Ecological change in the native Scottish pinewoods since 1971 - data from the Bunce 2018-2022 re-survey

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Abstract.

The native pinewoods of Scotland are acknowledged to be an important ecological resource, both for their biodiversity value and as a cultural and amenity resource. Due to the unique nature of the habitat and its limited range, it plays a critical role as an early warning system for broader environmental issues. In the late 1960s and 70s, increased concern was expressed regarding a decline in the status and management of the pinewoods. In response to the concerns, an ecological monitoring survey was initiated by R.G.H. Bunce of the Nature Conservancy in 1971, recording ground flora, tree information, soils and other descriptive attributes. Since that time, interest in the pinewoods has increased further, and there is a general consensus that the habitat is more vulnerable than ever. Thanks to a recent repeat survey between 2018 and 2022, questions addressing the threats and changes occurring in the pinewoods can now be explored in a statistically robust way. These questions include issues surrounding the impacts of deer grazing, regeneration, the balance between native and exotic species, local disturbances, trends in ground flora species occurrences, climate change and recovery from acidification. The new data from the 2018-22 survey are now publicly available via the following DOI: https://doi.org/10.5285/5e268e86-4a4f-4112-bf2d-c3b0179c915c 'Habitat, vegetation, tree and soil data from Native Pinewoods in Scotland, 2018-2022'. Change data are available at: https://doi.org/10.6084/m9.figshare.34574874.

1 Introduction

The Caledonian Pinewoods are a globally unique habitat. They are usually dominated by native Scots pine (*Pinus sylvestris*) but often have diverse canopies that include birch (*Betula* spp.), rowan (*Sorbus aucuparia*), alder (*Alnus glutinosa*), willow (*Salix* spp.), holly (*Ilex aquifolium*) and hazel (*Corylus avellana*). In Scotland, the native pine woodlands are included on the Scottish biodiversity list (Naturescot, 2024). They are identified as a priority habitat in the UK Biodiversity Action Plan (Maddock, 2008), and as an Annex I Habitat in the EU Habitats Directive (Caledonian Forest 91C0) (Romão, 2013). The restoration and resilience of this habitat is vital for halting biodiversity loss and contributing to reaching net zero, as well as being valued for cultural and recreational reasons. As a rare and unique habitat, the pinewoods act as an early warning system for many wider environmental issues. Several issues impacting the Scottish pinewood habitat have been identified including non-native tree species planting, regeneration of native species, deer density and management, ground flora species decline and climate change. In the last 50 years, statistically robust data regarding ecological changes in the habitat had been lacking that would allow investigation of changes over time related to these themes. The repeat of the 'Bunce Scottish Pinewood Survey', completed in 2022, provides the evidence to explore a wide range of questions when analysed in conjunction with the 1971 dataset (as described in Wood and Bunce, 2016).

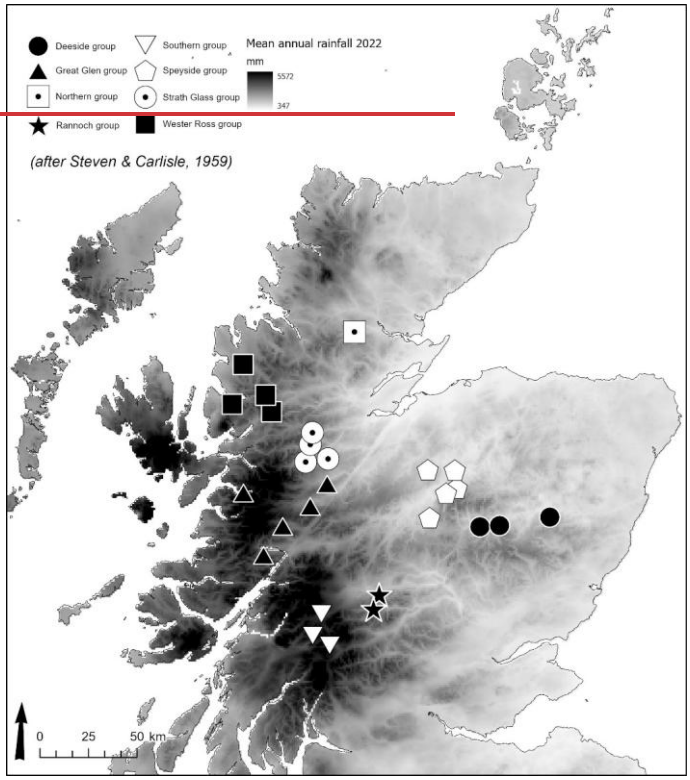
In the 1960s and 70s, concerns were expressed as to the decline in the native pinewoods, and as a result, an ecological survey (the 'Bunce Scottish Pinewood Survey') was initiated in 1971 by Professor R.G.H. Bunce of the Nature Conservancy (later the Institute of Terrestrial Ecology and the UK Centre for Ecology & Hydrology). This baseline survey and dataset is described in detail in Wood and Bunce (2016) and aimed to build on the comprehensive 'Native pinewoods of Scotland' book published in 1959 (Steven and Carlisle, 1959). The initial 1971 survey led to a symposium in 1975, bringing together key stakeholders and raising the profile in conservation terms of this biodiverse and valued habitat. Ongoing concern about the current state of the woodlands led to 'Scotland's Pinewood Conference', convened in Fort William, Scotland in October 2024, the third of its kind since 1975. Attendees included conservationists, foresters, land managers and academics. The repeatable methods used in the 1971 survey have enabled a re-survey of the Bunce sites, starting in 2018. The survey was completed in 2022, and was largely funded by Woodland Trust, with a contribution from the Cairngorms National Park Authority. At the same time, a complementary survey of broadleaved woodlands was carried out, the 'Bunce Woodland Survey of Great Britain', also initiated in 1971 using the same methods (Wood and Bunce, 2016; Smart et al., 2024). That survey had been repeated in 2001 (Wood et al., 2015; Kirby et al., 2005), however the Bunce pinewood survey had never been repeated aside from two sites (Mar Lodge and Shieldaig) undertaken as part of a pilot study in 2000 (Smart et al., 2001).

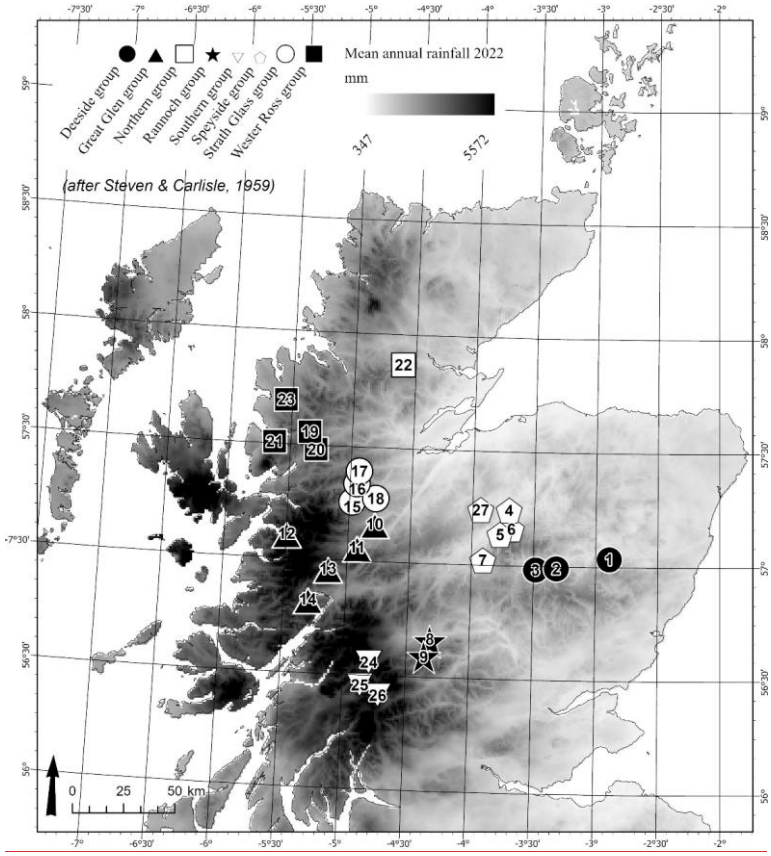
The main aims of the 2018-22 re-survey were to provide an evidence base for understanding the effects of multiple drivers and threats within a habitat of high conservation importance, and to gain a unique perspective on how understanding the past aids interpretation of the present. In particular, to investigate the status of native and non-native tree species, to collect evidence on the impacts of deer grazing, to test whether vegetation changes in the understorey have stabilised or been reversed due to local disturbance or management, to collect evidence of ongoing recovery from acidification by atmospheric sulphur and nitrogen deposition, to characterise the nearly 50-year trend in terms of variables that reflect links to ecosystem services (such as carbon storage in canopy and

soils), and the changing role of woodlands as refuges for distinctive species. A substantial benefit of the Bunce survey is that change since 1971 can be directly assessed. The survey complements other recent work carried out in the pinewoods – the 'Caledonian Pinewood Survey' (Rainey and Holmes, 2023) and the 'Native Pine Survey', part of the Native Woodland Survey of Scotland (NWSS) (Patterson et al., 2014) in addition to many smaller studies such as Bruce and Servant (2003); Froyd and Bennett (2006); Bain (1987).

