Therefore management options with respect to tree species diversity to increase food availability for red squirrels need to be carefully considered.

5.4.4 Issues and constrains

In both cases (i.e. Kidland and Abernethy Forests) VORTEX predicts a reduction in mean squirrel population over time. The fact that this occurs in both Kidland and Abernethy Forests could be indicating a feature of the model or life history parameter ranges used that fail to sufficiently account for site specific events (Rushton *et al.* 2006b). It would therefore be interesting to contrast these results with empirical data (i.e. field surveys and trap data giving details on population number, proportion of animals breeding etc.), in particular for Kidland Forest where monitoring will continue to be carried out on an annual basis (Lurz, pers. com; 2012). Furthermore, some of the specific input parameter ranges (i.e. observed ecological data for fecundity or mortality) used to run the model could also be having an effect on the model predictions. Previous studies on red squirrel population dynamics found that predicted population size for the Mt. Graham red squirrel in the United States was sensitive to variations in parameters such as adult mortality, juvenile mortality, fecundity and proportion of females breeding (Rushton *et al.*; 2006b); while in Italy, the predicted total population size of grey squirrels were influenced by mean fecundity and mean proportion of females with a first litter (Lurz *et al.*, 2001).

In the current study, all parameters related to fecundity and mortality used to run the model were gathered from published work on red squirrels in comparable forest habitats. However, the use of site-specific data on red squirrel in for example Kidland or Abernethy would certainly improve the accuracy and therefore the reliability of the model predictions.

5.4.5 The use of LiDAR remote sensing for PVA

The main aim of this Chapter was .to assess the potential of LiDAR derived habitat suitability data to assist red squirrels population viability analysis. Mills *et al.* (1996) highlighted the importance of minimising the effects of projecting uncertainty stemming from lack of accurate information in key parameters such as, for example, carrying capacity when using PVA models. This study illustrates the risks of overestimating habitat quality by, for example, not taking into consideration forest structure. This overestimation of habitat quality and therefore, of carrying capacity can lead to unrealistic projections and underestimate the actual risk of extinction of local populations.

The use of LiDAR remote sensing in this context allows for a more refined assessment of habitat quality by identifying patches that are of low suitability for the species. This in turn allows for a more realistic estimation of carrying capacity. In this way, this study also illustrates the potential of remote sensing, in particular LiDAR, to produce more realistic estimates of carrying capacity, leading to more realistic predictions of probability of extinction and population size when modelling PVA for endangered species.

Abernethy Forest is one of the potential red squirrel strongholds in Scotland. Management for strongholds at the stand level is contemplated in terms of conifer species and age diversification to provide a continuous food supply (http://www.scotland.gov.uk/Publications/2009/04/Red-Squirrel-Strongholds).

Habitat quality at the sub-stand level is not currently considered in management plans, partly due to a lack of cost-efficient method to collect data and to generate habitat quality information. The use of LiDAR remote sensing allows for the identification of areas where forest structure management at the sub-stand level is required. This is due to the capability of LiDAR to map habitat heterogeneity. In the particular case of Abernethy, when habitat suitability is assessed considering the species preferences in terms of forest structure and using LiDAR derived data, approximately 70% of the forest (see Chapter 4) is not capable of sustaining red squirrel populations in the long term. This highlights not only the need for management for the forest, but also the advantages of using remote sensing to map habitat quality at large scales.

To the author's knowledge, the current study represents one of the few that have used remote sensing to assist PVA. One such study was carried out by Haines *et al.* (2006). They incorporated remotely sensed data into a spatially-explicit package (RAMAS/GIS) to model population viability for the endangered ocelot in USA. Based on the species habitat preferences, habitat suitability data was incorporated to the model as a land-cover map derived from LANDSAT ETM+ data where those areas with canopy cover > 75% (identified by performing a supervised classification) were (more details in Section 5.1.4.1) The current study illustrates the potential of remote sensing as a tool to assist PVA modelling even when a no spatially-explicit package such as VORTEX is used.

Overall, the results of this Chapter highlight the need for considering forest structure when planning management for potential red squirrel reserves and the usefulness of using LiDAR remote sensing to assess habitat quality at the forest scale.

CHAPTER 6

Discussion and conclusions

This thesis has addressed two critical gaps in red squirrel habitat management in the UK. First, the study has investigated and quantified the relationship between red squirrel habitat use and forest structural parameters, namely canopy closure, tree density and canopy height. Second, the thesis has explored the use of remote sensing –in particular LiDAR- to assist management of red squirrel habitat for the species conservation. A population viability analysis was carried out to illustrate one of the potential applications of LiDAR-derived habitat quality data. This chapter summarises the findings of this research and discusses the limitations of the approach. Further research needs and potential applications beyond the scope of this study are also highlighted. Finally, overall conclusions and key recommendations are provided.

6.1 Forest structure and red squirrel habitat preferences

This thesis investigated the effects of forest structure on red squirrel (*Sciurus vulgaris)* habitat preferences. A general linear model (GLM) was used to relate red squirrel feeding signs (as an indicator of local patch use; see Doumas & Koprowski 2012 for a similar approach) to forest structural parameters for Scots pine (*Pinus sylvestris*). The statistical analysis of field-collected data showed that canopy closure and number of trees are significant predictors ($p < 0.01$ and 0.03 respectively; n=52) of the number of cones stripped by squirrels. Although strictly not significant (at the 0.05 significance level) tree height ($p < 0.058$) was retained as it is the only structural variable considered in the model which is related to seed quality (Grönwall, 1982).

The statistical model (GLM) performance was assessed using a leave-one-out (LOO) cross-validation approach (Arlot & Celisse, 2010). The correlation between field-collected stripped cones and those predicted by the model was found to be moderate (r_s = 0.4, p <0.004, n=52, RMSE = 20). In ecological and biological field studies variance in data is highly influenced by randomness and noise (i.e. outliers) and therefore the levels of variance explained by statistical models are generally lower than those in other sciences were experiments are carried out in controlled environments (Møller, & Jennions, 2002). The three forest structural variables considered in this study explained 43% of the variance in the number of cones stripped by squirrels. This indicates that these are important factors that shape red squirrel feeding behaviour at the sub-stand level.

The model developed in this study considered three forest structure parameters. Other structural variables not considered in this study might also influence the species habitat preferences at the plot level. Research by Nelson *et al.* (2005) found that Delmarva fox squirrel (*Sciurus niger cinereus*) prefer open understory in Maryland's Eastern Shore, USA. In the UK, Gurnell *et al* (2002) suggested that red squirrel avoided open stands not only because of the open canopy, but also because understory vegetation (in particular bracken) becomes denser in open stands making it more difficult for the squirrels to move across quickly if needed. Future research could explore the impact of understory vegetation in red squirrel habitat selection in the UK.

Tree seeds are red squirrel main diet (Gurnell, 1987; Lurz *et. al.*, 1995) and therefore the question of whether squirrels would use more those plots where food is more abundant, regardless the structure, has also been addressed in this thesis: the relationship between total cone crop and number of stripped cones (per plot) was assessed and results showed a weak to moderate correlation (r_s=0.37, p<0.007; n=52, Figure 6.1) between the total cone crop and the number of stripped cones per plot for both Abernethy and Aberfoyle data together. If the presence and abundance of food explained habitat use by red squirrel at the plot level, a much stronger correlation would be expected.

In addition to this, and using the data from the survey that has been carried out at Kidland Forest for the last 11 years (2001 to 2011; Lurz, 2011) the relationship between mean annual mean cone density and red squirrel density for the whole forest and considering all tree species together was also assessed. In this case, and as observed by Lurz (2011), a much stronger correlation was found (r_s=0.87, p<0.001; n=11).

These results suggest that while annual variations in food availability shape the number of red squirrels at the forest level, at the sub-stand level, and provided food is available, forest structure matters and has an impact on habitat selection by red squirrels.

The current study is based on 2 years of fieldwork and further research is required to test the robustness of the predictions. For example, whilst squirrels were seen to avoid open areas that contain food, it is unknown what would happen in times of food shortage, and what risks they would be prepared to take. Furthermore, in times of scarce resources, subordinate individuals in a population (i.e. sub-adults and juveniles) have limited access to those resources (i.e. food), which would also be the case if high densities of squirrels occur (Gurnell, 1987). It would be interested to explore if squirrels would exploit isolated stands or open forest in those situations.

Whilst this investigation of squirrel habitat use based on feeding signs represents a first and relatively crude approach, the findings confirm previous research by Gurnell *et al* (2002). The latter reported that red squirrels in Thetford Forest were observed to avoid old stands of Scots pine (*Pinus sylvestris*) that had been intensively thinned (i.e. few trees and open canopy). This thesis, however, goes one important step further by quantifying the effect of forest structure on red squirrel habitat use.

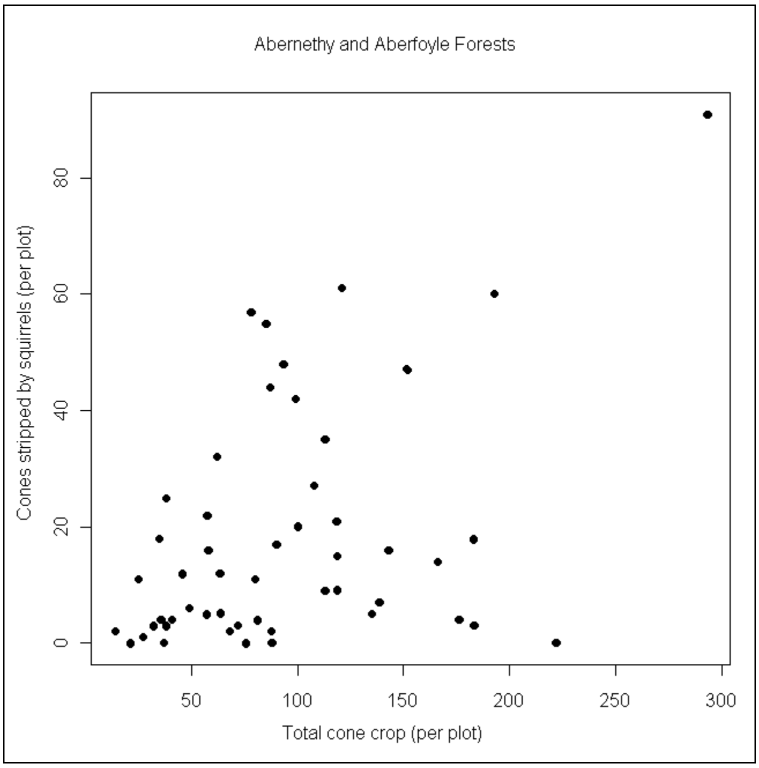


Figure 6.1: Scatter plot of number of stripped cones and total cone crop per plot for Scots pine (r_s=0.37, *P*<0.007; *n*=52). Abernethy and Aberfoyle Forest, Scotland

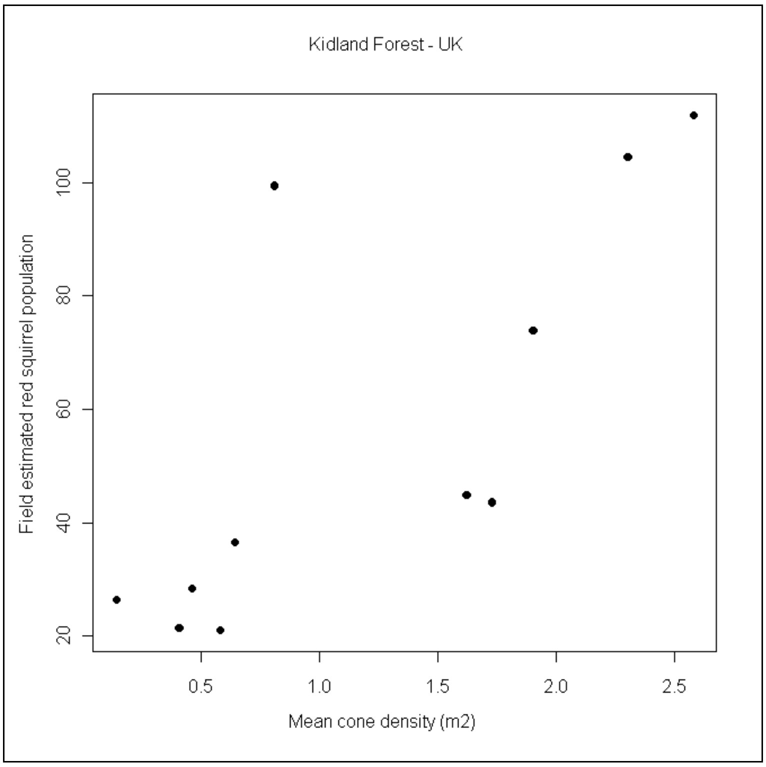


Figure 6.2: Scatter plot of field estimated red squirrel population and mean cone density (m^2) for all tree species together – annual values (r_s=0.87, *P*<0.001; *n*=11). Kidland Forest, England.

6.2 The use of LiDAR remote sensing

In this thesis, LiDAR remote sensing was used to i) retrieve forest structural parameters that relate to red squirrel habitat use, more specifically, the three variables discussed in the previous section: canopy cover (as a surrogate for canopy closure, see Chapter 3), number of trees and tree height; and ii) to map habitat suitability over the whole study areas using the LiDAR derived variables and the GLM.

