Determining the risk of Pinewood deterioration based on tree size (DBH), structure and regeneration density data.

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Contents

1. Executive Summary

Under the Habitats Directive (Article 6.2) it is the obligation of Member States to ensure appropriate steps are taken to avoid ‘deterioration’ of qualifying habitats and habitats of species within Natura sites (Special Areas of Conservation (SAC) and Special Protection Areas (SPA)). ‘Deterioration’ under the Deer (Scotland) Act (1996) (Anon, 1996) relates to the future condition of the habitat relative to the time at which the site was designated. Repeated measurements of a range of values will allow damage to be detected, and therefore ‘deterioration’ to be identified. However, repeat measurements need to be separated by a suitably long time period. Early detection of sites that could potentially ‘deteriorate’ if management conditions remain unchanged, would allow suitable changes to management prescriptions or new regimes to be put in place to avoid the deterioration, or at the very least alleviate it.

This project used data from long term monitoring plots in a range of native pinewood to parameterise a stand dynamics model to demonstrate the detrimental impact of deer browsing on the forest cycle. This project tested the possibility of predicting the probability that a candidate population was self-sustaining, and that over appropriate periods of time the distribution of tree size present on site now was maintained through adequate regeneration recruitment and growth. If it is accepted that these structural changes, affected by tree growth and mortality without new recruitment, constitute ‘deterioration’ of the habitat then predictions can be made on when regeneration is necessary in a population to avoid ‘deterioration’ occurring.

- Destructive sampling in Black Wood of Rannoch and Glen Affric revealed that trees that successfully transited from seedlings to saplings to trees took on average 52 years and 48 years respectively to grow into the lowest inventoried size class (7 cm DBH).

- Seedling mortality over a 22 year period in Black Wood of Rannoch was estimated at 50% in stands undergoing stem exclusion and 48% in stands entering the understorey reinitiation phase.

- The degree of tree canopy cover was used to determine when sites were no longer classified as woodland. Canopy cover values were calculated from tree DBH, which is significantly positively correlated with crown radius. Crown radius was calculated for the mid-value of each DBH size.

- Growth transition matrices were developed from repeat measurements of individuals present over a 22 year period for the two stand dynamics phases. The dbh distributions generated from these matrices were modified by density dependant mortality (self thinning).

- Data from long-term studies in native pinewoods and yield data from unthinned Scots pine commercial plantations were used to estimate the slope of the self-thinning line. At high stem densities (>6.35 ln stems ha^{-1}) native pinewoods and commercial plantations achieved similar mean quadratic DBH; however, the majority of the pinewoods occur below the commercial maximum density line. Only limited data exists on density dependency in native pinewoods for Scotland, therefore the assumptions made in this report need further study to ensure their consistency across different site types and stand conditions.

- The final model outputs were not realistic over the time periods reported. The final DBH distributions produced at year 50, 100 and 150 were identical in shape and proportion between dbh classes; and vary only in the number of trees represented in each class. The outcome is a set of non-random growth and mortality modifiers; which lead to the homogeneity of data predictions and is therefore of limited value for the purpose it was intended.

2. Background

Under the Habitats Directive (Article 6.2) it is the obligation of Member States to ensure appropriate steps are taken to avoid ‘deterioration’ of qualifying habitats and habitats of species within Natura sites (Special Areas of Conservation (SAC) and Special Protection Areas (SPA)). Ensuring that the integrity of the site is maintained and the site makes an appropriate contribution to achieving favourable conservation status for each of the qualifying interests.

Most of the native pinewoods in Scotland have been designated as SAC’s or SPA’s and therefore need to comply with the conservation objectives specified within the Habitats Directive; particularly Annex I: “ *to avoid deterioration of the qualifying habitat thus ensuring that the integrity of the site is maintained and the site makes an appropriate contribution to achieving favourable conservation status (FCS) to each of the qualifying interests* ”; and Annex II “ *to avoid deterioration of the habitats of the qualifying species or significant disturbance to the qualifying species, and thus ensuring that the integrity of the site is maintained and the site makes an appropriate contribution to achieving FCS for each of the qualifying interests* ”.

‘Deterioration’ under the Deer (Scotland) Act (1996) (Anon, 1996) relates to the future condition of the habitat relative to the time at which the site was designated. Damage is specifically ‘deterioration’ which can be measured from an evidence baseline (Anon, 2007). Repeated measurements of a range of values will allow damage to be detected, and therefore ‘deterioration’ to be identified. However, repeat measurements that will detect any change in the tree population need to be separated by a suitably long time period (Edwards and Mason, 2000). Even so, in some situations there is a need to predict future condition of the site relative to the current point in time, to avoid ‘deterioration’ of the habitat or any significant disturbance to the qualifying species. Early detection of sites that could potentially ‘deteriorate’ if management conditions remain unchanged, would allow suitable changes to management prescriptions or new regimes to be put in place to avoid the deterioration, or at the very least alleviate it.

The Deer Commission Scotland (DCS) have received Expressions of Concern regarding deer impacts within a variety of designated habitats within Upper Deeside in 2003. After consideration, DCS, Forestry Commission Scotland (FCS) and Scottish Natural Heritage (SNH) decided there was a basis for investigating further under published joint-working guidelines. DCS, FCS and SNH have begun working together to assess deer impacts on Natura interests within parts of Upper Deeside, using information collected from the parent trees and regeneration as a surrogate for woodland condition (Edwards, 2006).

Baseline studies were established in two major native pinewoods, Ballochbuie (Edwards & Duncan, 2007) and Mar Lodge (Edwards and Davies, 2008), with further baselines to be established in additional sites at a later date. These Baseline studies enable the Joint Working Group to determine the level of 'damage' in a site under The Deer (Scotland) Act (1996), (S7 and S8), but only with respect to another assessment of the same variables at a future date. The ability to predict the probability of future changes to the habitat from a single baseline study would ensure sites that are already damaged, and in risk of further deterioration, have appropriate management operations put in place as early as possible.

Stand development patterns in pinewoods pass through four distinct phases classified by Oliver and Larson (1996) as stand initiation, stem exclusion, understorey reinitiation, and old growth, which are an emergent property resulting from tree-to-tree interactions that modify recruitment (ingrowth) rates, growth of surviving trees, and mortality over time. This project uses data primarily from the Black Wood of Rannoch native pinewood to parameterise a stand dynamics model to demonstrate the detrimental impact of deer browsing on the forest cycle.

This project was funded to look at the prospect of using information on stand structure within native pinewoods, to predict the probability that the candidate population was self-sustaining, and that over appropriate periods of time the distribution of tree size present on site now was maintained through adequate regeneration recruitment and growth. The project aimed to determine if information on tree growth, tree mortality, and new seedling regeneration could be used to predict the future dynamic state of a native Pinewood. By modelling each of these three components of a dynamic system (Regeneration, Tree Growth, Tree Mortality) a series of 'what if?' scenarios can be designed and compared for particular woodland at a given point in time.

By preventing any regeneration to occur in the model the effect of tree growth and continued mortality on the probable stand structure can be calculated. If it is then accepted that these structural changes, affected by tree growth and mortality without new recruitment, constitute 'deterioration' of the habitat then predictions can be made on when regeneration is necessary in a population to avoid 'deterioration' occurring. The effects of delaying regeneration recruitment for a given period of time, or of increasing regeneration through assisted recruitment, can also be calculated.

For example, if the level of deer browsing on a site is particularly high and is preventing new regeneration becoming established and growing in size into the small tree class, then the effect of this continued lack of recruitment on the future stand structure could be predicted over the next 50 years. In the same way the potential effect of allowing a pulse of regeneration to establish on a site now in 50 years or in 100 years could be modelled and the probable effects on future stand condition forecast.

Because neither an independent tree growth model, nor a stand growth model exists for the native pinewoods a new population model had to be developed using existing Forest Research datasets. Similarly no models exist for pinewood regeneration or mortality. The regeneration model was built following destructive analyses of trees at two sites, and Forest Research datasets and published yield models were used to calculate density dependant mortality.

The potential use of the risk model is further explained in the discussion section of this report.

3. Project objectives

The project had four main objectives:

1. Collect and analyse relevant new and existing independent (i.e. collected outwith priority site / joint working process) data on tree age and condition.

2. Collect and analyse relevant new and existing independent data on recruitment.

3. Collect and analyse relevant new and existing independent data on growth and mortality.

4. Develop and apply criteria (including exploration of a 'phase approach' - i.e. areas at phase 1, 2 etc.) for identification of spatial temporal priority 'risk' areas (i.e. mapping areas where there is a need for regeneration within 10, 50, 100 years etc.).

This report explains how the first three objectives noted above were met. The final objective was not completed because the steering group could not agree on the use of ≥ 20% canopy cover as an indicator of woodland, and therefore on the allocation of priority 'risk' areas.

4. Method

Study area

This project focuses on the Black Wood of Rannoch (Figure 1) as an example of a typical native pinewood in Scotland for which long-term study data is available. Four large (0.85 ha) monitoring plots were established in 1948 (Arkle and Nixon, 1996), and resurveyed in 1956, 1983, 1994, and 2005. The plots are located in a reserve on the southern shores of Loch Rannoch in the Tummel Valley, Perthshire (Edwards and Mason, 2006). Ownership of the Black Wood of Rannoch has changed periodically through the centuries, resulting in periods of felling and overgrazing (Edwards and Mason, 2000). The last extensive felling episode was carried out by Canadian Forestry Corps in 1941-1942, since then the site has been ring fenced but no further interventions or management operations, except for deer control, have taken place (Edwards and Mason, 2006). Four plots were selected to represent stands in the stem exclusion and understorey reinitiation phases of stand development.

The Black Wood of Rannoch long term datasets were supplemented with information from destructive sampling of small trees from Black Wood of Rannoch and Glen Affric, as well as data from yield tables of unthinned Scots pine, and short and long-term study plots established in the following native pinewoods across Scotland: Abernethy long term plot on RSPB site, Glen Garry long term plot, Glenmore long term plot, Glen Affric long term plot, Glen Affric stand structure survey, Ballochbuie stand structure survey, and Kinveachy structure survey.

Regeneration dynamics

Forty Scots pine (*Pinus sylvestris*) and seven birch (*Betula* spp.) trees (>7 cm DBH, >3 m height) were destructively sampled to determine the time required to reach (*i*) 1.3 m in height (i.e., transition from a seedling to a sapling) and (*ii*) 7 cm DBH (i.e., transition from a sapling to a tree) for individuals that successfully transitioned from seedling to sapling to tree. Trees were randomly selected from a range of site conditions at Black Wood of Rannoch and Glen Affric to capture growth rate variability in response to light availability. Individuals were photographed insitu, and site conditions (open ground, canopy gap, and closed canopy), ground vegetation (species cover and height), and deer presence (deer scat, browse line) assessed prior to destructive removal. Trees were extracted with roots intact to ensure correct identification of the root collar and total tree height and root collar diameter recorded. Back at the laboratory individuals were sectioned and diameter measured using a calliper to 0.1 mm accuracy at the following distances from root collar: 5 cm if severe basal sweep occurred, 10 cm intervals up to 1.0 m, 1.3 m, and then every 0.5 m from 1.5 m to 3.0 m. Dried sections were sanded to a grit of 60 using a fixed sander, and then handed sanded using grits of 150, 320, and 600 as per standard dendrochronological preparation procedures (Swetnam *et al*. 1985). Annual ring counts were assessed on three trajectories from pith to bark using a 40x light microscope (Wild Heerbrugg) and aged relative to root collar. Tree ring data were used to reconstruct height and diameter profiles over time. Growth rate at DBH, calculated as diameter divided by the number of annual rings, was used to predict the time required to reach 7 cm DBH. This method assumes a constant growth rate from pith to bark, which may over simply the situation for individuals that undergo growth release following escape from browsing pressure.