1.1 Sites

The sites chosen for inclusion in the Bunce survey are a set of 27 sites chosen from 35 included as maps in the seminal text of Steven and Carlisle (1959), which were identified as the major areas of native pine woodland in Scotland. Since 1971, the pinewoods originally surveyed have undergone substantial changes in management and ownership, and therefore it is expected that changes in the ground flora, trees and other ecological aspects have also changed in line with these drivers, as well as wider external factors such as climate change and atmospheric deposition. These sites (Table 1) were divided into groups by Steven and Carlisle as shown in Fig. 1, and it is helpful to summarise the sites on this basis, as they represent different gradients in potential change drivers, such as rainfall, as illustrated, and other geographical variability, such as soil type. Each group also has some similarities in ownership and management as outlined below.





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Figure 1. Pinewood site groups shown in Steven and Carlisle (Steven and Carlisle, 1959) groupings displayed with mean annual rainfall for 2022 (Met Office, 2024) . See Table 1 for a site listing.

Table 1. List of sites included in the survey

Site Number	Name	OS Grid ref.	WGS84 (lat/long)
1	Glen Tanar	NO459941	57.016073,-2.874452
2	Ballochbuie	NO200897	56.989726,-3.318191
3	Mar	NO099892	57.019797,-3.591042
4	Abernethy	NH970183	57.241517,-3.675155
5	Rothiemurchus	NH925065	57.150132,-3.786736
6	Glenmore	NH981091	57.160484,-3.688023
7	Glen Feshie	NN841939	57.067504,-3.90647
8	Rannoch	NN582542	56.674128,-4.319107
9	Meggernie	NN553467	56.579112,-4.353992
10	Glen Moriston	NH313117	57.167624,-4.796578

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11	Glengarry	NH226003	57.065924,-4.920907
12	Barrisdale	NG883071	57.069544,-5.482271
13	Loch Arkaig and Glen Mallie	NN085900	56.942474,-5.009908
14	Ardgour	NM986750	56.788414,-5.34149
15	Glen Affric	NH203225	57.255437,-5.076864
16	Glen Cannich	NH227315	57.323318,-5.057618
17	Glen Strathfarrar	NH238375	57.41206,-4.715275
18	Guisachan and Cougie	NH318241	57.270359,-4.824274
19	Coulin	NG997568	57.546826,-5.35218
20	Achnashellach	NH028483	57.470562,-5.278451
21	Shieldaig	NG825522	57.50915,-5.641018
22	Amat	NH454895	57.832453,-4.595224
23	Loch Maree	NG881727	57.594118,-5.331424
24	Black Mount	NN284441	56.572352,-4.687331
25	Glen Orchy	NN240330	56.483488,-4.843483
26	Tyndrum	NN328279	56.414601,-4.708621
27	Dulnain	NH831185	57.237704,-3.940105

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The sites in the Deeside Group: Glen Tanar, Ballochbuie, and Mar Lodge, are the most easterly of the pinewoods, experiencing lower rainfall and lower winter temperatures compared to the other sites. All sites were in private ownership in 1971. Since then, Glen Tanar was partially acquired by the Scottish nature conservation agency, NatureScot, in 1978, and Mar Lodge has been acquired by The National Trust, a charity whose aims include nature conservation. Ballochbuie is still under the private ownership of the Crown Estate. Management of these sites has increasingly focused on conservation in the last few decades.

Abernethy, Rothiemurchus, Glenmore, Glen Feshie and Dulnain are all in the Speyside Group, and include some of the largest pinewoods. Along with the Deeside sites, the Speyside sites are located in areas with the lowest rainfall and winter temperatures compared to the other Groups. The majority of these sites are in public ownership, owned by Forest and Land Scotland (FLS) (formerly Forest Enterprise Scotland (FES) and before that, the Forestry Commission (FC)) and therefore subject to changing FLS, FES and FC policies over the years. In the past, felling and planting of non-native species particularly, for example at ~~at Abernethy and~~ Glenmore occurred. FLS policies in recent years have been based more around conservation objectives than in the past, when timber production was paramount.

The Great Glen Group contains sites located in the valleys of the glen, with rainfall values ranging from moderate to very high and relatively mild winters. The sites are under a mixture of ownership. Barrisdale and Ardgour are in private ownership and are both relatively remote sites with scattered pine trees. The Loch Arkaig & Glen Mallie site was recently acquired by the Woodland Trust, and the removal of non-native tree species is a management priority here, as well as continuing to recover from a widespread and devastating fire in 1942.

The Strath Glass Group contains Glen Affric, Glen Cannich, Glen Strathfarrar and Guisachan & Cougie. These receive moderately high rainfall, with cold winters. All are in public (FLS) ownership with the exception of Glen Strathfarrar. Non-native conifer planting has occurred in these sites, and their removal has been ongoing. Deer fencing and pinewood restoration ~~management~~ has been a priority in recent decades.

The Wester Ross Group contains Shieldaig, Loch Maree, Coulin and Achnashellach, and consists of sites with high rainfall and mild winters at the western edge of the Scots pine range. Ownership is a mix of public (FLS) and private.

In the Rannoch Group, the Black Wood of Rannoch has been declared a Site of Special Scientific Interest and a Forest Nature Reserve. This group includes the Old Wood of Meggernie, belonging to a private estate.

The privately owned Amat forest is in the Northern group. The Amat forest and the woods within the Rannoch Group experience average rainfall for Scotland but relatively cool winters – although not as cold as those in the Deeside, Speyside or Strath Glass Groups. ~~It~~Amat has suffered from felling and fires in the past, but now has deer fencing in place, and natural regeneration reportedly occurs.

The Southern sites are Black Mount, Glen Orchy and Tyndrum. All of these experience very high rainfall and relatively mild winters. Glen Orchy is publicly owned by FLS and has suffered in the past from non-native conifer planting. The other two sites are privately owned and have been subject to deer fencing. In terms of rainfall, these are some of the wettest sites.

1.2 Changes in the pinewood habitat since 1971

At the time of the first Bunce survey in 1971, conservationists and woodland managers realised that the pinewoods were under threat from ploughing and planting of non-native conifer species and overgrazing from deer and also sheep. In 1963, alarmingly, McVean came to the conclusion that the 'existing pure pine stands are largely artifacts and they have a limited future as self-maintaining entities; intensive management will be required for the native forests to be retained as they are' ~~and it may well be that the native pine, *Pinus sylvestris,* will only achieve self-perpetuation in a forest of mixed composition and intimately mixed age structure which has yet to be produced'~~ (McVean, 1963). In 1975, the only forest with a plan for expansion of native *Pinus sylvestris* was the Black Wood of Rannoch (Bain, 2013).

At the 2024 Fort William conference, a number of key issues were discussed. Each of these issues has affected the tree structure and composition of the pinewoods, the ground flora and soils in different ways since the 1970s. These key themes, which are often interrelated, are outlined as follows:

Non-native tree planting and removal: In the 1960s and 70s, there was much planting of Sitka spruce (*Picea sitchensis*) and other non-native conifers particularly in the west of Scotland, with extensive planting of Scots pine (*Pinus sylvestris)* around other pinewoods, often in the Central and Eastern Highlands~~ and other non-native conifers across Scotland, including around the pinewoods~~ (Bunce et al., 2014). Coniferous planting has a considerable effect on the associated ground flora, with little able to survive in the dense shade (Carey et al., 2008). It also has considerable effects on many aspects of landscape ecology, such as drainage patterns (Bunce et al., 2014). In 1977, the Forestry Commission's Native Pinewood Grant Scheme encouraged landowners to restore and increase the extent of pinewoods in specific areas. Only locally sourced seeds were allowed to be planted (Bain, 2013). Further protection was forthcoming in the 1980s, when sites designated as Sites of Special Scientific Interest (SSSI) were protected from felling and other harmful activities. Grants were made available for deer fencing (Bain, 2013).

Regeneration of native tree species: Regeneration depends on both the growing conditions, and external factors, such as incentives for the encouragement of natural regeneration. ~~On thinner soils or light heather cover, regeneration can be plentiful (Scott et al., 2000; Miles and Kinnaird, 1979; Mcvean, 1963).~~ In the 1990s, the UK

Biodiversity Action Plan (BAP, 1994) specified objectives to maintain remnant native pinewood areas listed on the Caledonian Pinewood Inventory and restore their natural diversity of composition and structure, regenerate and expand the current wooded area of remnant native pinewoods, and encourage natural regeneration (B~~ap~~AP, 1994). State support for Caledonian Pinewood restoration improved, with a series of Caledonian Forest Reserves being established in state owned forests, targeted felling of non-natives was supported as a management practice, along with attempts to control deer populations (Rainey and Holmes, 2023). These interventions were supported by improved Woodland Grant Schemes (1988-2003). However, the 2000s did not bring much further improvement in support (Bain, 2013).