Forest structural parameters

The statistical analysis of the relationship between forest structure and red squirrel habitat use focused on Scots pine. However, data on forest structure was also collected for sitka spruce (*Picea sitchensis*) at Aberfoyle. Field collected data for both tree species were used to validate LiDAR derived explanatory variables, and in both cases (i.e. field and LiDAR data), mean values at the plot level were used. A summary of the main findings is provided below:

Field-measured canopy closure and LiDAR-derived canopy cover were found to be strongly correlated when all Scots pine plots were considered together (r_s= 0.71; n=52, P< 0.00). Large LiDAR scan angles (i.e. > 18°) are thought to produce slightly biased canopy cover estimates (Korhonen *et al.*, 2011). Scan angles for Abernethy and Aberfoyle LiDAR data were 18° and 20° respectively and therefore, correlations were also assessed for Scots pine at each forest separately with similar results (r_s= 0.65 & 0.73; n=32 & 20, p<0.00 for Abernethy and Aberfoyle respectively). These results are not conclusive and only suggest that no substantial differences were observed between canopy cover derived from LiDAR data acquired at scan angles of 18° and 20°. However, the optimal scan angle is 12° and a maximum of 15° is recommended to avoid bias in the estimation of forest structural parameters (Evans *et al.,* 2009). The results of this thesis suggest that strong correlations between LiDAR canopy cover and field canopy closure are observed with scan angles larger than those recommended for vegetation applications. Nevertheless, future research should explore the correlation between canopy cover and canopy closure using LiDAR data acquired at scan angles <15°.

The correlation between canopy cover and canopy closure was assessed also for sitka spruce plots only and was found to be weaker (r_s=0.40, p< 0.015, n=36). As the key tree species in this project is Scots pine, this was not further investigated. However, tree species can differ significantly with respect to crown structure as illustrated by Scots pine and sitka spruce. If the approach is intended to be applied to other tree species or mixed woodlands, the relationship between canopy closure and canopy cover needs to be carefully explored in each case.

Local maxima algorithm provides an operational approach to retrieve the number of trees using LiDAR data. The level of accuracy achieved in Abernethy Forest (71,1%, LiDAR data resolution: 2 pulses/m^2) lies within the range of values found in the literature (e.g Gaulton *et al*, 2008; García *et. al.*, 2007). However, the percentage of trees correctly detected in Aberfoyle is considerably lower (47.7%). The main reason for this is likely to be the lower LiDAR data resolution (1 pulses/m^2). Higher point densities (i.e. >1 pulses/m^2) would potentially improve the number of detected trees (this is further discussed later in this section). The performance of local maxima is also likely to improve if a variable-size search window is used, as opposed to the fixed-size window that was used in this study. Provided that reliable allometric relationships are available, search-window size could be a function of the tree height (this has been discussed in more detail in Chapter 3). Finally, the use of a different approach or a combination of techniques (e.g. local maxima and image segmentation, see Chapter 3) might also produce more accurate results.

Accurate mean tree height at the plot level can be estimated by using 95th percentile of LiDAR height. This correlation was investigated for plots consisting of Scots pine only at Abernethy and for both Scots pine and sitka spruce plots together at Aberfoyle. Results were very similar in both cases (r=0.92 and 0.94; n= 32 and 56 respectively, P< 0.001) suggesting that 95th percentile of LiDAR height accurately represents mean tree height at the plot level for those three species. Future research could investigate the use of LiDAR percentiles for different types of forest; e.g. even aged plantations and natural mixtures with a variety of ages and species.

GLM implementation

The LiDAR derived explanatory variables were used to implement the general linear model and map habitat suitability in both Abernethy and Aberfoyle Forests (Chapter 4). As the GLM was originally developed for Scots pine only, in Aberfoyle, only Scots pine stands were used to implement the model. LiDAR performance was assessed by exploring the correlation between field-predicted and LiDAR-predicted number of stripped cones. Correlations were assessed for each study area separately and were found to be strong ($r_s = 0.59$ for Abernethy and $r_s = 0.54$ for Aberfoyle, n= 32 and 20; RMSE= 12.3 and 11.9 respectively). Assuming the number of stripped cones as an index of habitat selection by red squirrels, these strong correlations highlight the usefulness of LiDAR as a tool to assist red squirrel habitat management at large-scale.

The recommended pulse density for vegetation applications is 4-6 pulses/m^2 (Evans *et al*, 2009). The current study suggests that accurate results can still be achieved using lower point densities (1 and 2 pulses/m^2 for Aberfoyle and Abernethy respectively). However, this study also illustrates some of the potential constraints. The number of trees is the parameter where the effect of low pulse density seems more evident, in particular for Aberfoyle. This was expected to have an effect on the performance of the LiDAR-based model predictions. In order to quantitatively assess this effect, the Aberfoyle LiDAR number of trees was calibrated using field data (see Chapter 4) and the GLM was also implemented using the calibrated LiDAR number of trees. This correction improved the model performance (r_s = 0.60) but it also increased the error (RMSE = 29.8). This suggests that while this calibration improves the spatial variation of LiDAR-derived number of stripped cones it also increases the difference between absolute values of field-predicted and LiDAR-predicted number of stripped cones. While these results are not conclusive in terms of the actual accuracy of the model, they do reflect that the poor performance of the LiDAR derived number of trees influences the accuracy of the habitat suitability maps. As this poor performance is likely to be caused by the low pulse density, this highlights the need for using higher resolution LiDAR data to assess and monitor habitat suitability for red squirrel. However, increasing point density (and decreasing scan angle as suggested above) also increases acquisition cost and data volume (Evans *et al.*, 2009). Since LiDAR data can be used for multiple applications (i.e. forest inventories, topography mapping) establishing collaborative projects to share data could potentially reduce the cost of data acquisition and processing.

This project aimed to assess the ecological relationship between red squirrel habitat use and forest structure, and therefore, this part of the project was developed first using data collected in the field. LiDAR data were used afterwards to extrapolate the analysis to both study areas by using LiDAR-derived explanatory variables which replaced the field-measured explanatory variables. Most studies have used a different approach by directly exploring the relationship between species presence/abundance (or habitat use) and LiDAR derived metrics (see. Hill *et. al.*, 2005; Clawges *et. al.*,2008; Goetz *et. al.*,2010 for examples). Future research could explore the applicability of the latter to the red squirrel in the UK. For instance, using squirrel survey techniques such as radio-tracking or camera-trap would provide information on specific patch use. Integrating this information and LiDAR derived metrics into a GIS would allow a better understanding of how three-dimensional forest characteristics (such as canopy height, canopy cover, tree density) shape squirrels space use and impact on aspects of for example population dynamics (and predation rates) or red-grey squirrel competition.

A synergetic approach using optical and LiDAR remote sensing could provide the opportunity to map not only forest structure (LiDAR) but also other aspects of red squirrel habitat preferences. Most studies carried out in the UK investigating the species habitat preferences have used forest stock maps (e.g. Lurz *et al,* 1995; Gurnell *et al*, 2002) or the National Inventory of Woodlands and Trees (NIWT, e.g. Poulsom *et al.*, 2003) to assess tree species composition. However, forests and woodlands can change over the years and forest stock maps have been found to be outdated in a number of occasions (Jo Ellis, personal Comm., 2009; author's personal observation). Updating this information is time consuming and requires extensive field surveys. For instance, the current National Forest Inventory began in 2009 and it is expected to be completed in 2014 (Forestry Commission, 2012).

A number of studies have used remote sensing to map forest species composition with reasonable levels of accuracy: Martin *et. al.*, (1998) used AVIRIS hyperspectral data (224 contiguous spectral bands ranging from 0.4 to 2.4 µm; 20m spatial resolution) to generate tree species maps of pure and mixed stands of conifer and deciduous forests in Massachusetts, US; with an overall accuracy of 75%; while Lucas *et. al.* (2006) used CASI data (14 spectral bands, 1 m spatial resolution) to accurately (70%) classify tree species composition in a natural forest in Australia. From a "remote sensing" point of view, northern hemisphere forests have the advantage of having a relatively simple species composition, which facilitates the discrimination and mapping of tree species (Lucas *et. al.* 2008). In the UK, a study by Hill *et al* (2010) reported a maximum overall accuracy of 82% when using time-series multispectral data (ATM, 11 spectral bands) to classify tree species at Monks Wood, an ancient semi-natural deciduous forest.

The above examples illustrate the potential of remote sensing to provide additional information to assist red squirrel habitat management. The combination of both forest structure and species composition derived from remote sensing data could substantially improve habitat assessment for red squirrel in the UK by providing accurate information on a range of habitat requirements that would be prohibitively expensive and time consuming to gather in the field. Furthermore, mapping species composition using remote sensing could also provide a tool to regularly update forest stock maps and forest inventories.

Habitat suitability and population viability analysis (PVA)

Habitat suitability maps were created for both study areas. Out of the total forest area, 27% at Abernethy Forest and 37% at Aberfoyle (considering only the un-calibrated number of trees) were classified as Medium-to-High suitability (Chapter 4). Assuming that only Medium-to-High suitability patches can support resident populations of squirrels in the long-term, this means that only approximately one third of the forests is actually suitable for the species. This is one of the key findings of this thesis and has implications for the conservation of the species, in particular in Abernethy Forest, which is one of the proposed red squirrel strongholds.

To i) illustrate one of the potential applications of LiDAR derived habitat suitability information and ii) assess the impact of forest structure on the long-term survival of the species, a PVA was carried out. Carrying capacity was calculated based on the LiDAR-derived habitat suitability data, and the viability and risk of extinction of the species populations at Abernethy Forest were estimated. In general, and for all modelled scenarios (Chapter 5), results of the PVA suggested a reduction in red squirrel population. It is not clear if this is indeed the case, or if the model predictions are influenced by input ranges in life history parameters which do not completely capture long term population dynamics at Abernethy Forest. However, these results support previous research by Summers (2011) who suggested a long-term decline in red squirrel population in the forest.

Being a mono-species forest, Abernethy is a good example of the constraints and challenges of single species management in confined locations. It would be interesting to model different scenarios, including diversification and changes in the proportions of different tree species to evaluate management options.

When LiDAR derived habitat quality data was used to estimate carrying capacity, results suggest a high risk of extinction (74%) for the species populations in 20 years and very low densities (approximately 10 individuals in each of the two populations modelled). While results from PVA need careful interpretation due to the high levels of uncertainty typically associated with these types of models, these results highlight the need for considering forest structure when managing forests for red squirrel conservation and the usefulness of LiDAR remote sensing to assist this management.

Further research could integrate LiDAR derived suitability maps into spatially-explicit PVA models (e.g. RAMAS/GIS) to model more complex spatial-scenarios such as the viability and potential dispersal of red squirrel meta-populations based on the size and habitat quality of different patches in a forest. Furthermore, if grey squirrel habitat preferences in terms of structure were known, potential risk-of-competition maps could be derived from LiDAR data and red squirrel population viability could be modelled by manipulating, for instance, *reproduction rates* (Gurnell *et. al.* 2004) to account for the competition with the greys. A similar approach could be used to assess the effects of predation on the viability of red squirrel populations by modelling, for example, different *mortality* scenarios.

6.3 Transferability, repeatability and further applications of methods

The data collection methodology used in this project can be only used in conifer forests as it relies on the presence of feeding remains (stripped conifer cones) to assess and quantify habitat use by red squirrel. The GLM was developed using data from two different study areas but focused on the same tree species (i.e. Scots pine).

Further research could aim to test the transferability of this methodology to more complex, heterogeneous conifer ecosystems.

The implementation of the GLM using LiDAR-derived explanatory variables proved transferable between the two study sites. The results were influenced by acquisition parameters such as LiDAR pulse density and potentially scan angle. Higher pulse densities are likely to improve the accuracy of LiDAR-derived variables and therefore, of the habitat quality data.

The methodology developed in this thesis can assist current management and future monitoring of strongholds to ensure that these reserves meet the species requirements.

The red squirrel is being replaced by the greys not only in the UK but also in other European countries such as Ireland, Italy and Switzerland (Lurz *et al*, 1995; Rushton *et al*, 2000; Gurnell *et. al.*, 2004; Teangana *et al.*, 2000). The methodology developed in this thesis can be applied to the same species in other countries.

The transferability of the LiDAR-based methodology to tree species other than Scots pine (and potentially sitka spruce) was not assessed in this thesis. If the approach is intended to be applied to other conifer species, mixed woodlands or deciduous forests, validation using field data would need to be performed in order to assess the extent to which LiDAR-metrics can be used as estimators of ground data.

6.4 Contribution of research

It had been previously suggested that red squirrels would avoid open stands (Gurnell *et al.*, 2002), however this had not been statistically analysed and quantified. This thesis has moved one step forward and has quantified the relationship between forest structure parameters such as canopy closure, tree density and tree height and red squirrel habitat use for Scots pine in the UK.

This thesis has also developed a methodology to assess habitat suitability for red squirrel over large areas by using LiDAR remote sensing. This methodology produces accurate results without demanding extensive field work, although –as in any remote sensing-based approach- field data needs to be collected to assess the accuracy of LiDAR derived data. This study also explores the potential of LiDAR derived number of trees as an input to assess red squirrels habitat quality.