Presence and timing of past injuries (external, wood still exposed; internal, injury now healed over) resulting from deer damage (deer browsing, antler rubbing and/or bark stripping) were identified from disrupted annual ring patterns. Deer damage intensity was expressed as the number of sections from root collar to 1.3 m height with disrupted annual rings.

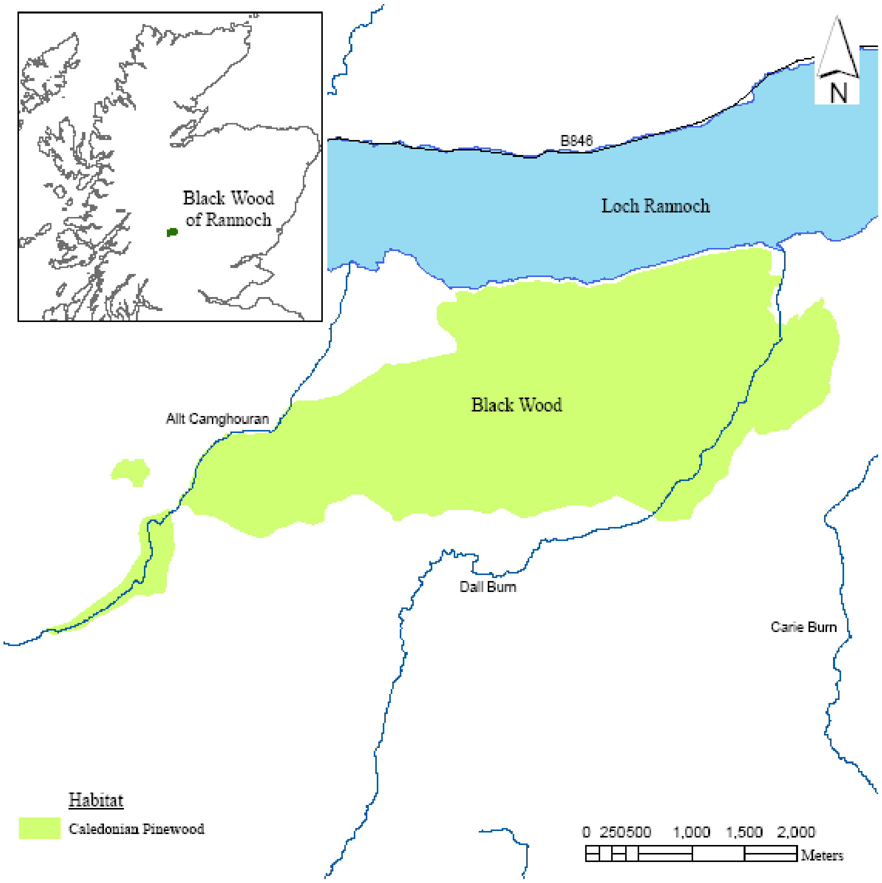

Figure 1. Location of Black Wood of Rannoch Caledonian Pinewood depicted by green shading.

Development of a growth transition matrix

Growth transition matrices (Lootens *et al.* 1999) were developed from repeat measurements of individuals present over a 22 year period for the two stand dynamics phases. Analyses were restricted to individuals present in 1983 that had grown into the smallest inventoried class (>7 cm DBH) by 2005. Lack of DBH and height data in 1983 meant that undersized individuals (i.e., <7 cm DBH) could not be classified into seedlings and saplings. Table 1 shows an example of a transition frequency matrix and corresponding transition matrix for stands entering the understorey reinitiation phase. Columns represent the distribution of individuals by size class in 1983 and rows show the corresponding size class in 2005. The grey shading indicates individuals that remained in the same size class over the 22 year period. Note that individuals can move more than one size class over the 22 year time period. For example, of the 4.2 stems ha^{-1} in 1983 that started out in the 61-70 cm DBH size class, 0.6 stems ha^{-1} are still in the 61-70 cm DBH size class, 1.4 stems ha^{-1} moved into the 71-80 cm DBH size class and 1.5 stems ha^{-1} moved into the >80 cm DBH size class (Table 1a). The corresponding transition matrix probabilities are 0.15, 0.32, and 0.35, respectively (Table 1b).

Total survivorship of individuals in a given size class is represented as the column sum, which is subtracted from one to get mortality. Thus, for individuals in the 61-70 cm DBH size class, survivorship over 22 years is 82% (i.e., 0.15 + 0.32 + 0.35 = 0.82), and mortality is 18% (i.e., 1-0.82 = 0.18). Mortality does not start to occur until trees are >60 cm DBH. However, percent mortality data derived from yield table data for non-thinned Scots pine planted with different initial spacing (0.9, 1.4, 1.8, 2.0, 2.4, 3.0 m) in a range of yield classes (YC 4, 6, and 8) indicate that mortality starts in the 11-20 cm DBH size class. Therefore, the probability values in the transition matrix were adjusted to account for 2.7, 7.5, and 6.7 % mortality in size classes 11-20, 21-30, and 31-40 cm DBH based on the yield table data. As the yield table data is based on commercial stands it did not extend into the larger diameter. Therefore, size-related mortality in the 41-50 and 51-60 cm DBH size classes was based on a weighted mean of the adjacent size classes. This mortality is in addition to density-dependent mortality resulting from competition between individuals, and is discussed later.

Recruitment and deer management

Destructive sampling captured regeneration dynamics of trees that successfully transitioned from seedling to sapling to tree. Therefore, the size class transition times and growth rates do not account for individuals that failed to grow into the smallest inventoried tree class as a result of poor light conditions or heavy deer browsing. Estimates of seedling and sapling mortality were based on repeat measurement surveys at Black Wood of Rannoch in 1994 and 2005. The 1983 data was excluded due to lack of DBH and height data for undersized individuals. Over the 11 year period 3.4 to 14.3% were still seedlings, 19.4 to 50.0% had transitioned to saplings, 11.9 to 28.4% had transitioned to trees, and the remaining 20.6 to 43.3% had died in the four plots (Edwards, C. unpublished data). Therefore, seedling mortality over a 22 year period (1983 to 2005) was estimated at 50% in stands undergoing stem exclusion and 48% in stands entering the understorey reinitiation phase. Seedlings that did not enter the system after two iterative runs (i.e., 44 years) were "killed", as seedlings were not found older than this. Survey data and yield tables support the case for zero mortality of individuals in the sapling and smallest tree size class (7-10 cm DBH). However, all saplings were killed 100 years after the first entered the system, since no saplings older than this were recorded in the field.

Stand dynamics models were run for three management scenarios: (a) deer pressure prevents regeneration, (b) regeneration set at optimum condition based on commercial planting, (c) natural regeneration from release of current seedling and sapling bank and rates expected based on stand basal areas. Scenario (a) assumes that deer browsing prevent seedlings from transitioning to saplings (i.e., 0% survivorship), in reality, a small proportion of the seedlings may escape browsing pressure by growing in protective sites such as gorse thickets. Commercial planting (b) was set to 1100 stems ha^{-1}, which represents the minimum density required to qualify for a regeneration grant. The abundance of natural regeneration in relation to current stand conditions was based on the average density of seedlings and saplings recorded in the 2005 survey for the two stand dynamics phases.

Published studies indicate that scots pine seedling growth only occurred at a basal area below a 25 m^2 ha^{-1} threshold (Mason *et al*., 2004a & b; Hale *et al*., 2004), however more recent studies in the Black Wood of Rannoch with natural regeneration suggests the threshold should be nearer to 20 m^2 ha^{-1} (Edwards, In Prep). Mean seedling densities dropped dramatically as basal area exceeded this threshold at Glen Affric and Ballochbuie. For example, stands in Ballochbuie with basal area of 10.1 to 20 m^2 ha^{-1} had mean seedling density of 778.5 stems ha^{-1}, while seedling density was reduced by two-thirds to 276.7 stems ha^{-1} for stands with basal areas of 20.1 to 30 m^2 ha^{-1} (Edwards and Duncan, 2006). The following mean seedling densities of 432, 377, and 508 stems ha^{-1} were used to populate natural regeneration when stands reached critical basal areas of 0, 0.1-10, and 10.1-20 m^2 ha^{-1}, respectively.

Table 1. Transition frequency table (a) and corresponding transition matrix (b) for stands entering the understorey reinitiation phase in the Black Wood of Rannoch. Grey shading indicates individuals that remained in the same size class during the 22 year measurement period from 1987 to 2005.

(a)

		Size class in 1983										
		<7[a]	7-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	>80	∑
Size class in 2005	<7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	7-10	13.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	18.6
	11-20	24.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	47.7
	21-30	15.4	0.0	5.7	1.9	0.0	0.0	0.0	0.0	0.0	0.0	67.8
	31-40	0.7	0.0	2.8	3.7	2.5	0.0	0.0	0.0	0.0	0.0	31.6
	41-50	0.0	0.0	5.1	4.8	3.7	5.5	0.0	0.0	0.0	0.0	24.0
	51-60	0.0	0.0	0.7	5.1	0.7	4.4	4.9	0.0	0.0	0.0	18.1
	61-70	0.0	0.0	0.0	0.0	0.6	3.7	3.7	0.6	0.0	0.0	10.1
	71-80	0.0	0.0	0.0	0.0	0.0	0.0	0.7	1.4	0.0	0.0	2.1
	>80	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5	0.6	0.6	2.7
	Dead	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.7	0.7	2.2
	∑	**54.3**	**0.0**	**14.4**	**15.5**	**7.5**	**13.7**	**9.4**	**4.2**	**1.4**	**1.4**	**224.8**

Note: *Number of stems per hectare by size class for individuals that were present in the 1983 survey and had transitioned into the smallest tree class (7-10 cm DBH) by the 2005 survey.*

[a] DBH and heights were not recorded for individuals with <7 cm DBH in 1983 so seedlings and saplings can not be distinguish.

(b)

$$\begin{bmatrix}
0.00 & R_{7\text{-}10} & R_{11\text{-}20} & R_{21\text{-}30} & R_{31\text{-}40} & R_{41\text{-}50} & R_{51\text{-}60} & R_{61\text{-}70} & R_{71\text{-}80} & R_{>80} \\
0.25 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 \\
0.45 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 \\
0.28 & 0.00 & 0.39 & 0.12 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 \\
0.01 & 0.00 & 0.20 & 0.24 & 0.33 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 \\
0.00 & 0.00 & 0.36 & 0.31 & 0.49 & 0.41 & 0.00 & 0.00 & 0.00 & 0.00 \\
0.00 & 0.00 & 0.05 & 0.33 & 0.10 & 0.32 & 0.53 & 0.00 & 0.00 & 0.00 \\
0.00 & 0.00 & 0.00 & 0.00 & 0.08 & 0.27 & 0.39 & 0.15 & 0.00 & 0.00 \\
0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.08 & 0.32 & 0.00 & 0.00 \\
0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.35 & 0.46 & 0.46
\end{bmatrix}$$

Note: Recruitment (R) from seed trees in each size class.