Impact of deer: In Scotland, it is estimated that deer numbers have doubled from 500,000 in 1990 to around 1 million now (Scottish Government, 2025). The effect of deer browsing in limiting regeneration is well documented, for example in Cameron (1995); Palmer and Truscott (2003); Palmer et al. (2007); Holloway (1967). Deer also have been shown to affect the composition of the ground flora in the pinewoods (Baines et al., 1994).

Climate change: Since 1970, Scotland's climatic trend has been towards warmer mean temperatures and higher rainfall, particularly in the winter (Met Office, 2025b). Both factors are likely to affect tree regeneration, and the composition of the associated ground flora, and to some extent, soil quality. The pinewoods are home to ~~a unique ground flora, including~~ nationally scarce species such as the creeping lady's-tresses orchid (*Goodyera repens)* (Wood and Bunce, 2016). Ground flora is likely to be affected by changes in climate, as well as grazing and the associated tree composition (Ford et al., 2018; Gill and Morgan, 2009) as the availability of shade will has significant effects on the ground flora assemblages (Peterken and Francis, 1999).

Additional threats: Threats such as tree disease, storm damage, atmospheric pollution and fire also pose challenges for the pinewood habitat.

1.3 Impact of changes in management, ownership and grants

Since 1971, there have been different approaches, interventions and incentives in response to the highlighted issues. At a local level, each pinewood is managed according to different objectives, and with a greater or lesser intensity. This is often dictated by ownership and also geographical factors. Some of the sites have been damaged by fire in the past, such as Loch Arkaig, and management objectives have included attempts to restore the damaged areas. Other management interventions have included deer culling and fencing, and assisting natural regeneration with the planting of native seed. In theory, the outlook for native pinewoods as a habitat should be better now than it has been for the last 300 years (Tayside Biodiversity Partnership, 2002). In recent years forestry policy has moved to recognise the value of native pinewood from a habitat, landscape and cultural perspective and has put in place a number of initiatives to protect and enhance its status and extent. The government, through Scottish Forestry, encourages forestry expansion through the payment of grants where creation of new woodland is in accordance with forestry and conservation policies. The Scottish Forestry Strategy contained a commitment to achieve ~~the current~~ Action Plan targets (Tayside Biodiversity Partnership, 2002). Financial and advisory support for native woodland management and establishment is also available (Scottish Forestry, 2025). In 1971, 68% of the pinewoods were in private ownership and 18% in the public sector. Now, ~~over~~ nearly 30% of the surveyed pinewoods are in the public ownership of FLS. Private ownership has dropped to around a third of the sites, and ~~there has been an increase in~~ sites owned by charities or conservation groups, including the public body

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responsible for nature conservation in Scotland – NatureScot) ~~which~~ make up the remainder. Several sites are under mixed ownership.

2. Data Collected

The Bunce survey collects a wide range of data that can aid the exploration of many of the issues facing the native pinewoods. The range of ~~repeat~~ measurements recorded in 1971, and now repeated in 2018-2022, include data on ground flora, trees, saplings and shrubs, habitat descriptions, and soil pH and loss on ignition. The methods for collecting these data are described fully in Wood and Bunce (2016). In summary, within each site 16 plots are laid out, originally placed in a random dispersed manner. Each plot is 200m square, with a concentric nested structure to aid botanical searching and that allows for the estimation of species-area relationships (Kunin et al., 2018). In 2018-22 ~~(later referred to as the '2022 survey')~~, plots were revisited as near as possible to the original 1971 position, based on plots marked on a 1:10 000 Ordnance Survey (the British mapping agency) map, previous surveyor notes, and to some extent, previous tree diameter at breast height (dbh) information (Smart and Wood, 2021). It is not possible to go back in time and understand fully how precisely the plots have been relocated and therefore some plot relocation error is inevitable given the nature of the information available and the nature of the original maps. However, work was undertaken in 2001 to understand the precision of plot relocation in the partner survey to this one, the Bunce Woodland Survey of Great Britain, which used exactly the same methods of relocation. Analysis of the 1648 plot records taken in 1971 and 2001, described fully in Kirby et al. (2005), demonstrated that the records may be treated as paired data (i.e. relocation error was not significant). In summary, the principal of autocorrelation (whereby plots near to each other are more similar than those further away) may be used to quantify the error in attempting to relocate the same vegetation plots.

A full census of the ground vegetation was recorded within these plots to the nearest 5% cover (or just 'present'); firstly presence and % cover in the inner 2 x 2 m nest, then presence in each subsequent nest, and finally the % cover for the whole 200m^2 quadrat. Litter, wood, rock, bare ground and water were also included where present (as a % cover), as well as bryophytes from a restricted list (Smart and Wood, 2021).

For tree recording, the 200m^2 plot was divided into 4 quadrants. Trees of >5cm diameter at breast height (dbh) were recorded from each quarter. Saplings (height <130cm and dbh <5cm)) and shrubs (species such as hazel (*Corylus avellana*) and juniper (*Juniperus* spp.) were recorded in quarters 1 and 3 only. A range of descriptive codes are recorded for each plot and site (including information such as presence of stumps, aquatic habitats, mammals, and land use).

A soil sample was taken from the centre of each plot, using a 5cm diameter plastic tube to sample the top 15cm of soil. Fresh plant litter was removed before sampling but decomposing plant litter was included within the sample. Soil samples were kept at around 4ºC until laboratory processing for pH and loss on ignition (LOI). Samples were sieved with a 2mm sieve, then 10cm^3 of the sample were added to a beaker containing 10ml of deionised water. A pH reading was taken with a standard pH probe (calibrated with buffer solutions of pH 4 and pH 7). Samples were then airdried at 25ºC for approximately 7 days. Another pH reading was taken from the dried soil at this point (Avery and Bascomb, 1974).

Loss on ignition and soil moisture were then determined. Loss on ignition is a simple method for determining soil organic matter. LOI was measured on a 5 g air-dried sub-sample taken after sieving to 2 mm, then dried at 105 ◦C

for 12 hours to remove moisture, weighed, and then combusted at 550 ◦C for 6 hours. The cooled sample was then weighed and the LOI (%) ~~and moisture content~~ calculated.

2.1 Data quality

During the survey seasons, all survey teams were initially trained in person by the project leader or deputy. Teams were in regular contact with the management team to ensure consistency and quality in data recording according to criteria laid out in the field handbook (Smart and Wood, 2021).

In 2018, the survey was undertaken for the first time using electronic data recording, using a bespoke recording form based on the ESRI Survey123 app (Esri, 2025) incorporating the 1971 methodology. Electronic recording meant that certain errors could be eliminated (such as those related to poor handwriting and coding errors). Data could also be checked as soon as records were submitted from the field to the central database to ensure completeness.

The soil pH and loss on ignition were analysed using standardised protocols (Emmett et al., 2008; Avery and Bascomb, 1974) incorporating quality control measures.

3. Summary of key findings

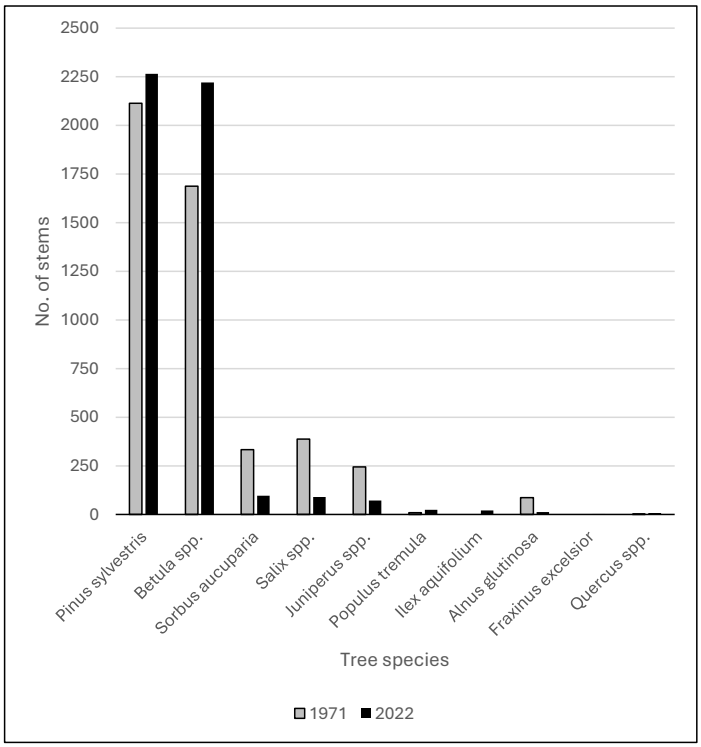
Key findings from the 2022 Bunce survey can be summarised in relation to changes in tree structure and composition, ground flora and soils in response to the pressures and themes identified above. Firstly, changes in non-native tree species and native species regeneration, and then deer management and climate change. There is also additional information included in the datasets that can be explored in future work, regarding threats such as tree disease, storm damage and atmospheric deposition.