When considered together, the quantification of the relationship between forest structure and habitat use by red squirrels, and the development of a methodology to implement the analysis over a large area, these findings allow for a more refined and integral assessment of habitat suitability at the sub-stand level considering not only food availability but also other factors such as the provision of shelter and reduced risk of predation. This study also represents the first to integrate remote sensing into habitat mapping for red squirrel in the UK.

Although PVA have been widely used to assess management strategies for endangered species conservation, few previous studies have incorporated information derived from remote sensing to assist species management. This thesis illustrates the potential of LiDAR derived data to assist PVA within a non-spatially explicit model as VORTEX by, for example, providing more accurate estimates of carrying capacity.

Finally, this study has contributed to address the challenge of multidisciplinary work involving the integration of ecology and remote sensing to map habitat and assist management for endangered species over large areas.

6.5 Overall conclusions

- Forest structure parameters, namely canopy closure, tree density and tree height, influence red squirrel habitat use at the sub-stand level for Scots pine. Further research is needed to test the robustness of the approach and its transferability to more complex mixed conifer forests

- Airborne LiDAR data can be used to assess habitat quality for red squirrel. Higher densities point data and smaller scan angles than those used in this study could potentially improve the effectiveness of the approach.

- Habitat quality for one of the 18 proposed strongholds (Abernethy Forest) was assessed and results showed that at present, less than one third of the forest is actually suitable for the species. Considering that these strongholds could potentially become the only hope for the species survival in the UK, this is one of the key findings of this thesis.

6.6 Key recommendations

From both previous research on red squirrel habitat preferences and the current study, managing forests for the species should considered the following:

1- Conifer forests > 2000 ha (Lurz *et al.*, 1995; Pepper & Patterson, 2001; Gurnell *et al.*, 2002; Bryce *et al.*, 2005)

2- Avoidance of large seeded broadleaves (i.e. oak, chestnut, beech and hazel; Lurz *et al.*, 1995; Bryce *et al.*, 2005;)

3- Mixture of conifer species and age structure to ensure food supply (Lurz *et al.*, 1995; Gurnell *et al.*, 2002; Bryce *et al.*, 2005)

1- Management for red squirrel also needs to contemplate the preference of the species for dense canopies (Flaherty *et al.*; 2012)

In terms of LiDAR data, key recommendations are:

1- LiDAR data point densities ≥ 2 pulses/m^2

2- LiDAR scan angles ≤ 15°

3- Collaborative data-sharing partnerships to reduce costs of data acquisition and processing

EPILOGUE

To a Squirrel at Kyle-na-gno

COME play with me;
Why should you run
Through the shaking tree
As though I'd a gun
To strike you dead?
When all I would do
Is to scratch your head
And let you go.

W.B. Yeats; *The Wild Swans at Coole*, 1919

REFERENCES

Abileah, R. 2001. Use of high resolution space imagery to monitor the abundance, distribution, and migration patterns of marine mammal populations. *OCEANS* 3: 1381-1387.

Agresti, A. 2002. *Categorical data analysis*, New York, Wiley-Interscience.

Ahokas, E., Yu, X., Oksanen, J., Hyyppä, J., Kaartinen, H. and Hyyppä, H. 2005. Optimization of the scanning angle for countrywide laser scanning. In Proceeedings of the International Archives of Photogrammetry, *Remote Sensing and Spatial Information Sciences*, G. Vosselman and C. Brenner (Eds). XXXVI, Part 3/W19, 115-119.

Andrén H. and Lemnell P. 1992, Population Fluctuations and Habitat Selection in the Eurasian Red Squirrel Sciurus vulgaris. *Ecography* 15: 303-307.

Arlot, S. and Celisse, A. 2010. A survey of cross-validation procedures for model selection. *Statistics Surveys* 4: 40-79.

Atkin, J.W., Radford, A.D., Coyne, K.P., Stavisky, J. and Chantrey, J. 2010. Detection of squirrel poxvirus by nested and real-time PCR from red (*Sciurus vulgaris*) and grey (*Sciurus carolinensis*) squirrels *BMC Veterinary Research* 6.

Baltsavias, E.P. 1999. Airborne laser scanning: basic relations and formulas. *Isprs Journal of Photogrammetry and Remote Sensing 54*: 199-214.

Begon, M., Harper, J. and Townsend, C. 1996, *Ecology: Individuals, populations and communities*, Blackwell Science, Oxford.

Bobyr, G.Y. 1978. A contribution to the ecology of the Altaian squirrel (Sciurus vulgaris altaicus) acclimatized. *Zoologichesky Zhurnal* 57: 253-259.

Bosch, S. & Lurz, P.W.W. 2012. *The Eurasian Red Squirrel Sciurus vulgaris* (First edition) Westarp Wissenschaften, Hohenwarsleben, Germany

Boyce, M. 1992. Population viability analysis. *Annual Review of Ecology and Systematics* 23: 481-506.

Bradbury, R., Hill, R., Mason, D.C., Hinsley, S.A., Wilson, J.D., Baltzer, H., Anderson, G.Q.A., Whittingham, M.J., Davenport, I.J. and Bellamy, P.E. 2005. Modelling relationships between birds and vegetation structure using airborne LiDAR data: a review with case studies from agricultural and woodland environments. *British Ornithologists' Union, Ibis* 147: 443-452.

Brito, D. and Grelle, C.E.V. 2006. Estimating minimum area of suitable habitat and viable population size for the northern muriqui (Brachyteles hypoxanthus), *Biodiversity and Conservation* 15: 4197-4210.

Broome, A., Hendry, S. and Peace, A. 2007. Annual and spatial variation in coning shown by the Forest Condition Monitoring programme data for Norway spruce, sitka spruce and Scots pine in Britain, *Forestry* 80: 17-28.

Brook, B.W., Lim, L., Harden, R., & Frankham, R. 1997. Does population viability analysis software predict the behaviour of real populations? A retrospective study on the Lord Howe Island woodhen Tricholimnas sylvestris (Sclater). *Biological Conservation,* 82: 119-128

Brook, B.W., Cannon, J.R., Lacy, R., Mirande, C. and Frankham, R. 1999. Comparison of the population viability analysis packages GAPPS, INMAT, RAMAS and VORTEX for the whooping crane (Grus americana), *Animal Conservation* 2: 23-31

Brook, B.W., O'Grady, J.J., Chapman, A.P., Burgman, M.A., Akcakaya, H.R., & Frankham, R. 2000. Predictive accuracy of population viability analysis in conservation biology. *Nature*, 404: 385-387

Brovelli, M.A., Cannata, M. and Longoni, U.M. 2002. Managing and processing LIDAR data within GRASS. Proceedings of the *Open source GIS - GRASS users conference 2002*, 1-29.

Burgman, M. and Possingham, H.P. 2000**.** Population viability analysis for conservation: the good, the bad and the undescribed**.** Pages 97-112 in: *Genetics, Demography and Viability of Fragmented Populations*. Eds Young, A.G & Clarke, G.M. Cambridge University Press, London

Burgman, M., Franklin, J., Hayes, K.R., Hosack, G.R., Peters, G.W., & Sisson, S.A. 2012. Modeling Extreme Risks in Ecology. *Risk Analysis* 32: 1956-1966

Bruemmer, C.M., Rushton, S.P., Gurnell, J., Lurz, P.W.W., Nettleton, P., Sainsbury, A.W., Duff, J.P., Gilray, J. and McInnes, C.J. 2010. Epidemiology of squirrelpox virus in grey squirrels in the UK. *Epidemiology and Infection* 138: 941-950.

Bryce, J., Cartmel, S. and Quine, C.P. 2005. Habitat use by red and grey squirrels: results of two recent studies and implications for management, Forestry Commission Information Note No. 76.

Carrascal, L.M. and Telleria, J.L. 1988. Relationships among birds and vegetation structure in the agricultural landscape of the atlantic basque country. *Ciencias Naturales* 40: 9-17.

Clawges, R., Vierling, K., Vierling, L. and Rowell, E. 2008. The use of airborne LiDAR to assess avian species diversity, density, and occurrence in a pine/aspen forest. *Remote Sensing of Environment* 112: 2064-2073.

Cook, J.G., Stutzman, T.W., Bowers, C.W., Brenner, K.A. and Irwin, L.L. 1995. Spherical densiometers produce biased estimates of forest canopy cover. Wildlife Society Bulletin 23: 711-717.

Crawley, M. 2007. *The R Book.* Chichester, England. John Wiley & Sons Ltd.

De Lamo, X. 2010. *Mapping red squirrel (Sciurus vulgaris) habitat suitability using GIS and remote sensing techniques* Edinburgh, UK University of Edinburgh, MSc.

Doak, D.F., Finkelstein, M.E. and Bakker, V.J. 2009. Population Viability Analysis, in Levin, S.A. (Eds) *The Princeton Guide to Ecology*, Princeton University Press, Princeton, 521-528.

Doo-Ahn Kwak, Woo-Kyun Lee, Jun-Hak Lee, Greg S. Biging, Peng Gong. 2007. Detection of individual trees and estimation of tree height using LiDAR data. *Journal of Forest Research* 12: 425-434

Doumas, S. & Koprowski1, J.L.; 2012, Return of Fire as a Restoration Tool: Long-Term Effects of Burn Severity on Habitat Use by Mexican Fox Squirrels, *Restoration Ecology,* DOI: 10.1111/j.1526-100X.2012.00864.x

Duca, C., Yokomizo, H., Marini, M.A., & Possingham, H.P. 2009. Cost-efficient conservation for the white-banded tanager (Neothraupis fasciata) in the Cerrado, central Brazil. *Biological Conservation*, 142: 563-574

Edelman, J., Koprowski, J.L. and Bertelsen, S.R. 2009. Potential for nest site competition between native and exotic tree squirrels. *Journal of Mammalogy* 90: 167-174.

Ene, L., Naesset, E. and Gobakken, T. 2012. Single tree detection in heterogeneous boreal forests using airborne laser scanning and area-based stem number estimates. *International Journal of Remote Sensing* 33: 5171-5193.

Evans, J.S., Hudak, A.T., Faux, R. and Smith, A.M.S. 2009. Discrete Return Lidar in Natural Resources: Recommendations for Project Planning, Data Processing, and Deliverables, *Remote Sensing* 1: 776-794.

Faraway, J.J. 2005. *Linear models with R*. Boca Raton, Florida, Chapman & Hall/CRC.

Faraway, J.J. 2006. *Extending the linear model with R*. Boca Raton, Florida, Chapman & Hall/CRC.

Fiegna, C. 2011. A *study of squirrelpox virus in red and grey squirrels and an investigation of possible routes of transmission*, Edinburgh, UK, University of Edinburgh, PhD.

Flaherty, S., Patenaude, G., Close A. and Lurz, P. 2012. The impact of forest-stand structure on red squirrel habitat use, *Forestry: An International Journal of Forest Research*, doi:10.1093/forestry/cps042.

Forestry Commission UK. 2006. The Scottish forestry strategy. http://www.forestry.gov.uk/sfs accessed 2012

Forestry Commission UK. 2009. Red squirrel strongholds consultation, http://www.forestry.gov.uk/ accessed 2012

Forestry Commission UK, 2012, http://www.forestry.gov.uk/inventory, accessed 2012

Garcia, C. 2006. *Locating potential red squirrel (Sciurus vulgaris) habitat in Kielder Forest, Northumberland with Quickbird imagery and object-oriented classification* Edinburgh, UK University of Edinburgh, MSc.

García, R., Suárez, J.C. and Patenaude, G. 2007. *Delineation of individual tree crowns for LiDAR tree and stand parameter estimation in Scottish woodlands.* Lecture Notes in Geoinformation and Cartography Part 2, 55-85.

Gaulton, R. 2008. *Remote sensing for continuous cover forestry: quantifying spatial structure and canopy gap distribution*. School of Geosciences. Edinburgh, Edinburgh, PhD

Gaulton, R., & Malthus, T.J. 2010. LiDAR mapping of canopy gaps in continuous cover forests: A comparison of canopy height model and point cloud based techniques. *International Journal of Remote Sensing* 31: 1193-1211

Gerber, L. & González-Suárez, M. 2010. Population Viability Analysis: Origins and Contributions. *Nature Education Knowledge,* 1(11):15

Goetz S.J., Steinberg D., Betts M.G., Holmes R.T., Doran P.J., Dubayah R. and Hofton M. 2010. Lidar remote sensing variables predict breeding habitat of a Neotropical migrant bird. *Ecology* 91: 1569-1576.

Graf, R.F., Mathys, L. and Bollmann, K. 2009. Habitat assessment for forest dwelling species using LiDAR remote sensing: Capercaillie in the Alps. *Forest Ecology and Management* 257: 160-167.

Grönwall, O. 1982. *Aspects of the food for red squirrels* (*Sciurus vulgaris* L.). Stockholm, Sweden.University of Stockholm. PhD: pp.131.

Gougeon, F.A., 1995. A crown-following approach to the automatic delineation of individual tree crown in high spatial resolution aerial images, *Canadian Journal of Remote Sensing*, 21(3):274–284.