Estimation of density-dependent mortality (self-thinning line)

Density-induced mortality or self-thinning is the result of competition between the individuals of a stand, which takes place if one or more of the resources (e.g., light) needed for tree development is insufficient for the needs of individuals and the stand as a whole (Rio *et al*., 2001). In this study the self-thinning line is expressed as the relationship between the stem density and square mean diameter (Reineke expression) on a double logarithmic scale (Reineke, 1933). Data from long-term studies in native pinewoods and yield data from unthinned Scots pine commercial plantations were used to estimate the slope of the self-thinning line (Figure 2).

At high stem densities (>6.35 ln stems ha^{-1}) native pinewoods and commercial plantations achieve similar mean quadratic DBH shown by self-thinning line 1 on Figure 2. However, the majority of the pinewoods occur below the commercial maximum density line, particularly stands with large diameter trees (>4.0 ln DBH). Hence, a second self-thinning line based on the upper limit of native pinewoods was adopted shown as self-thinning line 2 on Figure 2. The self-thinning lines were to keep the stand projections within bounds. It has been suggested that the self-thinning line in natural stands diverges from the straight line found in plantations. Only limited data exists on density dependency in native pinewoods for Scotland, therefore the assumptions made in this report need further study ensure their consistency across different site types and stand conditions.

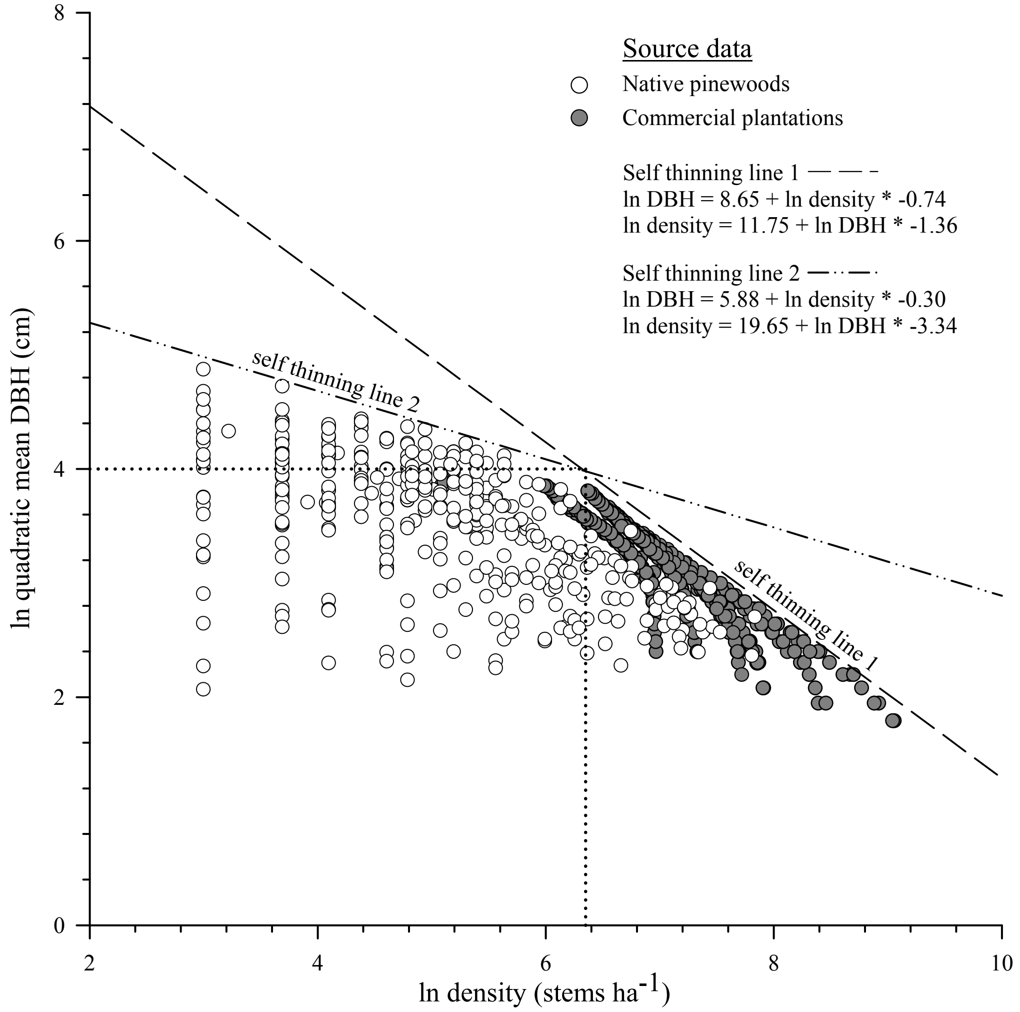

Figure 2. Self thinning lines (upper limit of stand density) based on long-term permanent sample plot data in native pinewoods across Scotland (Black Wood of Rannoch, Kinveachy, Ballochbuie, Glen Affric, Glen Garry, and Glenmore) and yield table data for 17 to 102 year old commercial unthinned Scots pine stands planted with different initial spacing (0.9, 1.4, 1.8, 2.0, 2.4, 3.0 m) in a range of yield classes (YC 4, 6, 8, 10, 12, 14). Density-dependent mortality in native pinewoods with large diameters (>4.0 cm ln DBH) is represented by self thinning line 2 as maximum densities inferred by self thinning line 1 from commercial stands are not attained.

Estimating crown closure – an indicator of pinewood loss

The degree of tree canopy cover is used to distinguish open habitats, such as grassland with scattered trees, from woodland habitat on ordnance survey maps. Therefore, once canopy cover opens up to below the minimum requirement, i.e. 20% cover (FC), the habitat will no longer be categorised as woodland and therefore the pinewood is effectively lost from the landscape. Crown dimensions and DBH data were available for 204 Scots pine ≥60 year old in Black Wood of Rannoch. DBH was significantly positively correlated with crown radius, and explained 81% of the variability of crown radius. Crown radius was calculated for the mid-value of each DBH size classes (i.e., mid-value of 10-21 cm DBH size class is 15.5 cm) using the following equation:

[Eq 1] $$\textbf{Crown radius} = 0.352 + 0.0691 * \textbf{DBH}$$

Size class frequency data generated by the projection model was multiplied by crown radius for each size class, and summed across the stand to get percent stand canopy cover levels assuming that tree crowns do not overlap. Canopy cover timeline graphs were plotted to estimate time required for a stand to pass below the minimum canopy cover threshold assuming continued deer browsing pressure prevents regeneration.

Statistical analysis

A range of shape and properties of the DBH distribution were calculated to examine the effect of different management scenarios on stand projections over 50, 100, and 150 years. Distributions were assumed to conform to the Weibull distribution, and mean, median, and range calculated. Lorenz curves, Shannon H, and the Gigi coefficient were calculated as described by Rouvinen and Kuuluvainen (2005) to examine differences in the shape of the distribution. In order to deduce how long it takes the stand to deteriorate under continued deer browsing pressure, stand projections were run for 300 years. A backward iterative process could then be used to determine how many seedlings need to be recruited to ensure tree reaches a given size class, to make the case for a one to one replacement.

5. Results

Regeneration dynamics

Trees that successfully transition from seedlings to saplings to trees take on average 52 years and 48 years to grow into the lowest inventoried size class (7 cm DBH) in Black Wood of Rannoch and Glen Affric, respectively (Table 2). Growth rates at DBH and time for a seedling to transition to a sapling varied by site conditions, which could be a function of light conditions and deer damage intensity (Table 2). Figure 3 compares growth curves (broken lines) from this study with published data from commercial plantations and natural regeneration in favourable and unfavourable conditions (solid lines). Regeneration dynamics were affected by site conditions, with trees growing in open conditions beneath overhead pylons attaining growth curves similar to commercial plantations for Black Wood of Rannoch (Figure 3a). At Glen Affric, trees located on steep eroding slopes in open conditions by roadsides achieved faster growth rates than commercial plantations (Figure 3b).

Effect of management on 50 year stand projections in Black Wood of Rannoch

Current DBH distribution depict a unimodal population with a modal DBH of 41-50 cm for both stand dynamics phases and a high proportion (44%) of stems with DBH >50 cm DBH (Figure 4a, 4e). Stands in the understorey reinitiation phase have lower basal areas (14.4 versus 26.3 m^2 ha^{-1}) and a higher density of natural regeneration (163.2 versus 41.4 stems ha^{-1} for seedlings and saplings combined) than stands in the stem exclusion phase. Small trees (7 to 10 cm DBH) are absent from both stand types indicating that deer browsing pressure is preventing the transition of natural regeneration into the tree population. Stand projections based on model parameters described in Table 3 were run at 22 year increments from 2005 up to 2049 to examine the response of the DBH distribution to three management scenarios. Continued deer browsing pressure prevents the influx of natural regeneration resulting in stands with a higher proportion of large individuals (Figure 4b, 4f). Deer exclusion permits the establishment of currently existing natural regeneration, however, due to low light levels this results in only minor changes to the DBH structure for stands in the stem exclusion phase (Figure 4c). Commercial planting dramatically changes the DBH structure, shifting the modal size class from 41-50 cm DBH in 2005 to 7-10 cm DBH in 2049, and a corresponding two-fold decrease in the proportion of stems >50 cm DBH to produce a bimodal population for stands in the understorey reinitiation stand (Figure 4d). Transition rates through the smaller size classes was slower for stands in the stem exclusion phase as values were based on trees that grew in overstorey conditions (Tables 2 and 3). Projected stands were beneath the maximum stand density line depicted in Figure 2.

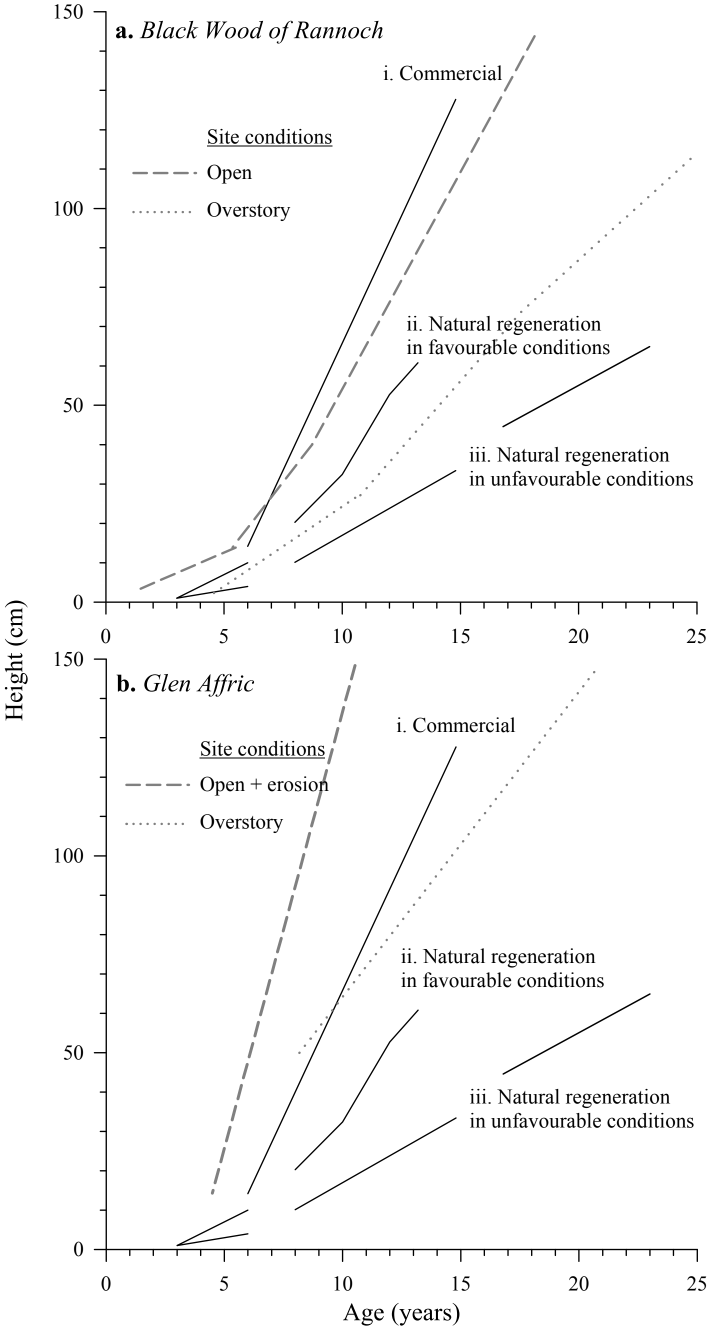

Figure 3. Comparison of results from the Black Wood of Rannoch (a) and Glen Affric (b) from this study to published Scots pine growth curves (i, ii, iii). Modified from Scott et al. (2000).