3.1 Tree structure and composition: native and non-native species

Overall, 5,527 tree/shrub stems were recorded in 1971 and 5,255 in the 2018-2022 survey~~s~~ - a decrease of 4.9 %. Scots pine (*Pinus sylvestris*) and birch (*Betula* spp.) were the most abundant tree species (78 % of all stems), with Scots pine (*Pinus sylvestris*) being recorded at all 27 sites. Trees, saplings and shrubs are included here, with trees being defined as stems of more than 5cm diameter at breast height, saplings as for trees, but with a height of less than 130cm and with a DBH less than 5cm and shrubs being shrub species such as hazel (*Corylus avellana*) and juniper (*Juniperus* spp.). The greatest positive changes in mean stem number are associated with birch (*Betula* spp.) (~~18.4~~19.1 stems per site) and Scots pine (*Pinus sylvestris*) (~~11.4~~24.3 stems per site). Fig. 2 illustrates an example of young Scots pine growth at the Glen Tanar site. Among the remaining native species, willows (*Salix spp.)* and rowan (*Sorbus aucuparia*) have declined markedly across all sites, willows by a mean of ~~6~~13.3 stems and rowan by a mean of ~~1~~8.8 stems. Juniper (*Juniperus communis*) has also declined. The major changes are shown in Fig. 3, and a summary table of the change in ~~average~~ mean stem count number between 1971 and 2018-2022 by species for each pinewood site may be found in the Supplementary Material (Table S1).



Figure 2. Young Scots pines at Glen Tanar



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Figure 3. Change in native tree species recorded

Non-native trees were present in 41% of the 27 pinewoods, a figure that overall hasn't changed markedly since 1971 (a slight decrease from 44%). However, the cover of those trees has declined (Fig. 4). Much of the decline in canopy cover is attributable to felling of densely planted, non-native conifers, including Douglas fir (*Pseudotsuga menziesii*), Japanese larch (*Larix kaempferi*), lodgepole pine (*Pinus contorta*), Norway spruce (*Picea abies*) and Sitka spruce (*Picea sitchensis*). An example of removal of non-native species at Glengarry is shown in Fig. 5, a site where this is particularly evident. While non-native conifers have generally declined across the Bunce sites, they have increased locally; larch (*Larix spp*.) at Abernethy, and Norway spruce (*Picea abies)* at Ballochbuie, Ardgour and Glen Orchy in particular. A summary table showing the changes in counts of non-native tree species may be found in the Supplementary Material (Table S2) and a figure showing changes in these by ownership (Fig. S1).

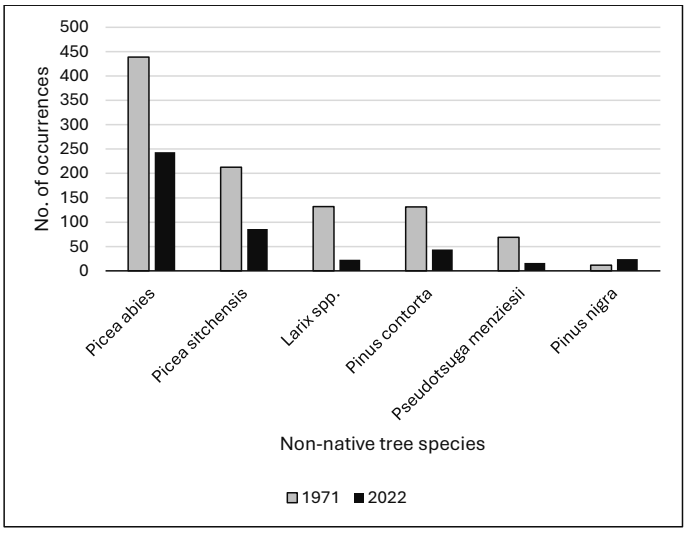


Figure 4. Change in non-native tree species (stem counts)



Figure 5. Felling at Glen Garry

The mean change in stem diameter per site ranges between -0.55 - 0.69 cm. Change was greatest for Scots pine (*Pinus sylvestris*), with a mean increase of 2.4 cm, whilst birch (*Betula* spp.) showed a minor increase of 0.5 cm. Very limited change in the diameter of the other broadleaved and native species was observed (<0.3 cm). Among the non-native conifers, only Douglas fir (*Pseudotsuga menziesii*), and Norway spruce (*Picea abies*) demonstrate a change in average stem diameter of greater than ±0.1 cm.

3.2 Regeneration of native species

Signs of regeneration may be investigated in the data by looking at the records of recent regeneration recorded in the plot descriptions, and also by looking at counts of seedlings and smaller stemmed trees and saplings. Over the longer-term, counts of stems likely to have appeared since 1971 give a picture of growth (including stem increase of established trees and regeneration of new, smaller trees) since that date. Whilst it is difficult to estimate tree age from the trunk diameter, we propose that Scots pine (*Pinus sylvestris*) stems with a diameter at breast ~~-~~height less than or equal to 20cm equate to individuals approximately 50 years old according to ~~the UK~~ a tree age calculator (~~Felling UK~~Virginia Tree Care, 202~~5~~6)~~,~~ in order to present an approximation of change since 1971. Fig. 6 shows a site example (Glen Tanar) which shows an increase in Scots pine (*Pinus sylvestris*) stems in the smaller dbh size classes, which indicates ongoing regeneration at that site.

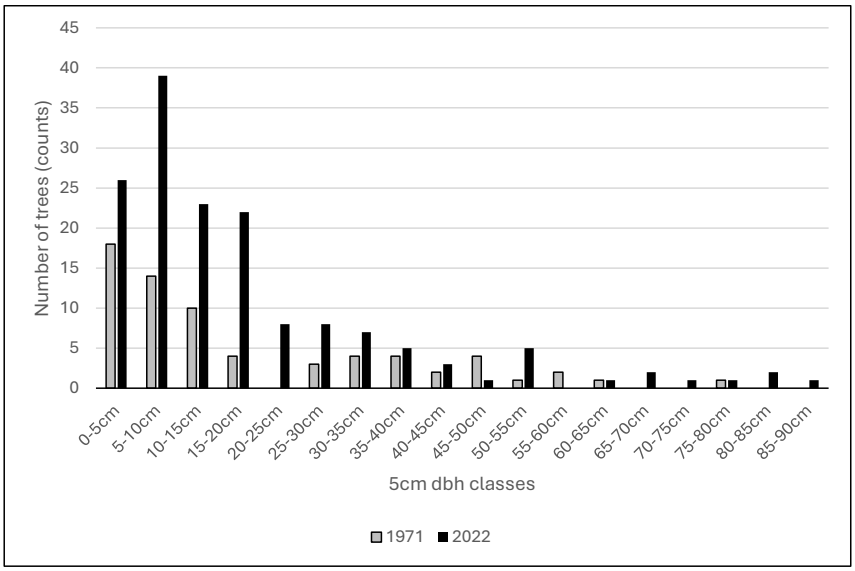
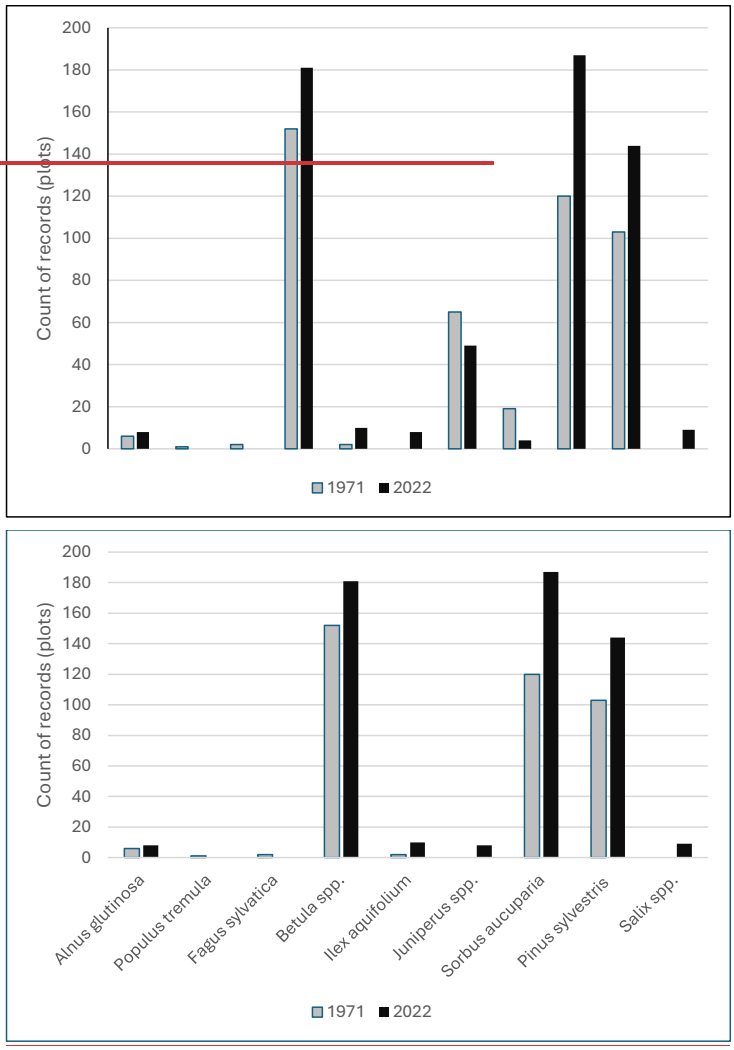