Gougeon, F.A. and Leckie, D.G. 2006. The Individual Tree Crown Approach Applied to Ikonos Images of a Coniferous Plantation Area. *Photogrammetric Engineering & Remote Sensing* 72: 1287–1297.

Gurnell, J. 1983. Squirrel numbers and the abundance of tree seeds. *Mammal Review* 13: 133-148.

Gurnell, J. 1987. *The natural history of squirrels*. Christopher Helm, London.

Gurnell, J. and Pepper, H.W. 1991. *Conserving the Red Squirrel*. Forestry Commission Research Information Note 205, HMSO, London.

Gurnell, J. and Pepper, H.W. 1993. A critical look at conserving the British Red Squirrel Sciurus vulgaris. *Mammal Review* 23: 127-137.

Gurnell, J., Clark, M.J., Lurz, P.W.W., Shirley, M.D.F. and Rushton, S.P. 2002. Conserving red squirrels (Sciurus vulgaris): mapping and forecasting habitat suitability using a Geographic Information System Approach. *Biological Conservation* 105: 53-64.

Gurnell, J., Wauters, L.A., Lurz, P.W.W. and Tosi, G. 2004, Alien species and interspecific competition: effects of introduced eastern grey squirrels on red squirrel population dynamics. *Journal of Animal Ecology* 73: 26-35.

Gurnell, J., Lurz, P.W.W., McDonald, R. and Pepper, H. 2009. Practical techniques for surveying and monitoring squirrels. Forestry Commission Practice Note 11, pp. 1-12, FC Alice Holt Lodge, Farnham, Surrey, UK.

Guo, J., Chen, Y. and Hu, J. 2002. Population viability analysis of giant pandas in the Yele Nature Reserve. *Nature Conservation*, 10: 35-40.

Haines, A.M., Tewes, M.E., Laack, L.L., Horne, J.S. and Young, J.H. 2006. A habitat-based population viability analysis for ocelots (Leopardus pardalis) in the United States. *Biological Conservation* 132: 424-436.

Halliwell, E.C. 1997. Red squirrel predation by Pine martens in Scotland. The Conservation of Red Squirrels, Sciurus vulgaris L. (Eds J. Gurnell and P.W.W. Lurz), pp.39-48 *Peoples Trust for Endangered Species*, London.

Hamby, D.M. 1995. A comparison of sensitivity analysis techniques, *Health physics* 68: 195-204.

Heblinski, J., Schmieder, K., Heege, T., Agyemang, T.K., Sayadyan, H. and Vardanyan, L. 2011. High-resolution satellite remote sensing of littoral vegetation of Lake Sevan (Armenia) as a basis for monitoring and assessment. *Hydrobiologia* 661: 97-111.

Hill, R.A., Hinsley, S.A., Gaveau, D.L.A. and Bellamy, P.E. 2004. Predicting habitat quality for Great Tits (*Parus major*) with airborne laser scanning data. *International Journal of Remote Sensing* 25: 4851-4855.

Hill, R.A., Wilson, A.K., George, M., and Hinsley, S.A. 2010. Mapping tree species in temperate deciduous woodland using time-series multi-spectral data. *Applied Vegetation Science* 13: 86-99

Holmgren, J. 2004. Prediction of tree height, basal area and stem volume in forest stands using airborne laser scanning. *Scandinavian Journal of Forest Research 19*: 543-553.

Hopkinson, C., Chasmer, L. and Hall, R.J. 2008. The uncertainty in conifer plantation growth prediction from multi-temporal lidar datasets. *Remote Sensing of Environment 112*: 1168-1180.

Hyde, P., Dubayah, R., Peterson, B., Blair, J.B., Hofton, M., Hunsaker, C., Knox, R. and Walker, W. 2005. Mapping forest structure for wildlife habitat analysis using waveform lidar: Validation of montane ecosystems. *Remote Sensing of Environment* 96: 427-437.

Hyyppa, J., Kelle, O., Lehikoinen, M. and Inkinen, M. 2001. A segmentation-based method to retrieve stem volume estimates from 3-D tree height models produced by laser scanners. *IEEE Trans. Geosci. Remote Sensing* 39: 969-975.

Hyyppa, J., Hyyppa, H., Leckie, D., Gougeon, F., Yu, X. and Maltamo, M. 2008. Review of methods of small-footprint airborne laser scanning for extracting forest inventory data in boreal forests. *International Journal of Remote Sensing* 29: 1339-1366.

Jain, A.K., Murty, M.N. and Flynn, P.J. 1999. Data Clustering: A Review. *ACM Computing Surveys* 31: 264-323.

Jennings, S.B., Brown, N.D. and Sheil, D. 1999. Assessing forest canopies and understorey illumination: canopy closure, canopy cover and other measures. *Forestry* 72: 59-73.

Jian, J., Jiang, H., Zhou, G.M., Jiang, Z.S., Yu, S.Q., Peng, S.L., Liu, S.Y. and Wang, J.X. 2011. Mapping the vegetation changes in giant panda habitat using Landsat remotely sensed data. *International Journal of Remote Sensing* 32: 1339-1356.

Ke, Y.H., Quackenbush, L.J. and Im, J. 2010. Synergistic use of QuickBird multispectral imagery and LIDAR data for object-based forest species classification. *Remote Sensing of Environment* 114: 1141-1154.

Kenward, R.E. and Hodder, K.H. 1998. Red squirrels (Sciurus vulgaris) released in conifer woodland: the effects of source habitat, predation and interactions with grey squirrels (Sciurus carolinensis). *Journal of Zoology* 244: 23-32.

Koprowski, J. 1991. Response of fox squirrels and grey squirrels to a late spring-early summer food shortage. *Journal of Mammalogy* 72: 367-372.

Korhonen, L., Korpela, I., Heiskanen, J. and Maltamo, M. 2011. Airborne discrete-return LIDAR data in the estimation of vertical canopy cover, angular canopy closure and leaf area index. *Remote Sensing of Environment* 115: 1065-1080.

Koukoulas, S. and Blackburn, G.A. 2005. Mapping individual tree location, height and species in broadleaved deciduous forest using airborne LIDAR and multi-spectral remotely sensed data. *International Journal of Remote Sensing* 26: 431-455.

Kraus, K. and Pfeifer, N. 1998. Determination of terrain models in wooded areas with airborne laser scanner data. *Isprs Journal of Photogrammetry and Remote Sensing* 53: 193-203.

Lacy, R.C. 1993a. VORTEX: A computer simulation model for Population Viability Analysis, *Wildlife Research* 20: 45-65

Lampio, T. (1965): Sex ratios and the factors contributing to them in the squirrel, *Sciurus vulgaris*, in Finland I. – *Finnish Game Research* 25: 5–90

Lee, H., Slatton, K.C., Roth, B.E. and Cropper, W.P. 2010. Adaptive clustering of airborne LiDAR data to segment individual tree crowns in managed pine forests. *International Journal of Remote Sensing* 31: 117-139.

Lefsky, M.A., Cohen, W.B., Parker, G.G. and Harding, D.J. 2002. LiDAR Remote Sensing for Ecosystem Studies. *Bioscience* 52: 19-30.

Lefsky, M.A. 2010. A global forest canopy height map from the Moderate Resolution Imaging Spectroradiometer and the Geoscience Laser Altimeter System. *Geophysical Research Letters* 37: 5.

Lesak, A.A., Radeloff, V.C., Hawbaker, T.J., Pidgeon, A.M., Gobakken T. and Contrucci, K. 2011. Modeling forest songbird species richness using LiDAR-derived measures of forest structure. *Remote Sensing of Environment* 115: 2823-2835.

Lillesand, T.M., Kiefer, R.W. and Chipman, J. 2004. *Remote sensing and image interpretation*. Fifth Edition. John Wiley and Sons, Inc., New Jersey.

Lim, K., Treitz, P., Wulder, M., St-Onge, B. and Flood, M. 2003. LiDAR remote sensing of forest structure. *Progress in Physical Geography* 27: 88-106

Lindenmayer, D.B., Clark, T.W., Lacy, R.C., & Thomas, V.C. 1993. Population Viability Analysis as a tool in wildlife conservation policy – with reference to Australia. *Environmental Management, 17*, 745-758

Lucas, R.; Bunting, P., Paterson M., Chisholm, L. 2007.Classification of Australian forest communities using aerial photography, CASI and HyMap data, *Remote Sensing of Environment*, 112: 2088-2103.

Lurz, P.W.W., Garson, P.J. and Rushton S.P.1995. The ecology of red squirrels in spruce dominated plantations: implications for forest management, *Forest ecology and management* 79: 79-90.

Lurz, P.W.W., Garson P.J. and Ogilvie J.F. 1998. Conifer species mixtures, cone crops and red squirrel conservation. *Forestry* 71: 67-71.

Lurz, P.W.W., Garson, P.J. and Wauters, L.A. 2000. Effects of temporal and spatial variations in food supply on the space and habitat use of red squirrels (*Sciurus vulgaris L.*). *Journal of Zoology* 251: 167-178

Lurz, P.W.W., Rushton, S.P., Wauters, L.A., Bertolino, S., Currado, I., Mazzoglio, P., & Shirley, M.D.F. 2001. Predicting grey squirrel expansion in North Italy: a spatially explicit modelling approach. *Landscape Ecology,* 16: 407-420

Lurz, P.W.W. & Lloyd, A., 2001, *Kidland Forest: Squirrel Monitoring Report*, Report to Forestry Commission

Lurz, P.W.W., 2002 to 2011, *Kidland Forest: Squirrel Monitoring Report*, Report to Forestry Commission

Lurz, P.W.W., Geddes, N., Lloyd, A.J., Shirley, M.D.F., Rushton, S.P. and Burlton, B. 2003. Planning a red squirrel conservation area: using a spatially explicit population dynamics model to predict the impact of felling and forest design plans. *Forestry* 76: 95-108.

Lurz, P.W.W., Gurnell, J., & Magris, L. 2005. Sciurus vulgaris. *Mammalian Species*, 1-10

Lurz, P., Shirley M. and Geddes, N. 2008a. Monitoring low density populations: a perspective on what level of population decline we can truly detect, *Animal biodiversity and conservation* 31: 29-39

Lurz, P.W.W., Koprowski, J.L., & Wood, D.J.A. 2008b. The use of GIS and modelling approaches in squirrel population management and conservation: a review. *Current Science* 95: 918-922

Lurz, P.W.W. and Cole, M. 2010. *Red squirrels.* Naturally Scottish, Scottish Natural Heritage, Scotland.

Mackinlay, L. and Patterson, A. 2011. *NTS Red Squirrel Conservation Action Plan 2011-2016*. National Trust for Scotland.

Maltamo, M., Mustonen, K., Hyyppa, J., Pitkanen, J. and Yu, X., 2004. The accuracy of estimating individual tree variables with airborne laser scanning in a boreal nature reserve. *Canadian Journal of Forest Research-Revue* 34: 1791-1801.

Manton, G. M., Angelstam, P. and Mikusinski,G. 2005. Modelling habitat suitability for deciduous forest focal species – a sensitive analysis using different satellite land cover data. *Landscape Ecology* 20: 827-839.

Martin, M.E., Newman, S.D., Aber, J.D., Congalton, R.G.; 1998, Determining Forest Species Composition Using High Spectral Resolution Remote Sensing Data, *Remote Sensing of the Environment*, 65: 249-254.

Martinuzzi, S., Vierling, L.A., Gould, W.A., Falkowski, M.J., Evans, J.S., Hudak, A.T. and Vierling, K.T. 2009. Mapping snags and understory shrubs for a LiDAR-based assessment of wildlife habitat suitability. *Remote Sensing of Environment* 113: 2533-2546.

Mather, P. 2004. *Computer Processing of Remotely-Sensed Images: an introduction,* Third edition. John Wiley and Sons, Inc., Chichester

Mather, P.M. 2004. *Computer processing of remotely sensed images: an introduction.* John Wiley and Sons, Chichester, West Sussex, England.

Mäkelä, A. and Vanninen, O. 2001. Vertical structure of Scots pine crowns in different age and size classes. *Trees* 15: 385–392.

Meng, X., Currit, N. and Zhao, K. 2010. Ground Filtering Algorithms for Airborne LiDAR Data: A Review of Critical Issues. *Remote Sensing* 2: 833-860.

McClain B.J. and Porter W.F. 2000. Using satellite imagery to assess large-scale habitat characteristics of Adirondack Park. *Environmental management* 26: 553-561.

McDermid, M.J., Franklin, S.E. and LeDrew, E.F. 2005. Remote sensing for large-area habitat mapping. *Progress in Physical Geography* 29: 449-474.

McGaughey, R.J., Carson, W.W., Reutebuch, S.E. and H-E. Andersen. 2004. *Direct measurement of individual tree characteristics from LIDAR data*. Proceedings of the Annual ASPRS Conference, Denver, May 23-28, 2004. American Society of Photogrammetry and Remote Sensing, Bethesda, MD.

McGaughey, R.J. 2009. *FUSION/LDV: Software for LIDAR Data Analysis and Visualization*. U.S. Department of Agriculture.