Table 2. Regeneration dynamics of saplings that successfully transitioned to trees based on height – diameter –age profiles for destructively sampled Scots pine and birch from the Black Wood of Rannoch and Glen Affric.

			DBH (cm)[a]		Growth	Time in years to reach[c]				Deer damage
Species	**Site conditions**	**N**	**Mean± SE**	**min - max**	**(mm/yr)[b]**	**1.3 m height**	**7 cm DBH**	**10 cm DBH**	**20 cm DBH**	**intensity[d]**
a. Black Wood of Rannoch										
Scots pine	Open[e]	15	30.2±2.6	13.3 - 42.8	1.6±0.1	17.1±1.2	42.8±2.8	53.6±3.6	89.4± 6.5	0.7±0.3
	Canopy gap	7	24.1±3.9	9.2 - 39.4	1.3±0.2	22.3±2.0	52.5±4.2	65.4±5.6	108.5±10.8	4.4±0.7
	Canopy edge	2	19.7±6.0	13.8 - 25.7	0.8±0.2	17.5±3.5	60.7±4.3	79.2±7.6	140.8±18.6	3.0±1.0
	Overstory	6	37.0±5.8	23.3 - 60.1	0.9±0.1	28.2±4.8	70.3±6.9	88.3±8.0	148.5±11.7	4.0±0.5
	All	30	29.5±2.1	9.2 - 60.1	1.3±0.1	20.8±1.4	51.7±2.9	65.0±3.7	109.1± 6.4	2.4±0.4
Birch	Canopy gap	1	60	--	1.7	16	37	46	76	--
b. Glen Affric[f]										
Scots pine	Open + erosion[g]	4	26.5±4.4	17.5 - 37.8	2.9±0.4	10.5±0.6	23.7±2.3	29.3±3.4	48.1±7.3	--
	Open[e]	2	24.1±5.6	18.5 - 29.7	1.1±0.1	21.5±7.5	54.3±10.6	68.4±11.9	115.3±16.2	--
	Overstory	4	38.3±5.8	22.3 - 48.5	1.9±1.2	26.3±4.5	68.9±10.1	87.2±16.2	148.1±36.7	--
	All	10	30.8±3.5	17.5 - 48.5	2.1±0.5	19.0±3.1	47.9±8.0	60.3±10.8	101.6±20.5	--
Birch	Open[e]	2	24.5±4.4	20.1 - 28.9	0.8±0.1	10.5±2.5	55.7±7.6	75.1±9.7	139.7±16.9	--
	Overstory	4	34.3±5.2	19.7 - 43.7	0.7±0.1	10.3±4.3	60.3±7.1	81.8±9.6	153.4±18.9	--
	All	6	31.0±4.0	19.7 - 43.7	0.8±0.1	10.3±2.8	58.8±5.0	79.6±6.7	148.8±13.1	--

[a] DBH of destructively sampled trees

[b] Growth rate calculated as (DBH / 2) / number rings at DBH

[c] DBH sections aged relative to root collar, additional time for projected growth at DBH calculated as (growth rate in mm/yr * 2) * diameter in mm

[d] Number of sections between root collar and 1.3 m height with signs of deer damage (i.e., exposed wood, disrupted annual rings)

[e] Woodlands bisected by overhead power lines (pylons)

[f] Growth rate and time in years to reach given height – DBH were based on sections taken at 1.5 m for Glen Affric, hence values slightly overestimate time to reach 1.3 m and are not directly comparable to data from Black Wood of Rannoch

[g] Growing on eroded steep slope >10 m from roadside

Table 3. Model parameters and transition matrix used for pinewood stand projections.

(a) Model parameters

Study area	Transition phases (years)[a]		Transition matrix[e]
	Seedling	Sapling	
Black Wood of Rannoch			
i. Stem exclusion	28[b]	42[b]	A
ii. Understorey reinitiation	19[c]	28[c]	B
Glen Derry, Mar Lodge			
i. pinewood with trees	19[c]	28[c]	B
ii. pinewood matrix (trees and open areas)	19[c]	28[c]	B
Ballochbuie			
i. Continuous cover	19[c]	28[c]	B
ii. Fragmented lowland	19[c]	28[c]	B
iii. Fragmented upland	42[d]	98[d]	B

[a] *Time required for an individual to transition through a phase based on destructive sampling of Scots pine at Black Wood of Rannoch.*

[b] *Transition phase based on Scots pine growing in overstorey conditions*

[c] *Transition phase based on Scots pine growing in open or canopy gap conditions*

[d] *Transition phase extrapolated from Scots pine growing in unfavourable conditions (Scott et al. 2000)*

[e] *Transition matrix for trees (DBH ≥7 cm) based on modified data from Black Wood of Rannoch*

(b) Transition matrix A

$$\begin{bmatrix}
0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 \\
0.70 & 0.28 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 \\
0.00 & 0.37 & 0.44 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 \\
0.00 & 0.19 & 0.36 & 0.49 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 \\
0.00 & 0.00 & 0.12 & 0.32 & 0.54 & 0.00 & 0.00 & 0.00 & 0.00 \\
0.00 & 0.00 & 0.00 & 0.05 & 0.22 & 0.78 & 0.00 & 0.00 & 0.00 \\
0.00 & 0.00 & 0.00 & 0.02 & 0.15 & 0.15 & 0.45 & 0.00 & 0.00 \\
0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.40 & 0.93 & 0.00 \\
0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.09 & 0.00 & 0.93
\end{bmatrix}$$

Note: *DBH classes: 7-10, 11-20, 21-30, 31-40, 41-50, 51-60, 61-70, 71-80, and 81-120 cm. Based on modified frequency data for stands in stem exclusion phase at the Black Wood of Rannoch*

(c) Transition matrix B

$$\begin{bmatrix}
0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 \\
1.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 \\
0.00 & 0.38 & 0.11 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 \\
0.00 & 0.19 & 0.22 & 0.31 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 \\
0.00 & 0.35 & 0.29 & 0.46 & 0.37 & 0.00 & 0.00 & 0.00 & 0.00 \\
0.00 & 0.05 & 0.31 & 0.09 & 0.29 & 0.45 & 0.00 & 0.00 & 0.00 \\
0.00 & 0.00 & 0.00 & 0.08 & 0.24 & 0.34 & 0.15 & 0.00 & 0.00 \\
0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.07 & 0.32 & 0.00 & 0.00 \\
0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.35 & 0.46 & 0.46
\end{bmatrix}$$

Note: *DBH classes: 7-10, 11-20, 21-30, 31-40, 41-50, 51-60, 61-70, 71-80, and 81-120 cm. Based on modified frequency data for stands entering understorey reinitiation phase at the Black Wood of Rannoch*

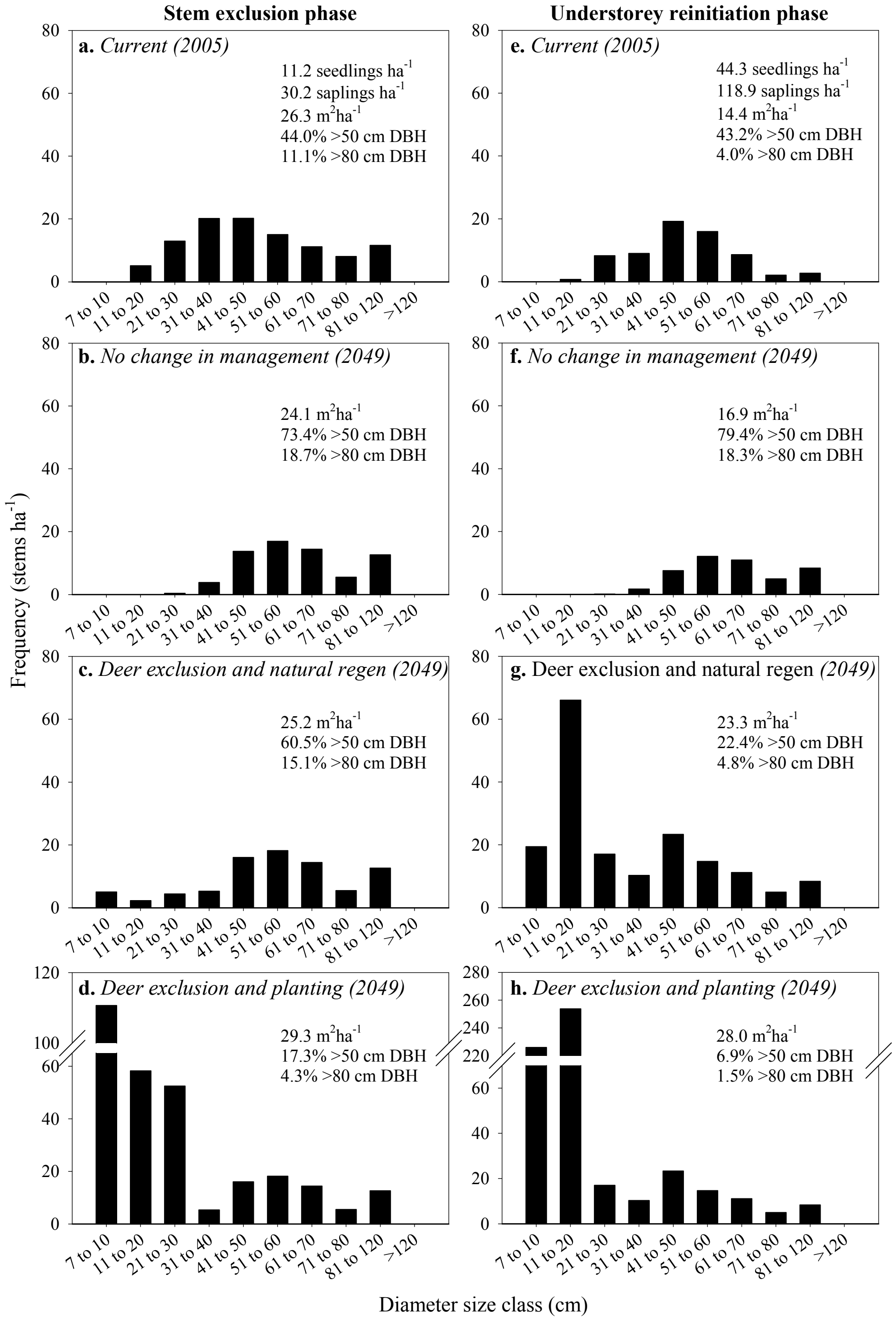

Figure 4. Current (2005) and projected (2049) diameter distribution under three different management scenarios based on stands in the stem exclusion phase (a to d) and understorey reinitiation phase (e to h) in Black Wood of Rannoch. See Table 3 for model parameter Current (2005) and projected (2049) diameter distribution under three different management scenarios based on stands in the stem exclusion phase (a to d) and understorey reinitiation phase (e to h) in Black Wood of Rannoch. See Table 3 for model parameters.