Figure 6. Counts of Scots pine stems at Glen Tanar, grouped in 5cm dbh classes

Overall, recent tree regeneration signs have increased by 33%, with increases demonstrated especially for the native species of Scots pine (*Pinus sylvestris*), birch (*Betula* spp.) and rowan (*Sorbus aucuparia*), and smaller increases in holly (*Ilex aquifolium*), alder (*Alnus glutinosa*), juniper (*Juniperus* spp.) and willow (*Salix* spp.). (Fig. 7), which matches the increase in the overall mean stem counts. Whilst the overall number remains very low, holly regeneration has increased by 400%. A marked increase in holly was particularly noted in the related Bunce Woodland Survey of Great Britain (Smart et al., 2024).

Mar Lodge (Fig. 8) is one of the sites demonstrating regeneration of Scots pine (*Pinus sylvestris*) and birch (*Betula* spp.) in the records of seedling frequency and regeneration. Recognised as an internationally important site, and having been acquired by the National Trust in 1995, the primary aim of the site is now focused on conservation. Large efforts have been made to control deer, which were previously hampering regeneration. ~~In t~~The Bunce data confirms a decrease in, signs of grazing animals ~~confirms a decrease there~~ since 1971.



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Figure 7. Change in signs of recent regeneration, 1971-2022



Figure 8. Birch and Scots pine regeneration at Mar Lodge

3.3 Deer management

Overall, a 14.7% decrease in signs of deer was noted between 1971 and 2021. Some sites, notably Mar Lodge, have made strong efforts to reduce the deer numbers. 1~~9~~4 of the Bunce sites recorded a~~n increase~~ decrease in signs of deer, and ~~only eight~~ nine recorded an increase ~~decrease~~. This appears to be reflected in the impact on ~~the number of smaller stems recorded~~regeneration of Scots pine. At sites where a decrease in deer was noted, the mean change in the number of ~~smaller stemmed tree species~~regeneration counts recorded was ~~16.4~~3.35, ~~and only 0.68~~but 1.11 at sites where deer had increased (Table ~~1~~2). There is also evidence that deer may have had a~~n~~ slight effect on the number of ground flora species found. At sites where there has been an ~~increase~~ decrease in deer, the mean change in absolute species numbers was a loss of ~~1.1~~2.07, versus a ~~g~~loss~~ain~~ of ~~0.98~~0.26 at sites where deer ~~decreased~~increased.

Table ~~1~~2. Effect of deer numbers on ~~small stems~~tree regeneration and ground flora, change in mean counts per site, 1971-2022

	~~In~~Decrease in signs of deer	~~De~~Increase in signs of deer
No. of Bunce sites	1~~4~~9	~~8~~9
Mean change in ~~no. of smaller stemmed tree~~regeneration ~~species~~ (Scots pine) counts	~~0.68~~3.35	1.11~~16.4~~
Mean change in no. of ground flora species	-2.07~~1.1~~	~~0.98~~0.26

The effects of deer impacts are complicated as other local factors should also be taken into account when undertaking analysis. It is also often difficult to determine exactly what the current levels of deer are at a plot level, as well as historical levels over the last 50 years due to a lack of data. Heavy deer grazing is known to reduce palatable species such as bilberry/blaeberry (*Vaccinium myrtillus)* and increase unpalatable ones, such as bracken

(Pteridium aquilinum) (Kirby, 2001). Across all sites i~~I~~n the Bunce pinewoods, both of these species have declined a very small amount overall~~, therefore it is difficult to discern an effect of deer grazing in relation to them~~. The data could, however, be used to investigate this issue in more detail at the individual site and plot level, including analysis of the trees and saplings. ~~Preliminary analysis of the data reinforces the finding by Kirby (2001) i~~In broadleaved woodlands, it has been found by Kirby (2001) that grasses tend to thrive under heavy grazing. You might expect more shade overall with fewer deer allowing the trees and shrubs to thrive, and therefore fewer grass species, being largely shade intolerant. In the pinewoods, ~~–~~Table ~~2~~3 demonstrates that sites with overall evidence of an increase in deer signs may have resulted in an increase ~~have a smaller loss~~ in the ~~occurrence~~ percentage cover of grass species (6.5%), but it also shows an increase (10.78%) for sites ~~than those in sites~~ with a decrease in deer signs. ~~The opposite is true i~~In terms of heather species (*Erica* spp. and *Calluna* spp.), ~~sites with an increase~~ in deer appear to demonstrate a smaller increase in these species, as ~~also might~~ may be expected, being palatable to the deer (Kirby, 2001; Baines et al., 1994). Table 3 suggests that *Vaccinium myrtillus* has increased slightly where signs of deer have increased. As a palatable species to deer, this is perhaps counterintuitive. Again, further detailed analysis is recommended as the situation is complex.

Table ~~2~~3. Effect of deer numbers on the change in the ~~overall mean~~ occurrence count of grass, ~~and~~ heather and bilberry/blaeberry species, ~~change in mean count per site,~~ 1971-2022

	~~In~~De~~c~~rease in signs of deer	~~De~~In~~c~~rease in signs of deer
~~No. of Bunce sites~~	~~19~~	~~8~~
~~Mean c~~Change in mean % cover of~~no. of~~ grass species ~~per site~~in plots	~~-5.28~~10.78	~~-9.88~~6.5
Change in mean % cover of ~~Mean change in no. of~~ heather species ~~per site~~in plots	5.99~~-2.83~~	1.13~~-0.75~~
Change in mean % cover of bilberry/blaeberry (*Vaccinium myrtillus*) counts per site	-0.21	2

3.4 Effects of climate change on ground flora

All sites were wetter in 2022 than they were in 1971, with a mean increase of 341mm overall when comparing the two years (Met Office, 2024). The wettest group (Southern Group) is also the group with the highest rainfall increase, i.e. the wettest sites are getting wetter. The mean daily temperature overall has risen from 7.5ºC in 1971 to 8.3ºC in 2022. Approximately one third of the sites have a mean winter minimum temperature above freezing point between 1991 and 2020 (Met Office, 2025b). This is an increase from only five sites between 1941 and 1970. These overall long-term trends are confirmed by other authors, for example, Wilson, (2023).

~~Wetland pl~~Plants associated with bogs and wet heaths ~~ants~~ are well-represented in the top 25 most frequently recorded species including deergrass (*Trichophorum germanicum*), purple moor-grass (*Molinia caerulea*) and star sedge (*Carex echinata)*. An increase in these species since 1971 is likely to be linked to the increase in climatic wetness.

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In terms of rare or plants diagnostic of the pinewood, two have increased: The orchid *Goodyera repens* was recorded 23 times (in 1971 it was recorded 14 times), and bearberry (*Arctostaphylos uva-ursi)* was recorded 59 times (in 1971, 12 times). Common cow wheat (*Melampyrum pratense)* was recorded 43 times, a decrease from 130 times in 1971. This species appears to be in decline overall based on other national surveys such as the GB Countryside Survey (UKCEH Countryside Survey, 2026) and the GB Broadleaved Woodland Survey (Smart et al., 2024). It is hemi-parasitic on the roots of other plants, including trees, ericaceous dwarf shrubs and Bog myrtle (*Myrica gale*). There has also been a major decline shown by Plant Atlas 2020 (https://plantatlas2020.org/atlas/2cd4p9h.yrz). They indicate that its large seeds are ant dispersed and so it is likely to have suffered from reduced dispersal opportunities if conditions in the understorey have become cooler and more shaded and reduced ant populations. Reasons for its decline in the pinewoods could be complex and would be worth investigating further in relation to a range of drivers. ~~This is a plant that thrives in open ground so perhaps indicates increased shade in the woods.~~

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3.5 Additional changes in ground flora composition

Species richness has declined across all sites from a mean of 18.6 species in 1971, to 17.5 species in the 2020s. However, this mean figure belies the large amount of variation between sites. A table showing the average number of species per site and relative and absolute change between surveys can be found in the Supplementary Material (Table S3), along with a list of the top 25 ground flora species recorded in the 2018-2022 survey (Table S4).