McInerney, D.O., Suarez-Minguez, J., Valbuena, R., & Nieuwenhuis, M. (2010). Forest canopy height retrieval using LiDAR data, medium-resolution satellite imagery and kNN estimation in Aberfoyle, Scotland. *Forestry, 83*, 195-206

McInnes, C.J., Coulter, L., Dagleish, M.P., Fiegna, C., Gilray, J., Willoughby, K., Cole, M., Milne, E., Meredith, A., Everest, D.J., MacMaster, A-M. 2009. First cases of squirrelpox in red squirrels (Sciurus vulgaris) in Scotland. *The veterinary record*, 164: 528-531.

McKinney, S.T. and Fiedler, C.E. 2010. Tree squirrel habitat selection and predispersal seed predation in a declining subalpine conifer. *Oecologia* 162: 697-707.

Metropolis, N. 1987. The Beginning of the Monte Carlo Method. *Los Alamos Science,* No. 15, p. 125.

Metropolis, N. and Ulam, S. 1949. The Monte Carlo method. *Journal of the American Statistical Association.* 44: 335-341.

Middleton, A.D. 1930. The ecology of the American grey squirrel (*Sciurus carolinensis* Gmelin) in the British Isles. Proceedings of the Zoological Society of London 2: 809-843.

Milazzo, A., Falleta, W. and Sara, M. 2003. Habitat selection of Fat dormouse (*Glis glis italicus*) in deciduous woodlands of Sicily. *Acta Zoologica Academiae Scientiarum Hungaricae* 49: 117-124.

Mills, L.S., Hayes, S.G., Baldwin, C., Wisdom, M.J., Citta, J., Mattson, D.J. and Murphy, K. 1996. Factors leading to different viability predictions for a grizzly bear data set. *Conservation Biology* 10: 863-873.

Miller, P.S., and R.C. Lacy. 2005. VORTEX: A Stochastic Simulation of the Extinction Process. Version 9.50 User's Manual. Apple Valley, *MN: Conservation Breeding Specialist Group (SSC/IUCN).*

Morsdorf, F., Frey, O., Meier, E., Itten, K.I. and Allgower, B. 2008. Assessment of the influence of flying altitude and scan angle on biophysical vegetation products derived from airborne laser scanning. *International Journal of Remote Sensing* 29: 1387-1406.

Moller, H. 1986. Red squirrels (Sciurus vulgaris) feeding in a Scots pine plantation in Scotland. *Journal of Zoology* 209: 61-84.

Møller, A.P. & Jennions M.D. 2002. How much variance can be explained by ecologists and evolutionary biologists? *Oecologia* 132: 492–500

Naesset, E.1997. Determination of mean tree height of forest stands using airborne laser scanner data, *ISPRS Journal of Photogrammetry & Remote Sensing,* 52: 49-56.

Naesset, E., Gobakken, T., Holmgren, J., Hyyppa, H., Hyyppa, J., Maltamo, M., Nilsson, M., Olsson, H., Persson, A., & Soderman, U. 2004. Laser scanning of forest resources: The Nordic experience. *Scandinavian Journal of Forest Research* 19: 482-499.

Nelson, R., Keller, C. and Ratnaswamy, M. 2005. Locating and estimating the extent of Delmarva fox squirrel habitat using an airborne LiDAR profiler. *Remote Sensing of Environment* 96: 292-301.

Nelson, R., Keller, C. and Ratnaswamy, M. 2005. Locating and estimating the extent of Delmarva fox squirrel habitat using an airborne LiDAR profiler. *Remote Sensing of Environment* 96: 292-301.

Ordnance Survey. 2001. Land-Form PROFILE User guide, V 4.0 (http://www.ordnancesurvey.co.uk/oswebsite/).

Paletto, A. and Tosi, V. 2009. Forest canopy cover and canopy closure: comparison of assessment techniques. *European Journal of Forest Research* 128: 265-272.

Palma, L., Beja, P. and Rodrigues, M. 1999. The use of sighting data to analyse Iberian lynx habitat and distribution. *Journal of Applied Ecology* 36: 812-824.

Parrott, D., Quy, R., Van Driel, K., Lurz, P., Rushton, S., Gurnell, J., Aebischer, N. and Reynolds, J. 2009. *Review of red squirrel conservation activity in northern England.* Natural England Contract No. 08/09/N/004. 2009. Report by Central Science Laboratory and Newcastle University.

Patenaude, G., Hill, R.A., Milne, R., Rowland, C.S., Dawson, T.P. 2004. Quantifying forest above ground carbon content using LiDAR remote sensing. *Remote Sensing of Environment* 93: 368-380.

Pearce, J. and Ferrier, S. 2001. The practical value of modelling relative abundance of species for regional conservation planning: a case study. *Biological Conservation* 98: 33-43.

Pepper, H. and Patterson, G. 2001. *Red squirrel conservation.* Forestry Commission Practice Note 5 Forestry Commission, Edinburgh.

Petty, S.J., Lurz, P.W.W. and Rushton, S. 2003. Predation of red squirrels by northern goshawks in a conifer forest in northern England: can this limit squirrel numbers and create a conservation dilemma? *Biological Conservation* 111: 105-114.

Popescu, S.C., Wynne, R.H. and Nelson, R.F. 2002. Estimating plot-level tree heights with lidar: local filtering with a canopy-height based variable window size. *Computers and Electronics in Agriculture* 37: 71-95.

Popescu, S.C., Wynne, R.H. and Nelson, R.F. 2003. Measuring individual tree crown diameter with lidar and assessing its influence on estimating forest volume and biomass. *Canadian journal of remote sensing* 29: 564-577.

Poulsom, L., Griffiths, M., Broome, A. and Mayle, B. 2005. *Identification of priority woodlands for red squirrels conservation in North and Central Scotland: a preliminary analysis.* Scottish Natural Heritage Commissioned Report No. 089 (ROAME No. F02AC334).

Rahman, M.Z.A. and Gorte, B.G.H. 2009. *Tree crown delineation from high resolution airborne LiDAR based on densities of high points* In, ISPRS Workshop Laserscanning ISPRS, France, pp. 123-128.

Rees, D.G. 1995. *Essential Statistics*. London, Chapman & Hall.

Reutebuch, S.E., McGaughey, R.J., Andersen, H.E. and Carson, W.W. 2003. Accuracy of a high-resolution lidar terrain model under a conifer forest canopy. *Canadian journal of remote sensing* 29: 527-535.

Reynolds J. and Bentley, S. 2001. Selecting refuge sites for red squirrels conservation, unpublished paper to the England Forum.

Richardson, J.J., Moskal, L.M. and Kim, S.H. 2009. Modeling approaches to estimate effective leaf area index from aerial discrete-return LIDAR. *Agric. For. Meteorol.* 149: 1152-1160.

Rosette, J.A., North, P.R.J., Suarez, J.C. and Armston, J.D. 2009. A comparison of biophysical parameter retrieval for forestry using airborne and satellite LiDAR. *International Journal of Remote Sensing* 30: 5229-5237.

Rushton, S.P., Lurz, P.W.W., Gurnell, J. and Fuller, R. 2000. Modelling the spatial dynamics of parapox virus disease in red and grey squirrels: a possible cause of the decline in the red squirrel in the UK?, *Journal of Applied Ecology* 37: 997-1012.

Rushton, S.P., Lurz, P.W.W., Gurnell, J., Nettleton, P., Bruemmer, C., Shirley, M.D.F. and Sainsbury, A.W. 2006a. Disease threats posed by alien species: the role of a poxvirus in the decline of the native red squirrel in Britain. *Epidemiology and Infection* 134: 521-533

Rushton, S.P., Wood, D.J.A., Lurz, P.W.W., & Koprowski, J.L. 2006b. Modelling the population dynamics of the Mt. Graham red squirrel: Can we predict its future in a changing environment with multiple threats? *Biological Conservation* 131: 121-131

Shaffer, M. 1981. Minimum Population Sizes. *BioScience* 31: No. 2.

Shorten, M. 1953. Notes on the Distribution of the Grey Squirrel (*Sciurus-Carolinensis*) and the Red Squirrel (*Sciurus-Vulgaris-Leucourus)* in England and Wales from 1945 to 1952. *Journal of Animal Ecology* 22: 134-140.

Singh, J.S., Roy, P.S., Murthy, M.S.R. and Jha, C.S. 2010. Application of Landscape Ecology and Remote Sensing for Assessment, Monitoring and Conservation of Biodiversity. *Journal Indian Society Remote Sensing* (Special issue on Biodiversity and Landscape Ecology) 38: 365-385.

Smith, A.A. and Mannan, R.W. 1994. Distinguishing characteristics of Mount Graham red squirrel midden sites. *Journal of Wildlife Management* 58: 437-445.

Smith, J. and Smith, P. 2007. *Environmental Modelling: An Introduction*, Oxford University Press, Oxford.

Stephens, P.R., Kimberley, M.O., Beets, P.N., Paul, T.S.H., Searles, N., Bell, A., Brack, C. and Broadley, J. 2012. Airborne scanning LiDAR in a double sampling forest carbon inventory. *Remote Sensing of Environment* 117: 348-357.

Suarez, J.C., Ontiveros, C., Smith, S. and Snape, S. 2005. Use of airborne LiDAR and aerial photography in the estimation of individual tree heights in forestry. *Computers & Geosciences* 31: 253-262.

Sulaiman, N.S., Majid, Z. and Setan, H. 2010. DTM generation from LiDAR data by using different filters in open- source software. *Geoinformation Science Journal* 10: 89-109.

Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F. and Ransome, D.B. 2009. Stand structure and the abundance and diversity of plants and small mammals in natural and intensively managed forests. *Forest Ecology and Management* 258: 127-141.

Summers, R.W. & Proctor, R. 1999. Tree and cone selection by crossbills *Loxia sp*. and red squirrels *Sciurus vulgaris* at Abernethy forest, Strathspey. *Forest Ecology and Management* 118: 173-182.

Summers, R.W. and Proctor, R. 2005. Timing of shedding seeds and cones, and production in different stands of Scots pines at Abernethy Forest, Scotland, *Forestry* 78: 541-549.

Summers, R.W. 2011. Patterns of exploitation of annually varying *Pinus sylvestris* cone crops by seed-eaters of differing dispersal ability. Ecography 34: 723-728.

Teangana, D.O., Reilly, S., Montgomery, W.I., and Rochford, J. (2000). Distribution and status of the Red Squirrel (Sciurus vulgaris) and Grey Squirrel (Sciurus carolinensis) in *Ireland. Mammal Review*, 30, 45-55

Tittensor, A.M. 1970. *The red squirrel (Sciurus vulgaris) in relation to its food resource*. PhD. Thesis University of Edinburgh, UK.

Tompkins, D.M., White, A.R. and Boots M. 2003. Ecological replacement of native red squirrels by invasive greys driven by disease. *Ecology Letters*l 6: 189-196.

Turner, W., Spector, S., Gardiner, N., Fladeland, M., Sterling, E. and Steininger, M. 2003. Remote sensing for biodiversity, science and conservation, *TRENDS in Ecology and Evolution* 18: 306-314.

Vauhkonen, J., Ene, L., Gupta, S., Heinzel, J., Holmgren, J., Pitkanen, J., Solberg, S., Wang, Y.S., Weinacker, H., Hauglin, K.M., Lien, V., Packalen, P., Gobakken, T., Koch, B., Naesset, E., Tokola, T., & Maltamo, M. 2012. Comparative testing of single-tree detection algorithms under different types of forest. *Forestry* 85: 27-40

Vierling, K.T., Vierling, L.A., Gould, W.A., Martinuzzi, S. and Clawges, R.M. 2008. Lidar: shedding new light on habitat characterization and modeling. *Frontiers in Ecology and the Environmet* 6: 90-98.

Wang, K., Franklin, S.E., Guo, X., He, Y. and McDermid, G.J. 2009. Problems in remote sensing of landscapes and habitats. *Progress in Physical Geography* 33: 747-768.

Watts, K., Humphrey, J.W., Griffiths, M., Quine, C. and Ray, D. 2005. Evaluating Biodiversity in Fragmented Landscapes: Principles, Forestry Commission Information Note No. 73.

Watts, K., Ray, D., Quine, C.P., Humphrey, J.W. and Griffiths, M. 2007. Evaluating Biodiversity in Fragmented Landscapes: applications of landscape ecology tools (PDF-1440K). Forestry Commission Information Note 85.

Wauters, L.A., Hutchinson, Y., Parkin, D.T. and Dhondt, A.A. 1994. The effects of habitat fragmentation on demography and on the loss of genetic variation in the red squirrel. – *Proceedings of the Royal Society London*, 255: 107–111

Wauters, L. A. 1997. The ecology of red squirrels in fragmented habitats: a review. The conservation of red squirrels Sciurus vulgaris L. (Eds. J, Gurnell and P. Lurz) pp.5-12 *People's Trust for Endangered Species*, London.

Wauters, LA., Gurnell, J., Martinoli, A. and Tosi, G. 2001. Does interspecific competition with introduced grey squirrels affect foraging and food choice of Eurasian red squirrels? *Animal Behaviour* 61: 1079-1091.

Wauters, L.A., Gurnell, J., Martinoli, A. and Tosi, G. 2002. Do introduced grey squirrels (Sciurus carolinensis) deplete tree seeds hoarded by red squirrels (S. vulgaris)? *Behavioural Ecology and Sociobiology* 51: 360-367.