The current parameterised transition matrix was used for long-term projections of stand development in Black Wood of Rannoch assuming continued deer browsing pressure. The outputs suggested the eventual collapse of stand structure if no further regeneration was to be recruited. Stands in the Understorey Reinitiation phase are already below the critical threshold (BA <20 m^2 ha^{-1}) at which regeneration would be expected to enter the system (Figure 5a). Stands in the Stem Exclusion phase drop below the critical threshold (BA <20 m^2 ha^{-1}) after only a further 66 years (Figure 6a). Basal area drops to 10 m^2 ha^{-1} after 110 years in stands in the stem exclusion phase and 100 years for stands entering understorey reinitiation (Figure 5a, 6a). The corresponding DBH distributions show a left skewed distribution with a modal DBH class of 81-120 cm DBH (Figure 5e, 6e). Projected stands are beneath the maximum density line (Figure 57b, 6b) and diminish to zero basal area after ~300 years. Thus, unless intervention occurs, the pinewood habitat will be lacking small trees up to 30 cm dbh within 50 years; will consist only of low density large dbh trees in 100 years, and will entirely lost in less than 300 years.

Understorey reinitiation phase, Black Wood of Rannoch

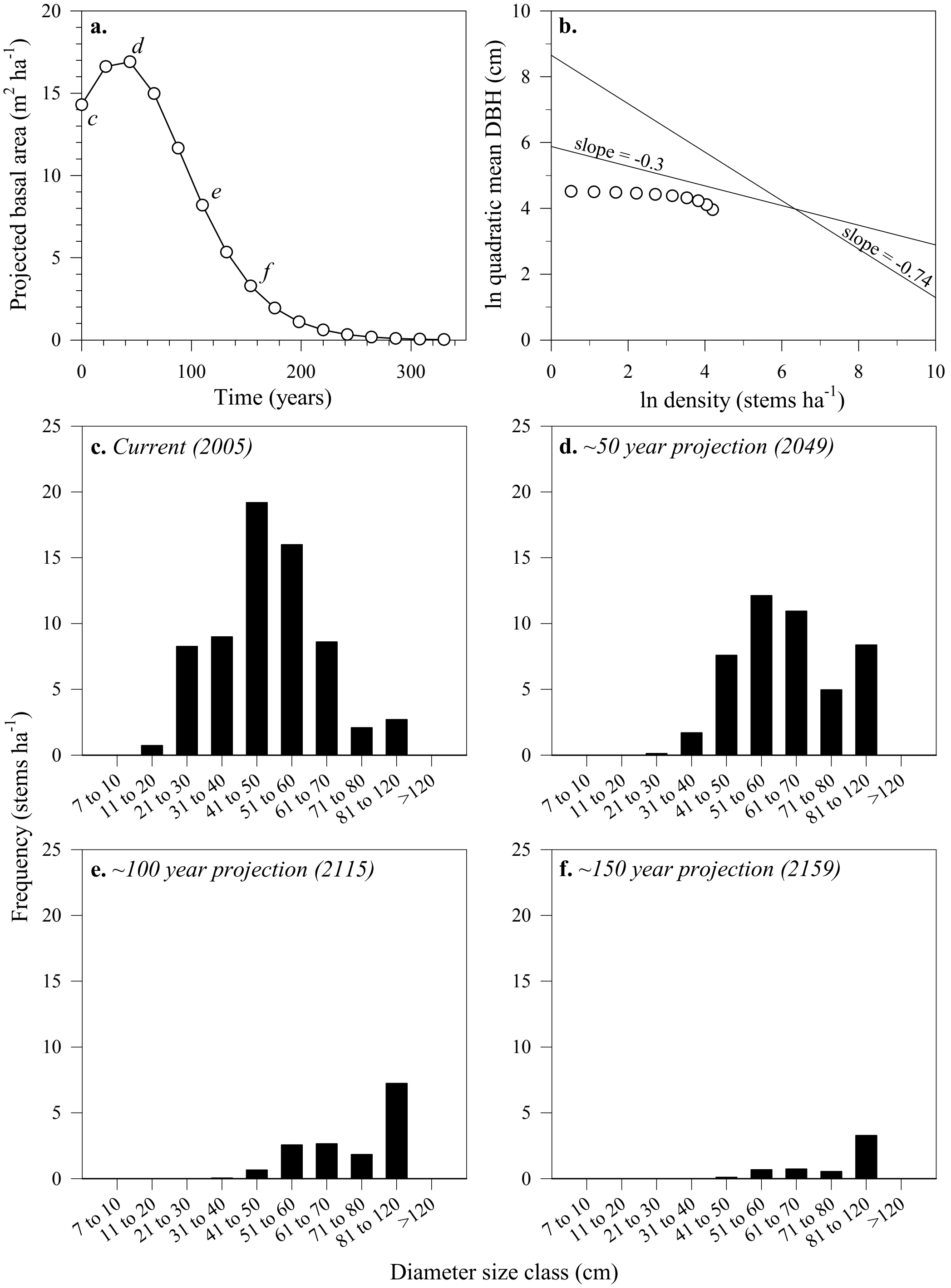

Figure 5. Projected stand development with continued deer browsing pressure over 300 years based on stands entering the understorey reinitiation phase at Black Wood of Rannoch. Self-thinning occurs when stands are above the maximum density line (b). Letters on (a) refer to current (c) and projected diameter distributions at 50 years (d), 100 years (e) and 150 years (f).

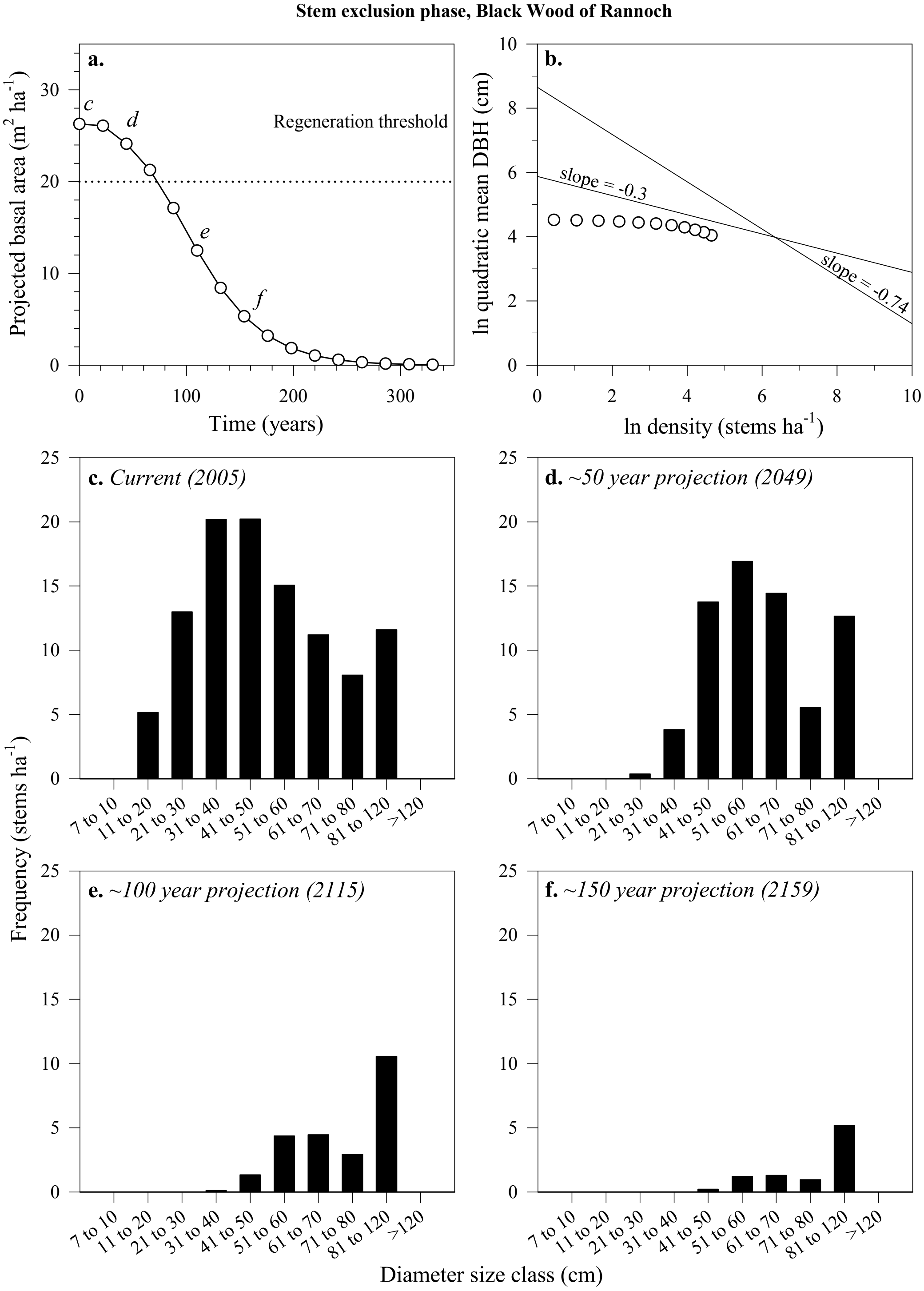
Stem exclusion phase, Black Wood of Rannoch

Figure 6. Projected stand development with continued deer browsing pressure over 300 years for stands in the stem exclusion phase at Black Wood of Rannoch. Self-thinning occurs when stands are above the maximum density line (b). Letters on (a) refer to current (c) and projected diameter distributions at 50 years (d), 100 years (e) and 150 years (f).

6. Use of the Model on extensive stands

Data sets from two baseline Stand Structure Surveys were available to test the assumptions of the model and the outputs generated by it. Ballochbuie pinewood (Edwards and Duncan, 2006) and Mar Lodge pinewood (Edwards and Davies, 2008) were both investigated under published joint-working guidelines (Figures 7 & 8).

Ballochbuie Caledonian Pinewood

In Ballochbuie pinewood tree'd areas with continuous cover occurred in the core region of the pinewood, while fragmented areas (open ground or canopy cover ≤20%) occurred on the pinewood margins. Stand projections varied greatly by scenario, with future loss of woodland predicted at ~200 years for continuous cover areas (Figure 9b), and in the current year for fragmented uplands (Figure 10b). Natural regeneration shown by the white bars, could contribute between 53 and 107 seedlings ha^{-1} if deer populations are controlled (Figure 9c, 10c). As it takes ~100 years for regeneration to reach the 20% canopy cover threshold, established regeneration needs to be in place 100 years before the current canopy trees deteriorate. However, even an influx of regeneration will not bring canopy cover above the woodland threshold in the fragmented uplands (Figure 10b). In such conditions, commercial planting would be the only means of restoring the habitat.