Several sites have shown an overall increase, in particular Glen Garry, Loch Arkaig & Glen Ma~~i~~llie, and Achnashellach. These are all sites where removal of non-native trees has taken place which may explain some of the increase. Despite the extensive removal of non-natives in Glenmore and Guisachan & Cougie, species richness declined. The biggest decreases in species richness have occurred in Ballochbuie, Glenmore, Guisachan & Cougie and Glen Orchy. Further investigation might look into the relationship between species richness and the impacts of deer at these sites.

In terms of the frequency of species recorded, the two most frequent have not changed since 1971, being heather (*Calluna vulgaris)* and bilberry/blaeberry (*Vaccinium myrtillus).* Purple moor grass *(Molinia caerulea)* has increased slightly while tormentil (*Potentilla erecta)* has decreased. Wavy hair-grass *(Deschampsia flexuosa)* remains the fourth most recorded species. Overall, the frequency of broadleaved grasses, ferns, sub-shrubs, wetland herbs and tree-seedlings has increased. Decreases in frequency were found for sub-shrubs (*Erica* spp.) and diminutive herbs.

In terms of overall change in the Top 15 species recorded in 1971 (Fig. 9), the most frequent species, heather (*Calluna vulgaris)* has not changed significantly. Bilberry/blaeberry (*Vaccinium myrtillus)* has increased slightly. Of the top 15, cowberry (*Vaccinium vitis-idea)* and dog bent (*Agrostis canina)* have declined the most markedly. Rowan (*Sorbus aucuparia)* recorded as saplings has increased whereas those recorded as shrubs have declined, potentially indicating increased initial regeneration, with a failure to thrive, most likely due to selective browsing by deer.

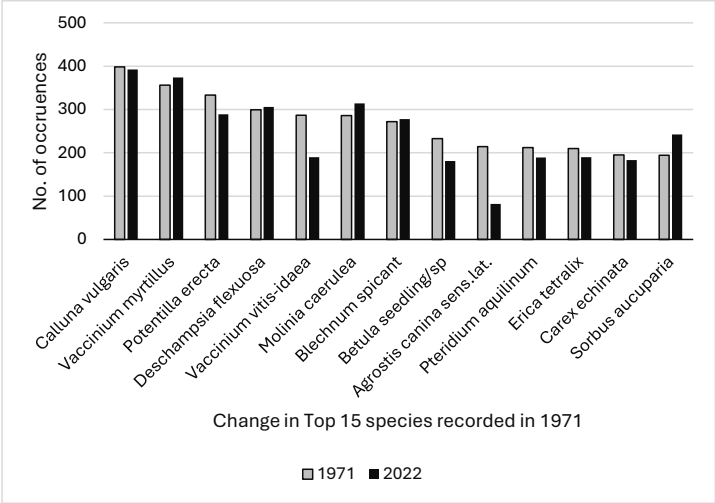


Figure 9. Change in the top 15 species recorded in 1971 to 2022

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3.6 Changes in soil condition

Change in soil pH was compared between 1971 and 2022 (Fig. 10) with repeat measurements following the same methods.~~.~~ Overall, there is a signal of a slight rise in the mean fresh soil pH value (0.15), which matches an increase detected in the GB Bunce Woodland Survey (1971-2022) (Smart et al., 2024; Kirby et al., 2005) and the GB Countryside Survey (1978-) and at least partly attributable to recovery from historically high atmospheric sulphur deposition in the past (Reynolds et al., 2013). This driver-response relationship has also been identified in other national surveys, for example, Kirk et al. (2010); Seaton et al. (2023). The Deeside Group in particular has shown a marked increase in soil pH which would be worth investigating further in relation to a range of potential drivers. The only geographical groupings showing a fall in pH were the Wester Ross and Speyside Groups. The Wester Ross Group is located in one of the wettest locations but had the smallest increase in mean annual rainfall between 1971 and 2022 (from 2095mm to 2158mm (Met Office, 2024)). The Speyside Group is located in one of the comparatively drier zones (mean annual rainfall 960mm for 2022 (Met Office, 2024)). At an individual site level, increased acidity was detected most markedly in the soil at Glenmore, Glen Moriston, Shieldaig and Glen Orchy.

~~Overall, loss on ignition in soils from the 2018 to 2022 survey have a mean value of 58.1% (with a wide range – minimum 1%, maximum 99%). Loss on ignition analyses were not undertaken in 1971, and the soil samples are no longer available for analysis, making comparison over that time-span impossible.~~

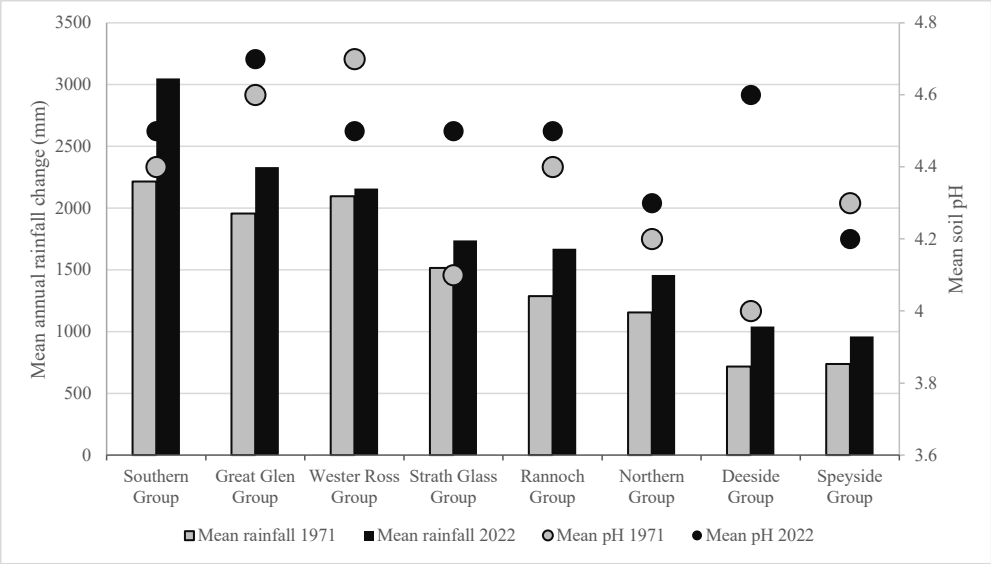


Figure 10. Change in soil pH across geographical groups, displayed with mean annual rainfall change 1971-2022

3.7 Additional threats: storm damage and disease

Winter storms were frequent during the period of the survey (Met Office, 2025a). Evidence of localised storm damage was apparent at two of the surveyed sites, Glen Moriston and Glen Garry, where trees had been blown down in the high winds.



Figure 11. Evidence of *Dothistroma* needle blight (DNB) at Shieldaig

In recent years, increasing attention has been focused on plant pathogens. In terms of the pinewoods, *Dothistroma* Needle Blight (DNB) was largely considered a problem in commercial plantations in the southern hemisphere until the mid -1990s (Bulman et al., 2013). Affecting *Pinus* species, it can lead to the death of foliage, the reduction of tree growth and sometimes widespread tree death (Marzano et al., 2017). In the Bunce survey, evidence of tree disease was recorded from around a third of sites (10), including Abernethy, Glenmore, Glen Feshie, Ballochbuie, Shieldaig (Fig. 11), Guisachan & Cougie (Fig. 12), Coulin, ~~Shieldaig (Fig. 12),~~ Loch Maree, Glen Orchy and Tyndrum, which additionally threatens the overall health of the pinewood habitat.



Figure 12. Tree disease affecting ~~the Scots~~ pines at Guisachan & Cougie

3.8 Other notable changes recorded

From the presence of recorded descriptive attributes, a range of conclusions can be made as follows. Signs of animals, including deer and livestock, rabbits, red squirrels and bones, have declined generally since 1971. However, evidence of deer remains high in some areas, for example, Glengarry. There are clear signs of fencing having taken place, being present within 9 recorded plots overall and present in 19 sites. An encouraging result is that rubbish was not recorded at any plot, having been recorded in 13 plots in 1971.

4. Result comparisons with other pinewood surveys

Aside from the Bunce survey, other surveys and reports have been published regarding the Caledonian pinewood habitat. Most recently, Trees for Life published findings from the Caledonian Pinewood Recovery Project (Rainey and Holmes, 2023) - a large-scale survey covering many aspects of the pinewoods. There have been other reviews (Bain, 1987) and inventories supported by the national public forestry agencies (Forestry Commission, 1994; Scottish Forestry, 2014); there have also been many local or targeted studies, for example Wilson and Puri (2001); Tayside Biodiversity Partnership (2002); Cameron et al. (2000); Scott et al. (2000). The Bunce survey is the only study that includes trees, ground flora, soils and other attributes, using statistically robust data from repeated plots over a 50 year time-span, giving an indication of change over that period. The Caledonian Pinewood Inventory (Forestry Commission, 1994) and Native Woodland Survey of Scotland (NWSS) (Scottish Forestry, 2014) provide information on the extent of pinewoods, invasive species and tree growth stages as part of canopy, but

lack detailed information on the composition of the woods – the ground flora, tree characteristics and soil metrics. The Trees for Life report (Rainey and Holmes, 2023) builds on the Caledonian Pinewood Inventory and identifies a few errors in the previous recording of sites, as well as discovering new pinewood fragments. Whilst it is wider ranging geographically than the Bunce survey, it doesn't sample soils or ground flora in as much detail nor can it provide the comparisons over time that the Bunce survey can. Some of the overall key messages are the same in both datasets, for example the same four species were recorded as the dominant ones in terms of cover in the pinewoods, namely ling heather (*Calluna vulgaris),* followed by purple moor grass (*Molinia caerulea)*, bilberry/blaeberry (*Vaccinium myrtillus)* and bracken (*Pteridium aquilinum)*.