Wauters, L.A., Matthysen, E., Adriaensen, F. and Tosi, G. 2004, Within-sex density dependent and population dynamics of red squirrels Sciurus vulgaris. *Journal of animal ecology* 73: 11-25.

Wauters, L.A., Verbeylen, G., Preatoni, D., Martinoli, A., & Matthysen, E. 2010. Dispersal and habitat cuing of Eurasian red squirrels in fragmented habitats. *Population Ecology,* 52: 527-536

Weiers, S., Bock, M., Wissen, M. and Rossner G. 2004. Mapping and indicator approaches for the assessment of habitats at different scales using remote sensing and GIS methods, *Landscape and Urban Planning* 67: 43-65.

Wood, D.J.A., Koprowski, J.L. and Lurz, P.W.W. 2007. Tree squirrel introduction: a theoretical approach with population viability analysis. *Journal of Mammalogy* 88: 1271-1279.

Zeide, B. 1995. A relationship between size of trees and their number. *Forest Ecology and Management* 72: 265-272.

Zuur, A.F., Ieno, E.N. and Smith, G.M. 2007. *Analysing Ecological Data*. New York, London, Springer**.**

Zuur, A.F.; Flaherty, S.; Lurz, P.; Patenaude, G., Ieno, E.N.; Hilbe, J. Generalized linear modelling with MCMC in JAGS applied on red squirrel data; In *A Beginner's guide to GLM using R and JAGS* , Zuur, A.F.; Ieno, E.N.; Hilbe, J., in preparation

APPENDIX A – Red squirrel sightings

During the field trip and to confirm the presence of red squirrels in both forests, visual-transects were walked at dawn time. Five visual-transects at Abernethy and three at Aberfoyle were walked in total. Red squirrels were also seen at other times and while field work was being carried out. All sightings were recorded using a GPS (Garmin GPS map 60CSx) or OS maps. To increase effectiveness, baited visual-transects were used at Aberfoyle (Gurnell *et al*, 2011). Figures A.1 and A.2 show the location of visual transects and red squirrels sightings, as well as plot locations for Abernethy and Aberfoyle Forests respectively. Tables A.1 and A.2 provide date, location and number of squirrels seen at each point.

Figures A.3 to A.6 show examples of cones and food remains (i.e. stripped cones, scales) found during the field work.

Table A.1: Squirrels sightings- date seen, coordinates in British National Grid and number of squirrels seen- Abernethy Forest, Scotland

Date	Easting	Northing	Number of Squirrels
14/10/2009	297817	817256	1
15/10/2009	299460	816648	1
16/10/2009	297781	818325	1
16/10/2009	299147	816693	1
10/10/2009	296880	819051	1
15/10/2009	296516	819372	2

Table A.2: Squirrels sightings- coordinates in British National Grid and number of squirrels seen- Aberfoyle Forest, Scotland

Date	Easting	Northing	Number of Squirrels
May 2010	249931	701079	2
May 2010	252481	701992	1

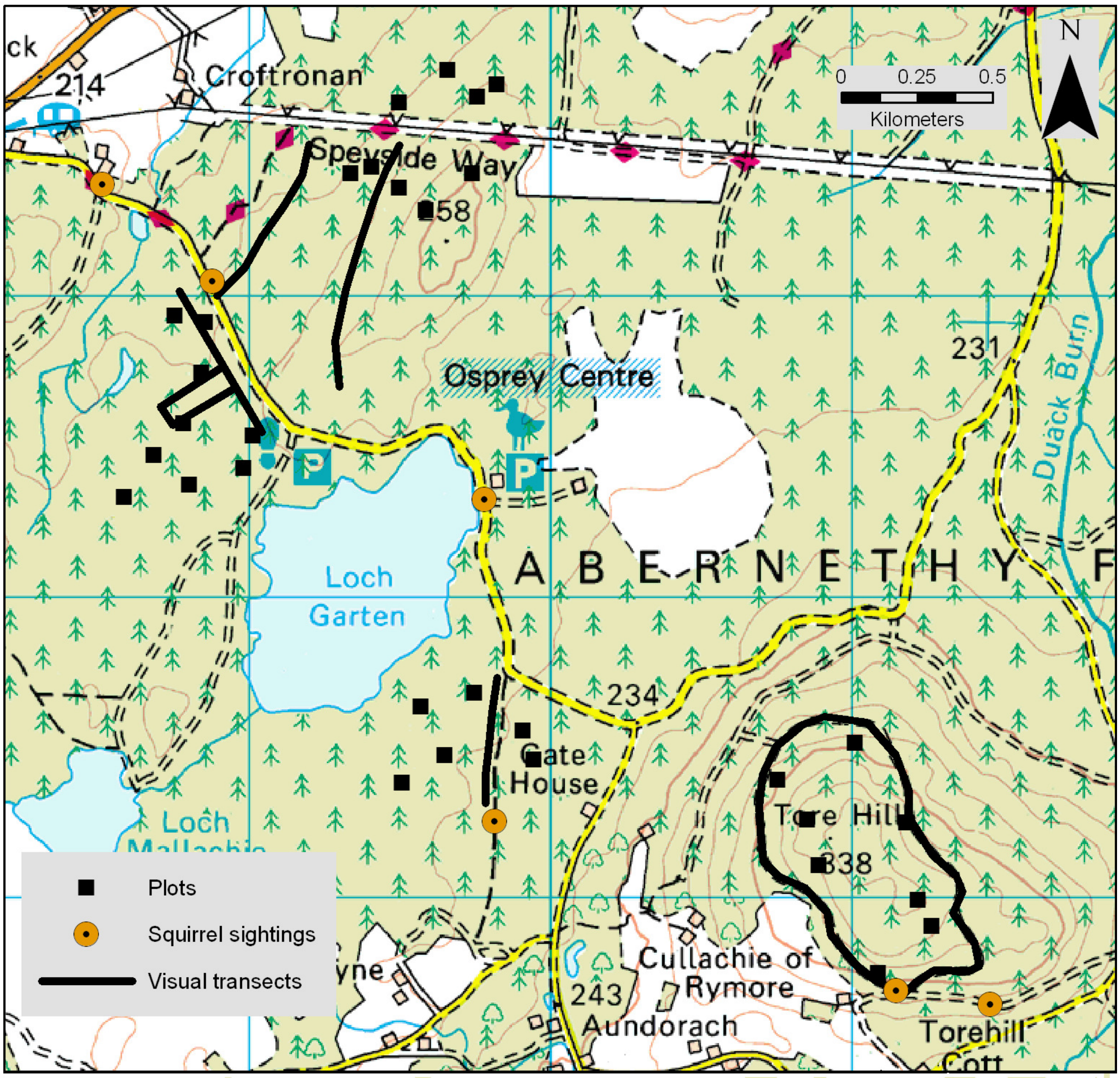


Figure A.1: Location of sampled plots, visual transects and red squirrel sightings – October 2009, Abernethy Forest, Scotland.

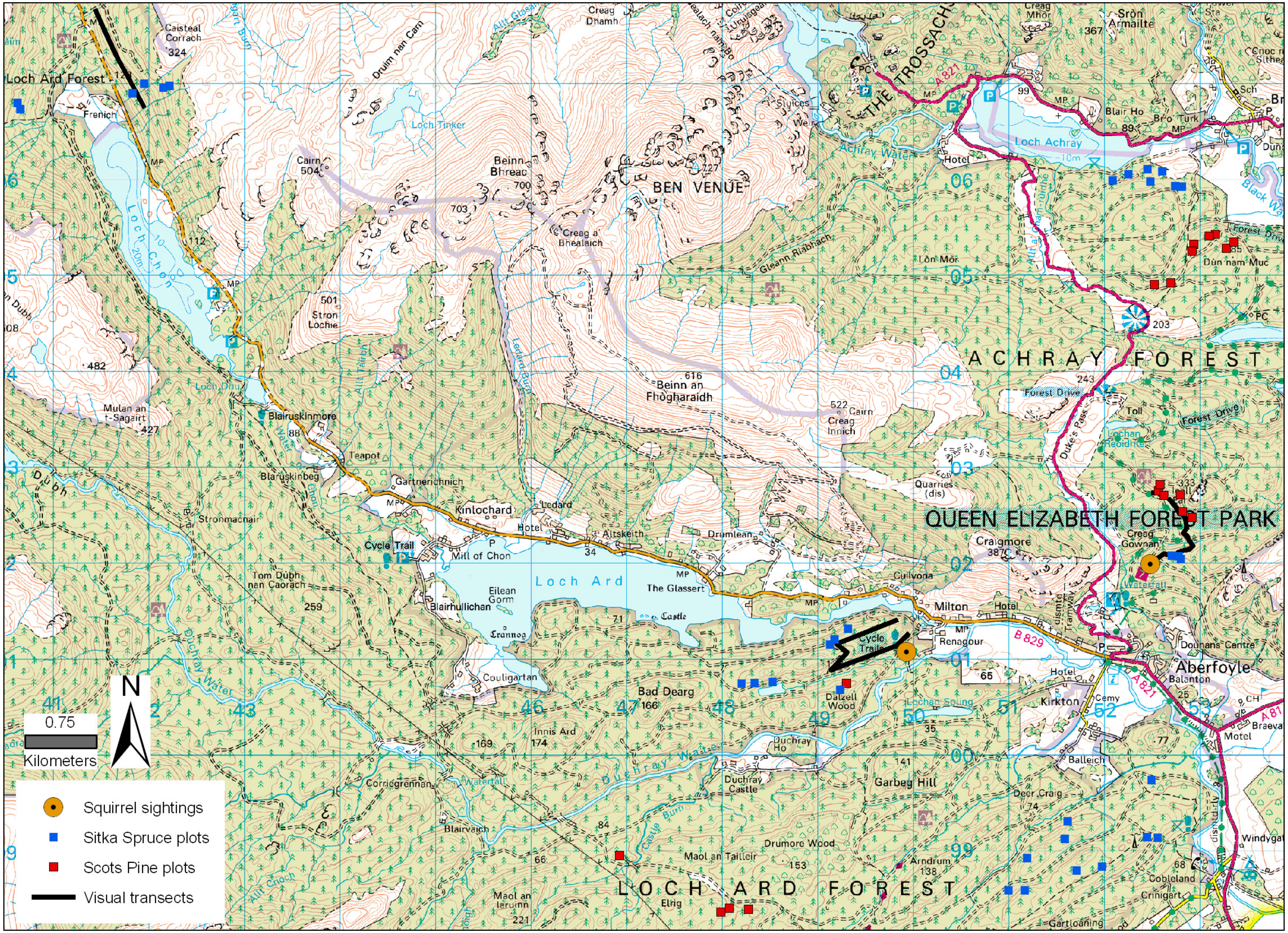


Figure A.2: Location of sampled plots, visual transects and red squirrel sightings – October 2009, Aberfoyle, Scotland

Figure A.3: Example of cones stripped by crossbill (first two, left) and by red squirrels (last two, right), Abernethy Forest, Scotland

Figure A.4: Scots pine scales on a stump, Abernethy Forest, Scotland**.** Squirrels feeding on the ground often carry cones to tree's stumps where feeding remains accumulate (Gurnell, 1987)

Figure A.5: From left to right: Example of uneaten Scots pine cones, cones stripped by squirrel and scales, Abernethy Forest, Scotland

Figure A.6: Sitka spruce cones stripped by squirrel on a stump, Aberfoyle Forest, Scotland

APPENDIX B – LiDAR & field values- Tables

Table B.1: Elevation (m) extracted from both DTMs: OS and LiDAR, and difference between the two, Abernethy Forest, Scotland. Mean difference, SD and RMSE are also provided.

Plot number	OS DTM	LiDAR DTM	Difference (OS – LiDAR)
1	224.4	221.9	2.5
2	227.6	227.0	0.6
3	233.9	232.9	1.0
4	247.6	247.9	-0.3
5	243.4	243.4	0.0
6	221.2	219.2	2.0
7	221.9	220.6	1.3
8	231.1	231.8	-0.7
9	231.1	228.2	2.9
10	218.8	216.3	2.5
11	228.6	220.5	8.1
12	229.0	226.7	2.3
13	227.9	226.6	1.3
14	227.9	221.0	6.9
15	231.1	228.7	2.4
16	230.0	225.9	4.1
17	229.0	225.5	3.5
18	230.0	228.9	1.1
19	227.9	227.7	0.2
20	229.0	228.4	0.6
21	228.6	224.9	3.7
22	229.0	223.9	5.1
23	229.0	226.4	2.6
24	228.6	224.9	3.7
25	302.5	304.6	-2.1
26	322.3	318.1	4.2
27	324.4	322.5	1.9
28	299.4	299.1	0.3
29	292.3	290.6	1.7
30	320.2	318.6	1.6
31	311.0	308.6	2.4
32	323.0	325.2	-2.2
Mean	**250.1**	**248.0**	**2.0**
SD	**37.1**	**37.8**	**2.2**
RMSE			**3.0**

Table B.2: Elevation (m) extracted from both DTMs: OS and LiDAR, and difference between the two, Aberfoyle Forest Park, Scotland. Mean difference, SD and RMSE are also provided.