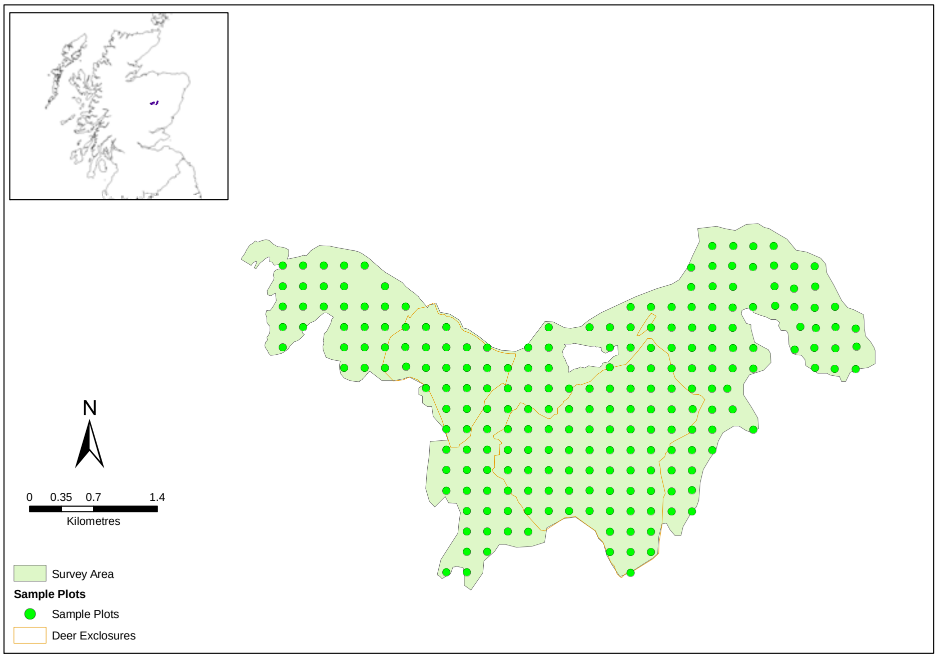

Figure 7. Location of stand structure sample plots in the Ballochbuie native pinewood.

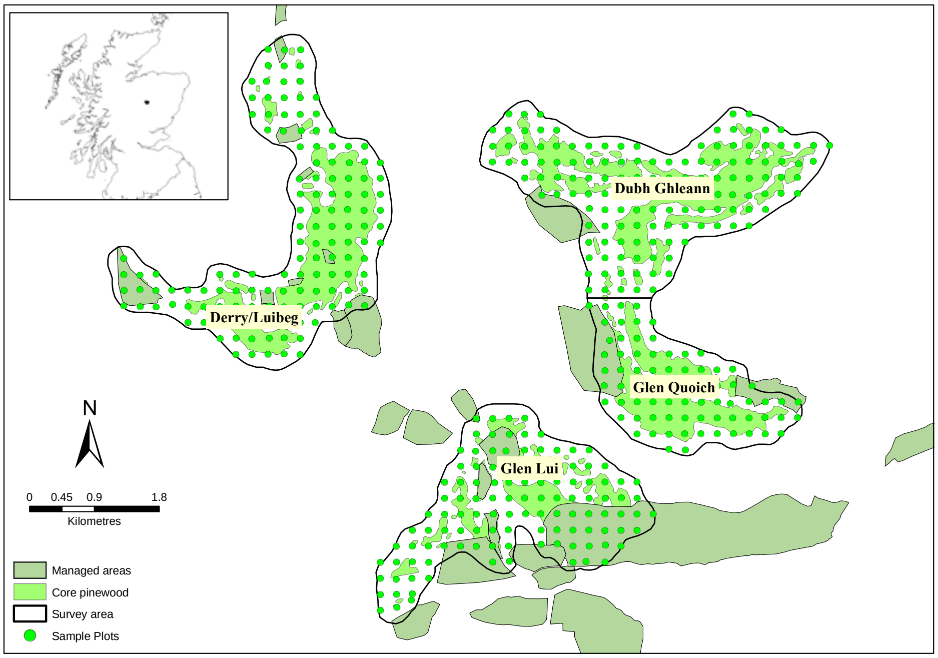

Figure 8. Location of sample plots and geographic sample regions in Mar Lodge native pinewood.

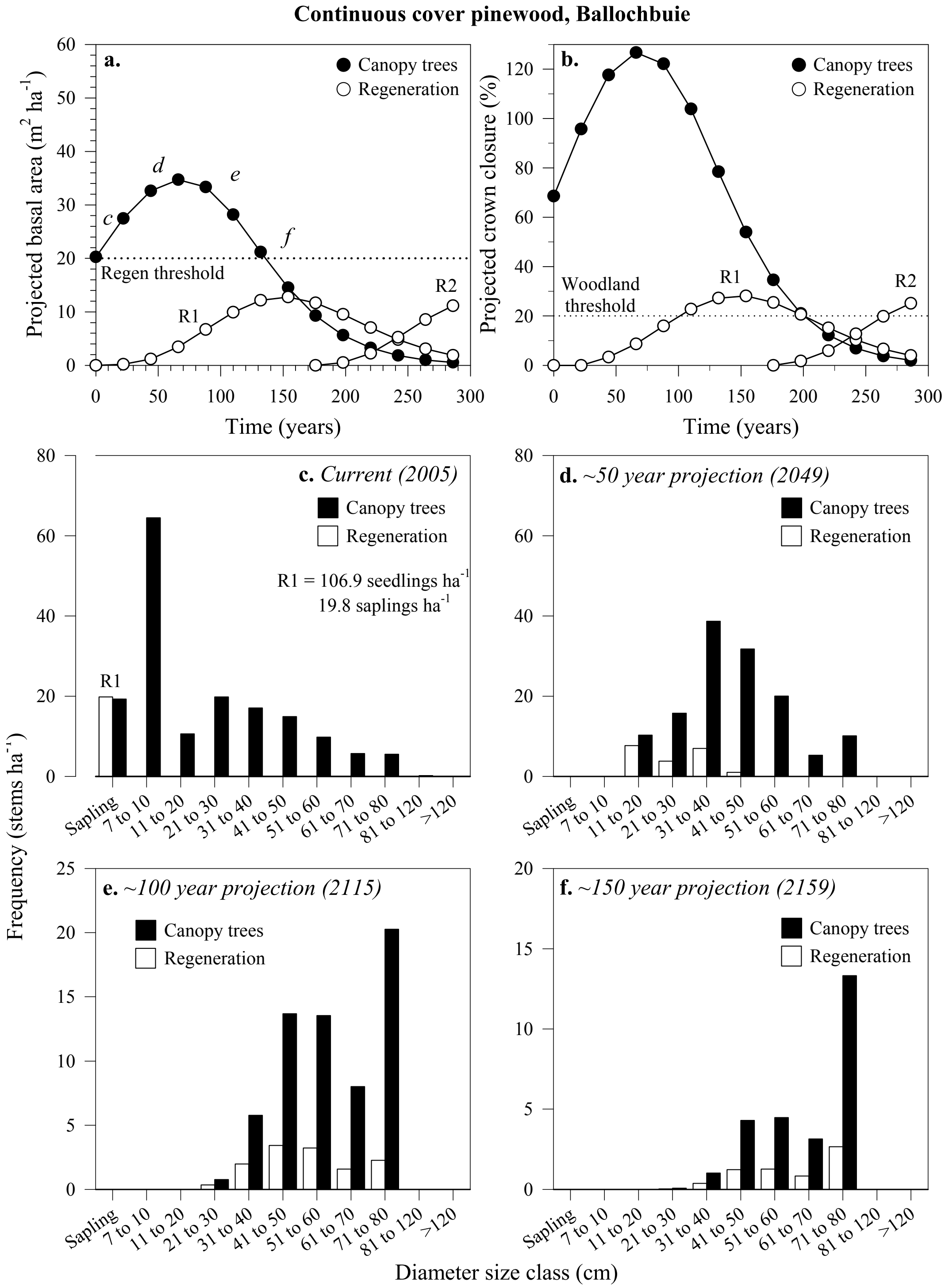

Figure 9. Model outputs for the lower altitude 'low risk' stands in part of Ballochbuie pinewood. Top graphs (a, and b) indicate the change in stand basal area, and predicted percentage canopy cover over a 300 year period from 2005. Lower graphs (c to f) show the current and predicted dbh distributions.

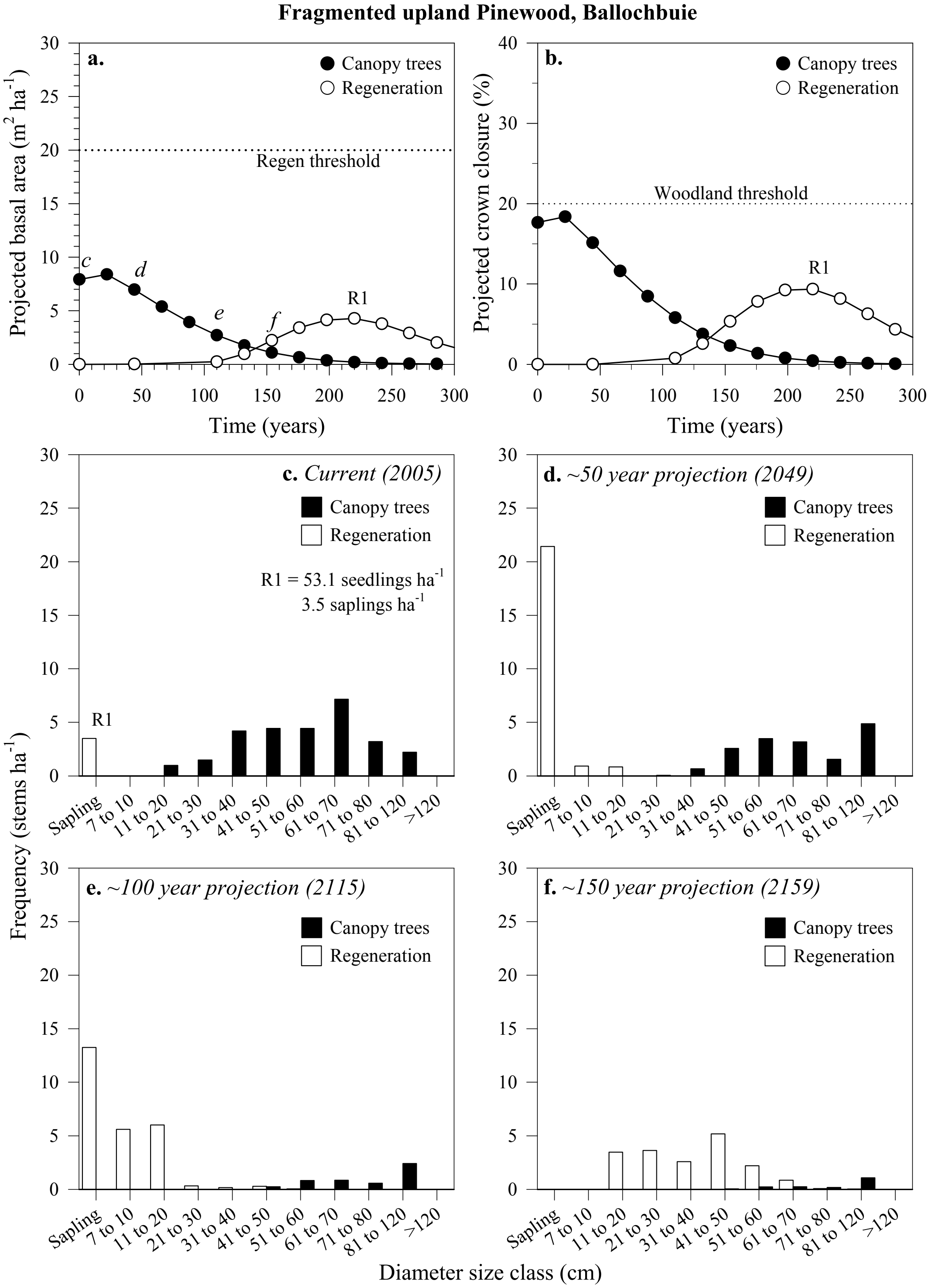

Figure 10. Model outputs for the upper altitude 'at risk' stands in part of Ballochbuie pinewood. Top graphs (a, and b) indicate the change in stand basal area, and predicted percentage canopy cover over a 300 year period from 2005. Lower graphs (c to f) show the current and predicted dbh distributions.