The Trees for Life survey reports a shift to birch dominated woods in the south west region. In the Bunce study, in the south western sites, we detect increases in birch at Ardgour, Glengarry and Barrisdale, but not at Glen Moriston or Loch Arkaig. It is likely that there are potential worthwhile opportunities to undertake joint analyses with the Bunce and Trees for Life survey data.

5. Conclusions

The Bunce pinewood survey provides an extremely rich dataset that will be an invaluable resource for exploring the responses of Scots pine woodlands to the changing environment, such as variations in canopy cover and the effects of shade on ground flora, the effect of storm damage and tree disease on ground flora, regional variations, climate change and deposition and pollution effects, as well as site level analyses. Since there is a large degree of spatial overlap in sites between this survey and the other recent surveys highlighted above there is additional scope for synergy and richer analyses resulting from combining datasets.

Whilst positive signs of change have been detected since 1971, there are still concerns regarding the health and resilience of the Caledonian pinewood habitat. It is encouraging to see an overall increase in Scots pine (*Pinus sylvestris*) and birch (*Betula* spp.) trees, replacing planted non-native species, largely as a result of policies initiated by public forestry bodies. However, there is still a significant presence of non-native trees at many sites. The greatest increase in stem counts were associated with Scots pine (*Pinus sylvestris*) and birch (*Betula* spp.), and the growing presence of their seedlings and saplings within the field layer augurs well for the future. Both species are more frequent in the 2022 Bunce survey, birch (*Betula* spp.) by 19 % and Scots pine (*Pinus sylvestris*) by 40 %. Rowan (*Sorbus aucuparia*) seedlings and saplings, and signs of regeneration, have also increased their frequency in the field layer so it is ~~likely~~ possible that rowan will become more frequent in the future canopy, assuming no other impacts upon the population, such as grazing or disease although unlikely in sites with signs of significant deer impacts. The overall stem count for rowan (*Sorbus aucuparia*) has decreased since 1971, so this may be the case, and would be worth investigating further. Black Mount, Glen Affric, Glen Feshie and Glengarry have all seen declines in Scots pine (*Pinus sylvestris*). At Glen Affric and Glen Feshie, the decline appears to be related to the loss of mature trees as stem dbh has respectively diminished by -14.70 cm and -0.26 cm. As these sites are considered successful examples of native pinewood restoration, it is noted that both of these sites show an increase in Scots pine saplings (Table S1) so the decline in dbh could be due to the recruitment of smaller age classes, thereby reducing the mean.

There is evidence to suggest that climate change may bring about an increase in winter storms (Slingo et al., 2014; Woth et al., 2006; Seidl et al., 2017), with the accompanying damage they cause. Plant pathogens are also increasing (Gougherty, 2023). In the pinewoods, *Dothistroma* Needle Blight (DNB) is already evident in nearly

a third of the Bunce sites. Climate change, as well as other factors such as nitrogen and sulphur deposition, are also likely to be affecting soil pH values, which overall showed an increase.

Deer pressure in the pinewoods is still evident despite signs of fencing, and an overall decrease of 14.7% in deer signs across all sites. At sites showing a~~, with 19 of the Bunce sites showing an increase in signs of deer since 1971, with these sites a~~n increase in deer,~~showing a minimal change in number of smaller stemmed tree species~~, there was a mean change in plot counts of regeneration seedlings of 1.11, versus an increase of 3.35 at sites where deer appear to have decreased.~~ At sites where an increase in deer signs was noted, the mean change in the number of smaller stemmed tree species recorded was only 0.68, but 16.4 at sites where deer had decreased.~~ In terms of the ground flora, slightly fewer species appear to have been lost in terms of ~~the mean change in~~ mean absolute species numbers ~~was higher~~ at sites with a deer increase. There is also evidence of ~~a~~ small ~~decrease~~ increases in heather cover (*Erica spp., Calluna spp.*) ~~palatable species such as bilberry/blaeberry (*Vaccinium myrtillus)*~~ and ~~an increase~~ in grass~~es~~ cover where deer have increased, although the situation is complex due to the range of potential variables involved and should be investigated further.

Overall, in line with many other plant studies in the UK (Maskell et al., 2010; Marrs et al., 2013; Carvalheiro et al., 2013; Seaton et al., 2025) species richness of the vascular plants in the field layer has declined, from an average of 18.6 species in 1971 to 17.5 species in the 2020s. This change equates to an average loss of 1.1 vascular species across all plots, or a reduction of 4.5 %. This coincides with an increase in species suited to warmer, wetter climates but also ~~may~~ is likely to be related to variations in canopy cover and composition and factors driving those, in particular the large amount of management changes since the 1970s.~~.~~

~~Whilst t~~There remains work to be done in conserving this precious habitat~~;~~. ~~t~~The Bunce dataset provides a critical source of evidence to direct decision-makers towards a better future in the Scottish pinewoods.

6. Data availability

The data sets have been assigned digital object identifiers and users of the data should reference the data as follows: Smart, S.M.; Wood, C.M.; Seaton, F.M.; McMullen, A.; Ward, S.E.; Ward, R.; Routledge, G.; Massey, K.; Everard, A.; Ross, L.; Benskin, C.M.H.; Dodd, B.A. (2023). Habitat, vegetation, tree and soil data from Native Pinewoods in Scotland, 2018-2022. NERC EDS Environmental Information Data Centre. https://doi.org/10.5285/5e268e86-4a4f-4112-bf2d-c3b0179c915c (Smart et al., 2023).

The 1971 data set is supplied as described in Wood and Bunce (2016). The data are provided under the terms of the Open Government Licence (https://eidc.ceh.ac.uk/licences/OGL/plain, https://www.nationalarchives.gov.uk/doc/open-government-licence/version/3/). The metadata are stored in the ISO 19115 (2014) schema (International Organization for Standardization, 2015) in the UK Gemini 2.3 profile (Uk Gemini, 2018). Data containing analyses of change are available via Figshare at: 10.6084/m9.figshare.34574874 (Wood et al., 2026).~~.~~ Users of the data will find the following document useful, supplied as supporting documentation with the data sets: 'National Woodland Survey & Native Pine Survey Field Handbook' (Smart and Wood, 2021).

Author contributions

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Claire Wood prepared the manuscript with significant contributions from all co-~~authors, and~~authors, and is the current database manager for the Land Use research group at CEH Lancaster. Simon Smart managed the survey in 2018-2022. Fiona Seaton and Clare Benskin managed the soil data. Andy McMullen and Sue Ward were part of the field survey team. Karen Hornigold and Chris Nichols provided support from the Woodland Trust.

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References

Avery, B. W. and Bascomb, C. L.: Soil survey laboratory methods, Rothamsted Experimental Station, Harpenden (UK), 1974.

Bain, C.: Native Pinewoods in Scotland: A Review 1957-1987, Royal Society for the Protection of Birds, Edinburgh, 1987.

Bain, C.: The Ancient Pinewoods of Scotland Sandstone Press Ltd, Dingwall, 2013.

Baines, D., Sage, R. B., and Baines, M. M.: The Implications of Red Deer Grazing to Ground Vegetation and Invertebrate Communities of Scottish Native Pinewoods, Journal of Applied Ecology, 31, 776-783, https://doi.org/10.2307/2404167, 1994.

BAP: Biodiversity: the UK Action Plan, London, 1994.

Bruce, M. and Servant, G.: Fire and pinewood ecology in Scotland: a summary of recent research at Glen Tanar Estate, Aberdeenshire, Scottish Forestry, 57, 33-38, 2003.

Bulman, L. S., Dick, M. A., Ganley, R. J., McDougal, R. L., Schwelm, A., and Bradshaw, R. E.: Dothistroma needle blight, in: Infectious forest diseases, CABI Wallingford UK, 436-457, https://doi.org/10.1079/9781780640402.0436, 2013.

Bunce, R. G. H., Wood, C. M., Smart, S. M., Oakley, R., Browning, G., Daniels, M. J., Ashmole, P., Cresswell, J., and Holl, K.: The landscape ecological impact of afforestation on the British uplands and some initiatives to restore native woodland cover, Journal of Landscape Ecology, 7, 5-24, https://doi.org/10.2478/jlecol-2014-0013, 2014.