Plot number	OS DTM	LiDAR DTM	Difference (OS- LiDAR)
1	99.1	99.4	-0.3
2	99.6	102.1	-2.5
3	86.0	91.4	-5.4
4	202.8	201.6	1.2
5	199.3	201.2	-1.9
6	201.0	195.6	5.4
7	167.4	170.8	-3.4
8	101.5	98.4	3.1
9	91.2	99.5	-8.3
10	111.1	116.0	-4.9
11	116.0	121.5	-5.5
12	118.8	117.1	1.7
13	122.1	117.7	4.4
14	119.9	116.4	3.5
15	102.8	101.0	1.8
16	64.0	59.5	4.5
17	83.7	84.7	-1.0
18	96.8	95.8	1.0
19	160.4	157.7	2.7
20	209.5	213.2	-3.7
21	277.4	280.0	-2.6
22	188.5	189.3	-0.8
23	178.2	181.3	-3.1
24	236.2	243.4	-7.2
25	238.6	241.7	-3.1
26	255.9	253.2	2.7
27	78.0	79.4	-1.4
28	108.0	106.8	1.2
29	111.0	110.1	0.9
30	98.0	98.7	-0.7
31	91.0	92.2	-1.2
32	47.0	46.1	0.9
33	81.0	80.6	0.4
34	86.0	86.8	-0.8
35	62.0	58.9	3.1
36	22.0	22.6	-0.6
37	252.1	256.2	-4.1
38	286.1	282.4	3.7
39	244.1	245.9	-1.8
40	284.7	284.8	-0.1
41	256.9	255.4	1.4
42	250.7	246.5	4.2
43	143.1	142.2	0.9
44	148.1	145.5	2.6
45	150.9	148.1	2.8
46	149.2	149.3	-0.1
47	131.5	136.6	-5.1
48	171.9	168.7	3.2
49	150.9	150.2	0.7
50	160.8	160.4	0.4
51	156.9	157.4	-0.5
52	103.3	101.7	1.6
53	108.0	108.8	-0.8
54	157.0	157.2	-0.2
55	162.0	163.0	-1.0
56	145.0	143.6	1.4
Mean	**148.7**	**148.9**	**-0.19**
SD	**65.3**	**65.5**	**3.04**
RMSE			**3.02**

Table B.3: Mean field canopy closure; mean LiDAR canopy cover and difference between both, Abernethy Forest, Scotland. Root mean square error (RMSE), mean and standard deviation (SD) of both LiDAR and field measured canopy density are also presented.

Plot ID	**Tree species**	**% Canopy closure (field)**	**% Canopy cover (LiDAR)**	**Difference (field - LiDAR)**
1	Scots pine	91.3	86.9	4.4
2	Scots pine	61.5	11.6	49.8
3	Scots pine	91.4	80.0	11.3
4	Scots pine	92.0	86.8	5.2
5	Scots pine	93.2	90.2	3.0
6	Scots pine	93.5	89.2	4.3
7	Scots pine	88.5	74.9	13.6
8	Scots pine	88.0	68.3	19.7
9	Scots pine	89.8	60.4	29.4
10	Scots pine	73.3	18.7	54.6
11	Scots pine	94.8	93.2	1.6
12	Scots pine	94.2	44.1	50.2
13	Scots pine	76.8	13.8	63.0
14	Scots pine	77.2	32.5	44.7
15	Scots pine	91.3	95.7	-4.4
16	Scots pine	92.2	81.1	11.1
17	Scots pine	91.8	77.6	14.2
18	Scots pine	88.6	83.1	5.5
19	Scots pine	92.4	87.0	5.4
20	Scots pine	85.2	55.8	29.4
21	Scots pine	92.9	85.3	7.5
22	Scots pine	91.5	84.4	7.1
23	Scots pine	90.7	84.7	6.0
24	Scots pine	89.0	76.4	12.6
25	Scots pine	93.5	72.2	21.3
26	Scots pine	91.9	74.4	17.6
27	Scots pine	90.7	81.2	9.5
28	Scots pine	90.4	81.0	9.4
29	Scots pine	69.9	42.7	27.3
30	Scots pine	92.6	79.5	13.1
31	Scots pine	91.4	89.6	1.8
32	Scots pine	89.2	65.5	23.7
Mean		**88.1**	**70.2**	**17.9**
SD		**7.7**	**23.1**	**17.3**
RMSE				**24.7**

Table B.4: Mean field canopy closure; mean LiDAR canopy cover and difference between both, sitka spruce plots- Aberfoyle Forest, Scotland. Root mean square error (RMSE), mean and standard deviation (SD) of both LiDAR and field measured canopy density are also presented.

Plot ID	**Tree species**	**%Canopy Cover (LiDAR)**	**% Canopy Closure (Field)**	**Difference (Field - LiDAR)**
1	Sitka spruce	66.9	94.3	27.4
2	Sitka spruce	40.4	93.2	52.8
3	Sitka spruce	45.6	93.8	48.3
4	Sitka spruce	82.6	93.7	11.1
5	Sitka spruce	91.9	93.9	2.0
6	Sitka spruce	82.1	92.5	10.4
7	Sitka spruce	88.1	93.3	5.2
8	Sitka spruce	78.4	93.4	15.0
9	Sitka spruce	81.9	91.8	9.9
10	Sitka spruce	67.8	92.0	24.2
11	Sitka spruce	69.4	91.6	22.2
12	Sitka spruce	70.7	90.9	20.1
13	Sitka spruce	86.3	89.3	2.9
14	Sitka spruce	88.7	91.8	3.1
15	Sitka spruce	83.2	92.4	9.2
16	Sitka spruce	49.3	92.7	43.4
17	Sitka spruce	80.5	87.9	7.4
18	Sitka spruce	65.6	86.5	20.8
19	Sitka spruce	96.0	94.0	-2.1
20	Sitka spruce	99.0	92.2	-6.8
21	Sitka spruce	98.6	94.0	-4.6
22	Sitka spruce	99.5	92.7	-6.8
23	Sitka spruce	100.0	92.9	-7.1
24	Sitka spruce	100.0	94.2	-5.8
25	Sitka spruce	99.4	94.3	-5.1
26	Sitka spruce	100.0	94.5	-5.5
27	Sitka spruce	94.4	91.8	-2.6
28	Sitka spruce	99.6	94.7	-5.0
29	Sitka spruce	88.9	92.5	3.5
30	Sitka spruce	76.5	92.5	15.9
31	Sitka spruce	80.5	91.7	11.2
32	Sitka spruce	95.2	92.7	-2.5
33	Sitka spruce	98.9	93.0	-5.9
34	Sitka spruce	82.1	93.0	10.9
35	Sitka spruce	96.4	93.4	-3.1
36	Sitka spruce	84.1	92.4	8.2
Mean		**83.6**	**92.5**	**9.0**
SD		**15.9**	**1.7**	**15.5**
RMSE				**17.7**

Table B.5: Mean field canopy closure; mean LiDAR canopy cover and difference between both, Scots pine plots- Aberfoyle Forest, Scotland. Root mean square error (RMSE), mean and standard deviation (SD) of both LiDAR and field measured canopy density are also presented.

Plot ID	Tree species	%Canopy Cover (LiDAR)	% Canopy Closure (Field	Difference (Field - LiDAR)
37	Scots pine	83.5	87.6	4.1
38	Scots pine	57.4	54.4	-3.0
39	Scots pine	88.3	93.1	4.8
40	Scots pine	96.4	90.2	-6.2
41	Scots pine	91.4	93.6	2.2
42	Scots pine	91.4	93.1	1.7
43	Scots pine	57.6	84.4	26.8
44	Scots pine	75.1	86.5	11.5
45	Scots pine	88.1	91.1	3.0
46	Scots pine	70.7	80.7	10.0
47	Scots pine	55.5	83.3	27.8
48	Scots pine	65.3	77.3	11.9
49	Scots pine	52.0	80.0	28.0
50	Scots pine	73.3	88.0	14.7
51	Scots pine	80.4	81.1	0.7
52	Scots pine	78.4	93.8	15.3
53	Scots pine	59.9	84.8	24.9
54	Scots pine	79.3	87.2	7.9
55	Scots pine	79.1	89.6	10.5
56	Scots pine	79.7	87.8	8.1
Mean		**75.1**	**85.4**	**10.2**
SD		**13.3**	**8.7**	**10.2**
RMSE				**14.3**

Table B.6: Number of trees per plot detected applying the local maxima approach to the CHM and to the cloud of points, using 3m and 2m radius windows. Results are presented in total number of trees per plot. Abernethy Forest, Scotland.

Scots pine		CHM approach		Cloud of Points approach	
Plot	**Field**	**Search Window 3m**	**Search Window 2m**	**Search Window 3m**	**Search Window 2m**
1	32	15	20	20	25
2	4	4	4	3	5
3	34	19	20	14	18
4	22	18	26	14	23
5	22	11	17	13	19
6	20	13	15	16	18
7	19	12	12	9	18
8	15	12	13	9	12
9	12	10	10	8	14
10	9	5	10	2	2
11	5	5	7	6	8
12	12	11	14	8	11
13	12	3	5	1	1
14	16	4	9	5	5
15	70	14	16	20	26
16	16	10	16	18	22
17	37	6	11	8	12
18	25	13	17	13	18
19	12	10	13	9	11
20	6	4	4	2	3
21	13	12	11	9	11
22	15	11	10	8	12
23	13	12	14	9	12
24	7	5	6	3	5
25	10	13	15	11	16
26	8	9	9	7	7
27	10	10	12	10	14
28	10	12	15	10	13
29	3	4	5	1	2
30	11	15	18	13	14
31	15	15	15	12	14
32	11	9	10	11	12
Total	**526**	**326**	**399**	**302**	**403**

Table B.7: Number of trees per plot detected applying the local maxima algorithm to the CHM and to the cloud of points, using 3m and 2m radius windows. Results are presented in total number of trees per plot. (Scots pine plots only) Aberfoyle Forest, Scotland.

Scots pine		**CHM approach**		**Cloud of Points approach**	
Plot	**Field**	**Search Window 3m**	**Search Window 2m**	**Search Window 3m**	**Search Window 2m**
1	14	6	8	6	8
2	13	1	2	1	3
3	7	5	9	5	6
4	22	4	4	5	9
5	18	3	9	5	9
6	18	5	12	7	11
7	9	3	6	3	5
8	11	5	7	5	9
9	16	6	12	5	9
10	11	2	5	4	8
11	12	5	8	3	9
12	8	4	5	4	6
13	9	4	6	4	5
14	9	3	8	2	5
15	12	1	4	6	7
16	28	6	13	4	9
17	30	5	9	5	8
18	30	2	6	6	7
19	36	6	10	6	10
20	11	5	9	5	10
Total	**324**	**81**	**152**	**91**	**153**

Table B.8: Number of trees per plot detected applying the local maxima algorithm to the CHM and to the cloud of points, using 3m and 2m radius windows. Results are presented in total number of trees per plot. (sitka spruce plots only) Aberfoyle Forest, Scotland.

Sitka spruce		**CHM approach**		**Cloud of Points approach**	
Plot	**Field**	**Search Window 3m**	**Search Window 2m**	**Search Window 3m**	**Search Window 2m**
1	49	3	5	4	9
2	22	1	2	2	4
3	9	2	2	2	3
4	3	3	4	3	4
5	4	2	3	3	4
6	5	4	4	4	7
7	5	1	6	2	5
8	21	3	6	3	7
9	8	5	7	5	5
10	9	4	8	5	8
11	5	3	10	3	5
12	16	3	6	4	5
13	5	3	8	4	7
14	7	2	7	2	7
15	5	2	4	3	4
16	8	2	3	1	2
17	7	3	8	3	9
18	6	2	3	2	5
19	38	6	7	8	8
20	49	2	10	7	9
21	70	8	15	7	15
22	30	6	10	4	10
23	38	5	8	4	8
24	67	5	12	5	9
25	73	4	12	5	13
26	83	4	14	5	6
27	36	6	12	4	7
28	46	5	8	6	10
29	10	3	9	6	7
30	22	2	7	5	7
31	15	3	10	5	12
32	28	3	10	4	8
33	64	8	10	7	13
34	12	5	8	6	8
35	7	4	10	4	10
36	8	4	4	4	9
Total	**890**	**131**	**272**	**151**	**269**

Table B.9: Field mean height and LiDAR 90th & 95th percentile canopy height -values per plot. Average and SD. Abernethy Forest, Scotland

Plot ID	**Tree Species**	**Field field mean height**	**LiDAR 90^{th} percentile**	**LiDAR 95th percentile**
1	Scots pine	20.3	18.4	18.4
2	Scots pine	15.2	15.3	14.6
3	Scots pine	16.1	18.2	17.2
4	Scots pine	22.4	19.4	18.5
5	Scots pine	19.5	18.2	18.7
6	Scots pine	22.9	18.6	19.3
7	Scots pine	21.1	17.6	18.1
8	Scots pine	20.6	18.2	18.6
9	Scots pine	21.6	19.1	19.8
10	Scots pine	7.5	8	6.7
11	Scots pine	24.5	21.5	20.5
12	Scots pine	12.6	11.3	10.6
13	Scots pine	13.5	10	7.4
14	Scots pine	12.7	11	12.6
15	Scots pine	17.9	17.2	17
16	Scots pine	15.9	13.5	13.9
17	Scots pine	13.9	12.1	13
18	Scots pine	14.6	13.1	13.5
19	Scots pine	17.2	17.1	16.8
20	Scots pine	18.3	16.3	17.1
21	Scots pine	20.2	17.5	17.9
22	Scots pine	15.6	13.1	14.4
23	Scots pine	20.1	17.6	19.3
24	Scots pine	19.2	13.6	14.1
25	Scots pine	21.1	17.9	18.3
26	Scots pine	20.5	17.1	19
27	Scots pine	21.9	16.9	18.3
28	Scots pine	22.8	19.7	19.2
29	Scots pine	20.4	17.1	16.3
30	Scots pine	19.4	18.7	19
31	Scots pine	24.5	21.9	21.9
32	Scots pine	19.1	17.5	18.5
Mean		**18.5**	**16.3**	**16.5**
SD		**3.9**	**3.3**	**3.6**