Tree'd areas were confined to the core regions of the Caledonian pinewood, and an open matrix occurred around the periphery (Figure 8). Current dbh-distributions have a bimodal distribution (Figures 11c & 13c), with a peak in the 7 to 10 cm size class for the Dubh Ghleann area of the pinewood (Figure 12c) and peak in 11 to 20 cm size class for the pinewood matrix as a whole (not shown). Long-term projections of stand development based on parameters derived from Black Wood of Rannoch (Table 3) suggest that stands fail to meet the 20% canopy cover requirement for woodland classification currently. Complete woodland loss is predicted to occur between 200 – 220 years, although low density woodland (i.e. < 10 trees ha^{-1}) will occur within 80 years (Figures 11 – 13). Projecting future distributions is irrelevant I these circumstances. Incorporating the very low levels of natural regeneration, currently just 44.1 seedlings ha^{-1} recorded, did not ameliorate future stand deterioration, since the density of regenerating tree seedlings does not reach the 20% critical canopy cover threshold. It is likely that the current seedling and sapling densities under-represent the potential natural regeneration of the site, since the pulse of small trees indicate that regeneration can successfully establish within the stand given adequate protection from browsing (Edwards, 2008). Future stand projections demonstrate a shift in the population from small to large dbh sizes, by 150 years 60% of the population is in the top 20% of the DBH size classes. Mean DBH increases over time from a current value of 22.5 cm to 79.2 cm in 150 years.

Pinewood matrix, Core Pinewood, Mar Lodge

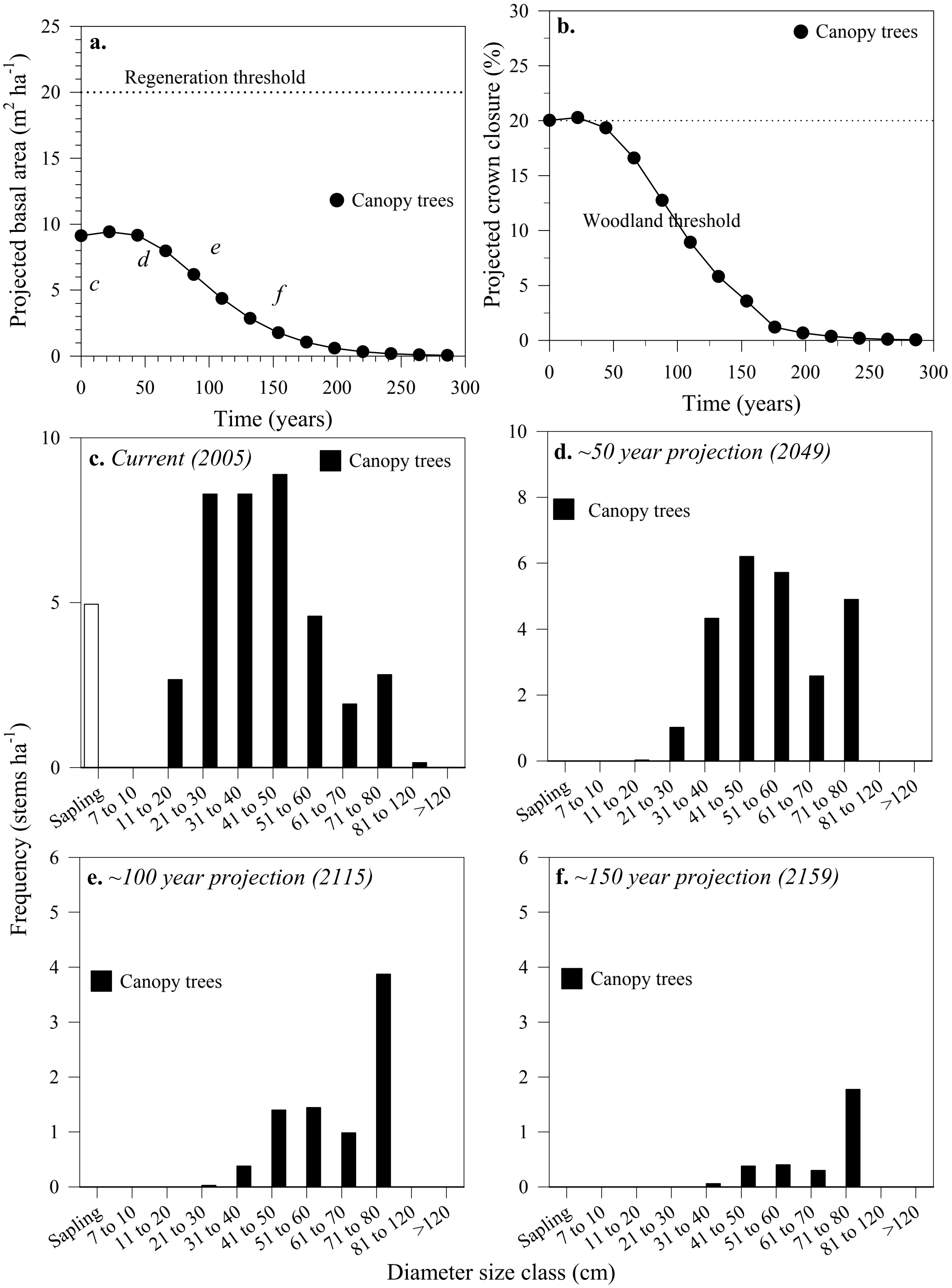

Figure 11. Model outputs for the core pinewood area of Mar Lodge. Top graphs (a, and b) indicate the change in stand basal area, and predicted percentage canopy cover over a 300 year period from 2005. Lower graphs (c to f) show the current and predicted dbh distributions.

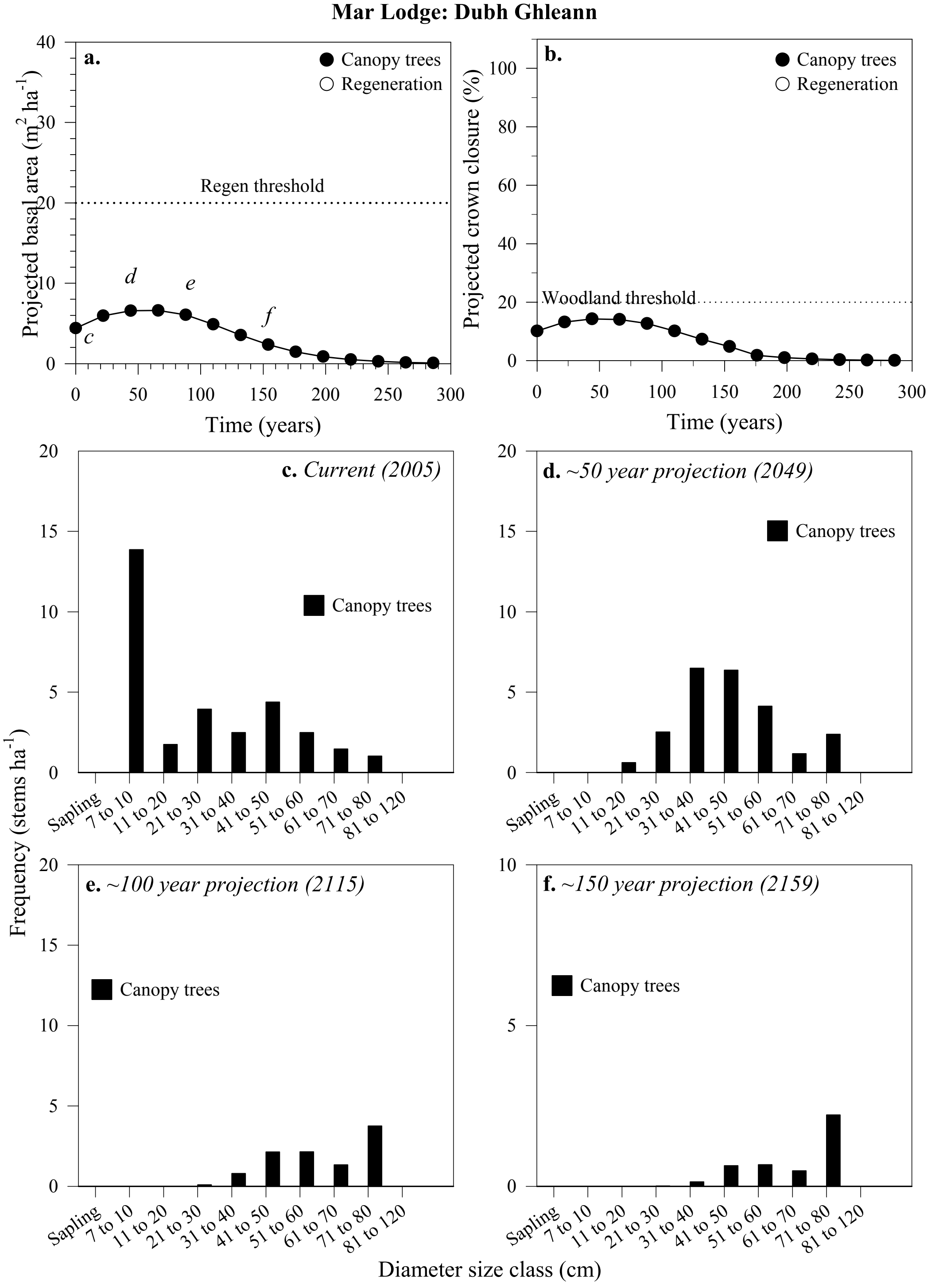

Figure 12. Model outputs for the Dubh Ghleann geographic area of Mar Lodge pinewood. Top graphs (a, and b) indicate the change in stand basal area, and predicted percentage canopy cover over a 300 year period from 2005. Lower graphs (c to f) show the current and predicted dbh distributions.

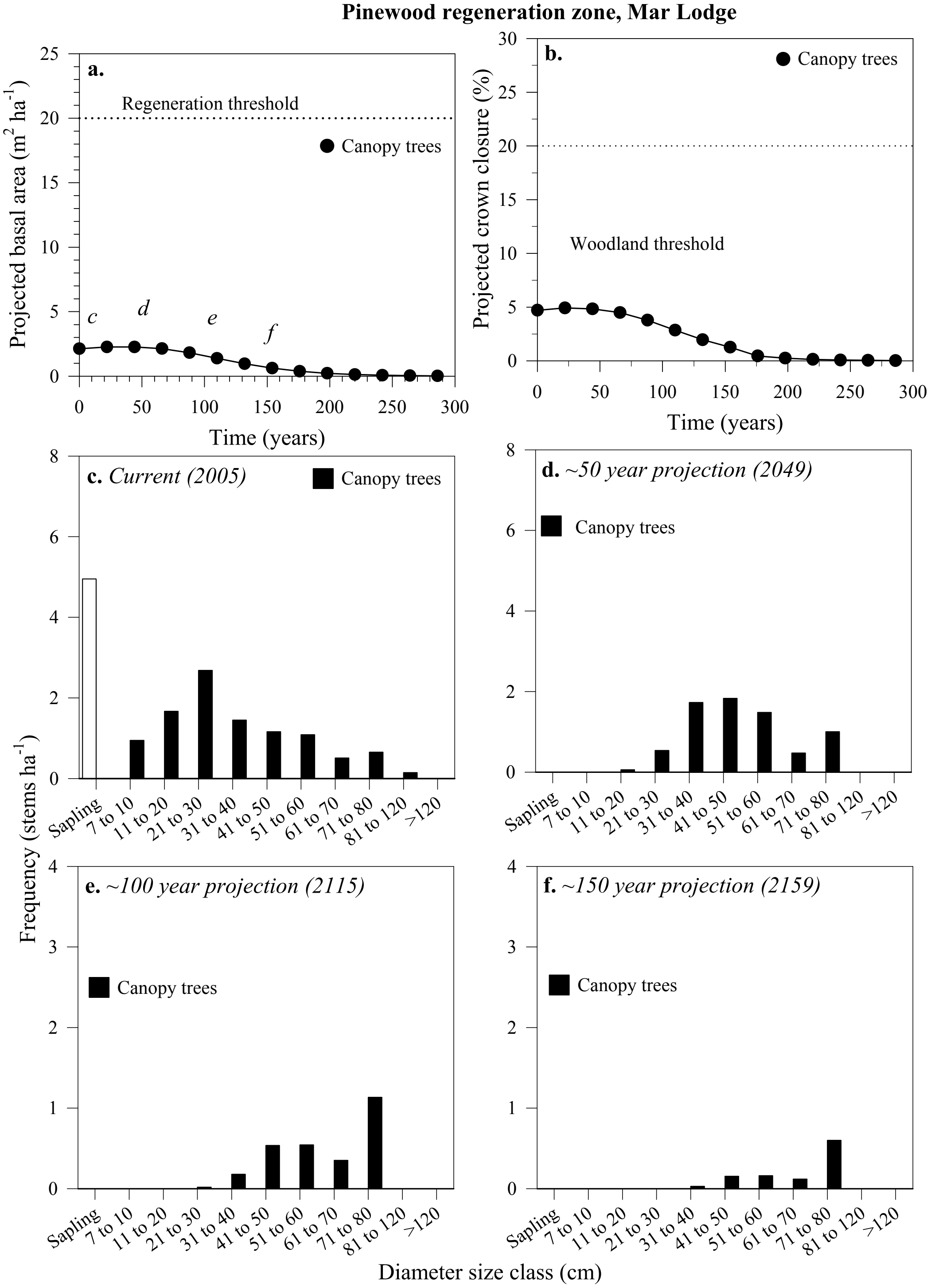

Figure 13. Model outputs for the regeneration zone in Mar Lodge pinewood. Top graphs (a, and b) indicate the change in stand basal area, and predicted percentage canopy cover over a 300 year period from 2005. Lower graphs (c to f) show the current and predicted dbh distributions.

7. Conclusions

Using the models to determine risk of Pinewood deterioration

It became clear when assessing the data from the two extensive stands, Ballochbuie and Mar Lodge that the model outputs were not realistic over the time periods reported. The final DBH distributions produced at year 50, 100 and 150 were identical in shape and proportion between dbh classes; and vary only in the number of trees represented in each class.

This occurred with all the data sets tested, irrespective of the starting distribution. The source of this irregularity appears to be a product of a number of faults within the current set of parameters being used. Above all it is due to the low number of data points used to populate the probability matrix for large trees (> 50 cm dbh), and because of the assumptions used to allocate mortality in larger dbh classes in the generation of future dbh distributions. The outcome is a set of non-random growth and mortality modifiers; which lead to the homogeneity of data predictions and is therefore of limited value for the purpose it was intended.

Although the current outputs are insufficient to be used on real sites, the general use of Matrix models is still sound. As seen in the short term Black Wood of Rannoch data, these do enable diameter distributions of pinewood stands to be projected under different management scenarios. If it is assumed that the future projected state of the woodland is significantly different from the current measured state of the woodland, i.e. there is no 1-for-1 continuation of the woodland, then deterioration can be said to occur. By incorporating the density of regeneration currently on the site into the regeneration model the effect of this recruitment on the future state can be also modelled. If sufficient regeneration is available to ensure that the distribution of current small diameter class trees are replaced by the regeneration as it grows in age, then it is likely that deterioration will be avoided (i.e. canopy cover will not fall below 20% the point at which the woodland can no longer be classified as woodland).

In circumstances where no natural regeneration is currently present, the effects of recruiting new regeneration on future site conditions can be predicted. This is achieved by modelling the effects off introducing either a single regeneration event, by planting, or by ensuring consistent conditions exist for continued low-level seedling recruitment. The Ballochbuie case study demonstrates that exclusion of deer may not be enough by itself to ensure survival of the pinewood (Figure 9). Pinewood degradation, such as establishment of a thick undergrowth of heather and/or increased wetness, may make conditions less favourable for seedling colonisation. Also, senescing canopy trees may not be producing viable seed. In such circumstances, planting is essential to ensure successful restoration of the pinewood.

It is also assumed that in a self sustaining pinewood that there will be a range of age classes to ensure replacement of each of the successional phases that naturally occur as growth and mortality affect the dynamics of the pinewood. There are published equations based on fire disturbance regimes that allow an estimate of the minimum area required in specified age classes to ensure the continued existence of various Old-Growth forests for any given disturbance cycle (Johnson *et al*, 1995; Seymour and Hunter, 1999). Assuming a disturbance return period of 150 years (equivalent to the average age at which Old Growth structures are believed to be reached in native pinewoods (Humphrey, 2003)), then the proportion of the forest expected to be in each growth phase (or equivalent DBH range) can be predicted.

One of the objectives not fully addressed in this project, was to '*Develop and apply criteria (including exploration of a 'phase approach' - i.e. areas at phase 1, 2 etc.) for identification of spatial temporal priority 'risk' areas (i.e. mapping areas where there is a need for regeneration within 10, 50, 100 years etc.)'* because the definitions to be used and criteria against which this process would be measured were not agreed upon by the steering group. During the development of parallel work on pinewood condition (Edwards and Davies, 2008) identifying at risk areas, to which the RISK model could be applied, used and refined the use of Successional Phases based on data collected during a Stand Structure Survey. The survey methodology is based on combining the procedure published in Forestry Commission Information Note 45 (Kerr *et al.*, 2002), with a modified tree crown scoring system based on the Assessment of Tree Condition (Innes, 1990). To make the assessments statistically viable circular plots, of adequate individual area to ensure that sufficient trees are located in each plot, are systematically distributed across the woodland area using ArcGIS to give a 1% sample of the total woodland area. This methodology allows the allocation of individual plots to one of seven phases (see Table 4) depending upon the relationship between tree density, tree size, basal area and the presence or absence of regeneration and deadwood. Overall the Successional Phase breakout can be used to determine the dynamics of the various stages and for these to be mapped. The RISK model, once a function version is available, should be applied to the plot data derived from the two degraded phases, Degraded Old Growth and Delayed Reinitiation. These are areas of the stand where it is argued regeneration recruitment has been limited by some external factor and by extension of this argument where regeneration is required before canopy tree mortality prevents the possibility of any natural seedling recruitment. Determining the probability of tree loss over a 50 year period (the period over which there is confidence the current RISK model could be applied) and comparison with the known rates of seedling growth and development, to the stage of being a tree with dbh > 10 cm) would indicate when the latest period of seedling establishment in these areas should be.

Table 4. Allocation of Structural phase, based on the relationship between tree density and seedling density. [1] Degraded old growth plots must either have fewer than 40 stems per hectare, or must have a maximum dbh ≥ 50 cm and > Dg, and must contain standing, fallen or torn stump deadwood. [2] Old growth plots must have a maximum dbh ≥ 50 cm and > Dg, and must contain standing, fallen or torn stump deadwood. [3] The transition from stand initiation to stem exclusion is characterised by changes in tree stocking density, mean tree size (Dg) and stand basal area. In this simplified scheme the role of Dg and BA is not quantified.

<table>
<tr><th colspan="2"></th><th colspan="4">Tree stocking density (stems per ha)</th></tr>
<tr><th colspan="2"></th><th>0</th><th>> 0, < 40</th><th>≥ 40, < 1,100</th><th>≥ 1,100</th></tr>
<tr><th rowspan="2">Seedling and sapling density (stems per ha)</th><th>< 100</th><td>Non-wooded</td><td>Degraded old growth</td><td>Delayed reinitiation
or
Degraded old growth[1]</td><td rowspan="2">Stem exclusion[3]</td></tr>
<tr><th>≥ 100</th><td colspan="2">Stand initiation</td><td>Understorey reinitiation
or
Old growth[2]</td></tr>
</table>

8. Future work

Additional tree diameter growth data sets and refinement of the mortality assumptions used in the current model are required before the model can be used with any confidence. Long-term data sets are also required to validate the outputs; ideally these should be stands that have not been subject to management interventions for a period of at least 50 years. Since all the available data sets were used to populate the transition matrix new data needs to be collected specifically for this purpose. It can come from two main sources; existing long-term monitoring stands or assessment of growth rates from increment cores. A number of additional long-term monitoring stands are available to assess if funding was available. The ability of these to generate growth data for the upper size-classes is not known, but it is assumed that only a relatively small proportion of these stands will have suitable large diameter trees measured over a sufficiently long period (ideally > 20 years).

Assessment of the available data from increment cores would generate growth data over the full range of dbh-classes required. If insufficient examples were available from current samples, additional trees of the required size could be sampled from current populations.

Destructive sampling

Due to time constraints, destructive analysis was limited to a small sample size (47 individuals), two species (Scots pine, birch), and two study areas (Black Wood of Rannoch, Glen Affric). In order to capture variation resulting from site conditions, stand dynamics, deer management, altitude, climate and soils, the analysis needs to be expanded to include a wider range of study areas dispersed across Scotland and larger sample sizes to ensure ~5 individuals per site condition. A wider range of species also need to be included, as many Scots pine stands have a significant hardwood component which needs to be incorporated into the stand dynamics model. We recommend that future dendrochronological analyses be carried out in winDENDRO^{TM} (Regent Instruments Inc., Blain, Quebec), a scanner-based image processing tree-ring measurement system (Guay *et al.* 1992) that outputs ring counts and individual ring widths facilitating the development of a mean standardised chronology. Ring width measurements would enable more accurate estimates of time required to grow into the 7 cm DBH size class, as the current approach assumes constant growth rates that do not take into account age-related growth trends (Holmes *et al*. 1986) or the effect of deer damage.

Model development

The model presented in this report represents a preliminary output with severe limitations due to the short time scale on which the frequency matrix was based (22 year period), narrow range of climatic conditions represented by the study area (Black Wood of Rannoch, Glen Affric), relatively small number of plots for which repeat measurement data was available, and assumptions on the allocation of mortality to trees on a size basis. A re-inventory of long-term study plots in Caledonian pinewoods across Scotland is currently being considered, and if this data was available could be used in an extension of this project. Incorporation of this data into the model parameterisation process would greatly improve predictive ability of the model.

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