Table B.10: Field mean height and LiDAR 90th & 95th percentile canopy height -values per plot. Average and SD. Aberfoyle Forest, Scotland

Plot ID	Tree species	Field mean height	LiDAR 90th percentile	LiDAR 95th percentile
1	Sitka spruce	25.0	19.5	20.1
2	Sitka spruce	27.3	23.0	29.1
3	Sitka spruce	35.0	20.0	35.8
4	Sitka spruce	34.2	32.0	36.4
5	Sitka spruce	37.5	32.0	34.3
6	Sitka spruce	43.7	35.3	32.7
7	Sitka spruce	36.9	31.0	32.4
8	Sitka spruce	36.9	30.5	33.7
9	Sitka spruce	33.1	32.0	32.0
10	Sitka spruce	32.9	28.0	30.0
11	Sitka spruce	33.7	30.0	31.7
12	Sitka spruce	20.8	19.5	17.9
13	Sitka spruce	36.2	31.2	33.2
14	Sitka spruce	31.0	31.6	30.3
15	Sitka spruce	31.1	31.8	31.7
16	Sitka spruce	40.1	33.7	37.7
17	Sitka spruce	33.2	28.6	34.2
18	Sitka spruce	37.2	29.8	36.8
19	Sitka spruce	37.0	29.3	31.9
20	Sitka spruce	25.5	23.3	24.0
21	Sitka spruce	19.9	17.7	19.0
22	Sitka spruce	31.0	29.6	30.2
23	Sitka spruce	29.7	28.8	28.7
24	Sitka spruce	27.6	24.7	26.0
25	Sitka spruce	24.8	21.6	22.6
26	Sitka spruce	29.3	24.8	27.9
27	Sitka spruce	23.5	21.0	22.4
28	Sitka spruce	24.4	23.0	23.3
29	Sitka spruce	23.8	20.4	23.9
30	Sitka spruce	25.0	20.0	23.3
31	Sitka spruce	24.6	18.7	21.8
32	Sitka spruce	28.0	22.3	24.4
33	Sitka spruce	24.7	21.4	22.2
34	Sitka spruce	25.0	20.8	22.4
35	Sitka spruce	30.5	27.8	30.1
36	Sitka spruce	26.4	22.5	24.8
37	Scots pine	23.0	22.7	23.2
38	Scots pine	17.5	21.0	21.6
39	Scots pine	22.3	20.9	22.3
40	Scots pine	15.6	16.6	19.4
41	Scots pine	21.0	19.4	21.7
42	Scots pine	19.2	18.6	21.5
43	Scots pine	24.1	19.3	20.5
44	Scots pine	22.7	18.6	21.5
45	Scots pine	21.3	19.2	20.3
46	Scots pine	21.7	20.8	21.9
47	Scots pine	21.5	19.8	20.0
48	Scots pine	21.9	19.7	20.6
49	Scots pine	21.7	17.0	20.4
50	Scots pine	23.3	19.1	22.1
51	Scots pine	22.8	18.8	21.0
52	Scots pine	18.5	18.0	18.3
53	Scots pine	16.2	16.9	16.9
54	Scots pine	19.5	15.3	16.6
55	Scots pine	17.1	15.5	18.1
56	Scots pine	21.4	20.0	20.5
Mean		**26.8**	**23.5**	**25.5**
SD		**6.7**	**5.5**	**5.9**

APPENDIX C – GLM validation – Tables

Table C.1: Field-predicted number of stripped cones, LiDAR-predicted number of stripped cones and difference between both. Mean values, standard deviation and RMSE. Abernethy Forest, Scotland.

Plot ID	**Field-predicted cones**	**LiDAR-predicted cones**	**Diff Field-LiDAR**
1	16	28	-11
2	1	0	1
3	14	19	-4
4	28	21	7
5	17	15	2
6	40	17	22
7	16	3	12
8	18	4	15
9	19	7	12
10	1	0	1
11	24	26	-2
12	11	0	11
13	3	0	3
14	2	1	2
15	45	1	44
16	18	10	9
17	28	5	23
18	15	14	1
19	13	9	4
20	8	4	4
21	24	13	12
22	17	4	14
23	15	10	5
24	11	4	7
25	16	7	9
26	14	2	12
27	21	9	12
28	15	11	4
29	2	1	1
30	19	13	6
31	27	32	-5
32	15	8	7
Mean	**17**	**9.2**	**7.5**
SD	**10**	**8.6**	**9.9**
		RMSE	**12.3**

Table C.2: Field-predicted number of stripped cones, LiDAR-predicted number of cones using un-calibrated LiDAR number of trees (GLM 1) and calibrated number of trees (GLM 2). Difference between *Field* and *GLM 1* and *Field* and *GLM 2*.Mean values, standard deviation and RMSE. Aberfoyle Forest, Scotland.

Plot ID	Field-predicted cones	LiDAR-predicted cones GLM 1	LiDAR-predicted cones GLM 2	Diff Field- GLM 1	Diff Field - GLM2
33	18	25	11	-7.0	7.1
34	1	7	2	-6.0	-0.7
35	27	47	147	-20.0	-119.9
36	14	20	41	-6.0	-26.8
37	29	50	31	-21.0	-1.9
38	38	23	72	15.0	-34.3
39	9	11	3	-2.0	6.4
40	22	7	7	15.0	15.1
41	21	3	23	18.0	-2.5
42	9	32	15	-23.0	-5.7
43	10	5	13	5.0	-3.4
44	8	2	3	6.0	4.6
45	9	1	0	8.0	9.0
46	15	3	12	12.0	3.2
47	11	5	1	6.0	9.8
48	40	33	27	7.0	12.7
49	10	0	0	10.0	10.0
50	13	16	18	-3.0	-5.0
51	17	8	4	9.0	13.0
52	9	5	29	4.0	-20.5
Mean	**16.5**	**15.2**	**23**	**1.4**	**-6.5**
SD	**10.3**	**15.3**	**34**	**12.1**	**29.8**
RMSE				**11.9**	**29.8**

Table C.3: Number of cones stripped by squirrels observed in the field and predicted using field data (LOO cross-validation). Abernethy Forest (plots 1 to 32) and Aberfoyle (plots 33 to 52)- Scotland

Plot Id	**Field-observed stripped cones**	**Field-predicted stripped cones (LOO cross-validation)**	**Difference (Field-observed – Field-predicted)**
1	61	16	45
2	4	1	3
3	15	14	1
4	9	28	-19
5	42	17	25
6	4	40	-36
7	12	16	-4
8	27	18	9
9	0	19	-19
10	4	1	3
11	91	24	67
12	20	11	9
13	5	3	2
14	14	2	12
15	35	45	-10
16	11	18	-7
17	47	28	19
18	17	15	2
19	16	13	3
20	0	8	-8
21	44	24	20
22	18	17	1
23	9	15	-6
24	16	11	5
25	60	16	44
26	3	14	-11
27	5	21	-16
28	5	15	-10
29	2	2	0
30	32	19	13
31	55	27	28
32	3	15	-12
33	18	18	0
34	0	1	-1
35	11	27	-16
36	0	14	-14
37	6	29	-23
38	4	38	-34
39	0	9	-9
40	48	22	26
41	7	21	-14
42	2	9	-7
43	3	10	-7
44	2	8	-6
45	21	9	12
46	22	15	7
47	4	11	-7
48	1	40	-39
49	3	10	-7
50	25	13	12
51	57	17	40
52	12	9	3
Mean	**17.9**	**16.6**	**1.33**
SD	**20.4**	**10.0**	**20.2**
		RMSE	**20.0**

APPENDIX D – VORTEX predictions – Abernethy Forest

Table D.1: VORTEX predictions for red squirrel populations at Abernethy Forest: Annual population size and standard deviation (SD) for Population 1 and Population 2, for each scenario *Basic* and *LiDAR* and for each sub-scenario: *catastrophe* and *no-catastrophe*

	Population 1 (No-Catastrophe)				**Population 2 (No-Catastrophe)**			
Year	**Basic Pop Size**	**Basic-SD**	**LiDAR Pop Size**	**LiDAR-SD**	**Basic Pop Size**	**Basic-SD**	**LiDAR Pop Size**	**LiDAR-SD**
1	260	90.3	87	42.6	254	78.4	78	21.2
2	228	112.3	77	44.8	217	104.7	60	30.6
3	202	117.4	62	46.6	197	109.2	56	32.7
4	179	120.0	57	45.8	172	112.5	48	34.0
5	162	122.7	49	47.1	160	115.6	44	34.8
6	146	121.5	46	46.3	140	116.1	38	34.3
7	136	120.9	38	42.2	132	114.8	35	34.2
8	124	118.8	37	43.8	122	113.0	30	33.0
9	110	117.2	31	41.0	107	111.9	30	33.5
10	104	110.7	30	39.4	101	106.6	24	30.8
11	92	110.0	25	38.6	89	108.1	23	31.4
12	82	110.8	24	38.5	81	104.3	20	30.0
13	75	103.0	20	34.2	74	100.2	19	28.7
14	69	104.5	20	35.7	67	101.4	17	28.2
15	62	101.3	18	34.3	62	96.2	16	27.7
16	57	98.8	17	32.6	56	95.1	15	27.3
17	49	100.8	17	34.4	49	93.0	16	27.7
18	45	101.9	16	33.4	44	99.1	13	25.6
19	42	99.2	13	29.2	42	94.8	13	25.5
20	42	95.0	13	30.2	42	91.8	11	24.1
	Population 1 (Catastrophe)				**Population 2 (Catastrophe)**			
Year	**Basic Pop Size**	**Basic-SD**	**LiDAR Pop Size**	**LiDAR-SD**	**Basic Pop Size**	**Basic-SD**	**LiDAR Pop Size**	**LiDAR-SD**
1	242	98.0	87	43.9	238	86.6	76	22.5
2	203	113.2	74	45.1	194	106.5	59	31.2
3	171	118.1	60	45.2	169	110.6	54	32.4
4	157	118.0	55	46.2	150	111.6	45	33.8
5	133	116.3	47	44.9	133	111.6	42	33.9
6	122	118.1	44	44.8	116	110.5	37	33.7
7	114	117.1	37	41.9	112	112.9	34	33.2
8	103	114.7	35	42.2	101	109.6	30	33.2
9	97	114.1	32	41.0	94	109.2	28	32.2
10	92	114.4	27	36.0	89	107.9	25	31.6
11	84	110.0	25	38.0	82	107.3	21	29.2
12	79	108.4	23	36.1	79	104.6	22	30.5
13	70	101.6	22	37.1	69	99.9	20	29.6
14	63	98.4	18	33.1	63	95.8	17	27.9
15	59	97.8	18	33.4	58	95.2	16	27.7
16	56	95.1	15	30.0	54	91.3	14	25.2
17	53	95.3	14	28.1	52	92.5	13	25.1
18	47	89.7	14	30.9	46	85.1	13	25.6
19	44	86.7	12	27.7	43	84.6	11	25.4
20	38	78.5	11	29.7	37	75.1	9	22.3

APPENDIX E – Related publications

The following publications contain work related to or derived from this thesis.

Peer-reviewed publications

Flaherty, S.; Patenaude, G., Close A. & Lurz, P. 2012. The impact of forest-stand structure on red squirrel habitat use*, Forestry: An International Journal of Forest Research,* Vol. 85, No.3, pp 437-444

Conference proceedings

Flaherty, S.; Patenaude, G., & Lurz, P. The use of LiDAR remote sensing for red squirrel habitat mapping in Abernethy Forest, Scotland. In *Proceedings of ForestSat 2010*, 7th -9th September, Lugo, Spain

Flaherty, S.; Lurz, P. & Patenaude, G. Implementation of a General Linear Model using LiDAR derived explanatory variables: a case study in Scotland. In *Proceedings of SPIE Remote Sensing*, 24 - 27 September 2012, Edinburgh, United Kingdom (Submitted)

In preparation

Flaherty, S.; Lurz, P. & Patenaude, G. Red squirrel habitat mapping using LiDAR remote sensing. To be submitted to the *Journal of Applied Remote Sensing*

Zuur, A.F.; Flaherty, S.; Lurz, P.; Patenaude, G., Ieno, E.N.; Hilbe, J. Generalized linear modelling with MCMC in JAGS applied to red squirrel data; In *A Beginner's guide to GLM using R and JAGS* , Zuur, A.F.; Ieno, E.N.; Hilbe, J.