Cameron, A. D., Miller, D. R., Ramsay, F., Nikolaou, I., and Clarke, G. C.: Temporal measurement of the loss of native pinewood in Scotland through the analysis of orthorectified aerial photographs, Journal of Environmental Management, 58, 33-43, https://doi.org/10.1006/jema.1999.0306, 2000.

Cameron, E. J. F.: The regeneration of existing pinewoods, Our pinewood heritage. Proc. conference, Inverness, 1994, 155-164, 1995.

Carey, P. D., Wallis, S., Chamberlain, P. M., Cooper, A., Emmett, B. A., Maskell, L. C., McCann, T., Murphy, J., Norton, L. R., Reynolds, B., Scott, W. A., Simpson, I. C., Smart, S. M., and Ullyett, J. M.: Countryside Survey: UK Results from 2007, NERC/Centre for Ecology & Hydrology, Lancaster, http://www.countrysidesurvey.org.uk/outputs/uk-results-2007, 2008.

Carvalheiro, L. G., Kunin, W. E., Keil, P., Aguirre-Gutiérrez, J., Ellis, W. N., Fox, R., Groom, Q., Hennekens, S., Van Landuyt, W., Maes, D., Van de Meutter, F., Michez, D., Rasmont, P., Ode, B., Potts, S. G., Reemer, M., Roberts, S. P. M., Schaminée, J., WallisDeVries, M. F., and Biesmeijer, J. C.: Species richness declines and biotic homogenisation have slowed down for NW-European pollinators and plants, Ecology Letters, 16, 870-878, https://doi.org/10.1111/ele.12121, 2013.

Emmett, B., Frogbrook, Z., Chamberlain, P., Griffiths, R., Pickup, R., Poskitt, J., Reynolds, B., Rowe, E., Spurgeon, D., and Rowland, P.: CS Technical Report No. 3/07: Soils Manual, Centre for Ecology & Hydrology Wallingford, UK, http://nora.nerc.ac.uk/id/eprint/5201/1/CS_UK_2007_TR3%5B1%5D.pdf, 2008.

ESRI: Survey123, https://survey123.arcgis.com/, 2025.

Felling UK: Tree Age Calculator https://felling.uk/calculator/tree-age, last access: 24/6/2025.

Ford, H., Healey, J. R., Markesteijn, L., and Smith, A. R.: How does grazing management influence the functional diversity of oak woodland ecosystems? A plant trait approach, Agriculture, Ecosystems & Environment, 258, 154-161, https://doi.org/10.1016/j.agee.2018.02.025, 2018.

Forestry Commission: Caledonian pinewood inventory, Forestry Commission, 1994.

Froyd, C. A. and Bennett, K. D.: Long-term ecology of native pinewood communities in East Glen Affric, Scotland, Forestry, 79, 279-291, https://doi.org/10.1093/forestry/cpl015, 2006.

Gill, R. M. A. and Morgan, G.: The effects of varying deer density on natural regeneration in woodlands in lowland Britain, Forestry: An International Journal of Forest Research, 83, 53-63, https://doi.org/10.1093/forestry/cpp031, 2009.

Gougherty, A. V.: Emerging tree diseases are accumulating rapidly in the native and non-native ranges of Holarctic trees, NeoBiota, 87, https://doi.org/10.3897/neobiota.87.103525, 2023.

Holloway, C. W.: The effect of red deer and other animals on naturally regenerated Scots pine, University of Aberdeen (United Kingdom), 1967.

Kirby, K. J.: The impact of deer on the ground flora of British broadleaved woodland, Forestry: An International Journal of Forest Research, 74, 219-229, https://doi.org/10.1093/forestry/74.3.219, 2001.

Kirby, K. J., Smart, S. M., Black, H. I. J., Bunce, R. G. H., Corney, P. M., and Smithers, R. J.: Long term ecological change in British woodland (1971-2001). A re-survey and analysis of change based on the 103 sites in the Nature Conservancy 'Bunce 1971' woodland survey. Final report, Peterborough: English Nature. (English Nature Research Reports Number 653), Peterborough, 139 + appendices, http://www.nmw.ac.uk/cehstaff/Library/cr/C02026/0507024.pdf, 2005.

Kirk, G. J. D., Bellamy, P. H., and Lark, R. M.: Changes in soil pH across England and Wales in response to decreased acid deposition, Global Change Biology, 16, 3111-3119, https://doi.org/10.1111/j.1365-2486.2009.02135.x, 2010.

Kunin, W. E., Harte, J., He, F., Hui, C., Jobe, R. T., Ostling, A., Polce, C., Šizling, A., Smith, A. B., Smith, K., Smart, S. M., Storch, D., Tjørve, E., Ugland, K.-I., Ulrich, W., and Varma, V.: Upscaling biodiversity: estimating the species–area relationship from small samples, Ecological Monographs, 88, 170-187, https://doi.org/10.1002/ecm.1284, 2018.

Maddock, A.: UK Biodiversity Action Plan; Priority Habitat Descriptions, Published online, http://jncc.defra.gov.uk/PDF/UKBAP_PriorityHabitatDesc-Rev2011.pdf, http://jncc.defra.gov.uk/PDF/UKBAP_PriorityHabitatDesc-Rev2011.pdf, 2008.

Marrs, R. H., Kirby, K. J., Le Duc, M. G., McAllister, H., Smart, S. M., Oksanen, J., Bunce, R. G. H., and Corney, P. M.: Native dominants in British woodland – a potential cause of reduced species-richness?, New Journal of Botany, 3, 156-168, https://doi.org/10.1179/2042349713Y.0000000028, 2013.

Marzano, M., Fuller, L., and Quine, C. P.: Barriers to management of tree diseases: Framing perspectives of pinewood managers around Dothistroma Needle Blight, Journal of Environmental Management, 188, 238-245, https://doi.org/10.1016/j.jenvman.2016.12.002, 2017.

Maskell, L. C., Smart, S. M., Bullock, J. M., Thompson, K., and Stevens, C. J.: Nitrogen deposition causes widespread loss of species richness in British habitats, Global Change Biology, 16, 671-679, https://doi.org/10.1111/j.1365-2486.2009.02022.x, 2010.

McVean, D. N.: Ecology of Scots Pine in the Scottish Highlands, J. Ecol., 51, 671-686, 10.2307/2257754, 1963.

Met Office: Past weather events: https://weather.metoffice.gov.uk/learn-about/past-uk-weather-events, last access: 24/06/2025.

Met Office: UK temperature, rainfall and sunshine time series: https://www.metoffice.gov.uk/research/climate/maps-and-data/uk-temperature-rainfall-and-sunshine-time-series, last access: 25/3/2015.

Met Office, H., D.; Carlisle, E.; Kendon, M.; Packman, S.; Doherty, A.: HadUK-Grid Gridded Climate Observations on a 1km grid over the UK, v1.3.0.ceda (1836-2023), NERC EDS Centre for Environmental Data Analysis [dataset], https://dx.doi.org/10.5285/b963ead70580451aa7455782224479d5, 2024.

~~Miles, J. and Kinnaird, J.: The establishment and regeneration of Birch, Juniper and Scots pine in the Scottish highlands, 1979. NatureScot: Scottish Biodiversity List: https://www.nature.scot/scotlands-biodiversity/scottish-biodiversity-strategy-and-cop15/scottish-biodiversity-list last access: 11/7/24.~~

Palmer, S. C. F. and Truscott, A. M.: Browsing by deer on naturally regenerating Scots pine (Pinus sylvestris L.) and its effects on sapling growth, Forest Ecology and Management, 182, 31-47, https://doi.org/10.1016/S0378-1127(03)00026-4, 2003.

Palmer, S. C. F., Broadhead, J. E., Ross, I., and Smith, D. E.: Long-term habitat use and browsing by deer in a Caledonian pinewood, Forest Ecology and Management, 242, 273-280, https://doi.org/10.1016/j.foreco.2007.01.061, 2007.

Patterson, G., Nelson, D., Robertson, P., and Tullis, J.: Scotland's Native Woodlands: Results from the Native Woodland Survey of Scotland, Forestry Commission, Edinburgh, 2014.

Peterken, G. F. and Francis, J. L.: Open spaces as habitats for vascular ground flora species in the woods of central Lincolnshire, UK, Biological Conservation, 91, 55-72, https://doi.org/10.1016/S0006-3207(99)00040-3, 1999.

Rainey, J. and Holmes, F.: Caledonian Pinewoods Findings from the Caledonian Pinewood Recovery Project, Trees for Life, Forres, Moray, 2023.

Reynolds, B., Chamberlain, P., Poskitt, J., Woods, C., Scott, W., Rowe, E., Robinson, D., Frogbrook, Z., Keith, A., and Henrys, P.: Countryside survey: national "soil change" 1978–2007 for topsoils in great britain—acidity, carbon, and total nitrogen status, Vadose Zone Journal, 12, https://doi.org/10.2136/vzj2012.0114, 2013.

Romão, C.: Interpretation manual of European Union habitats, version EUR 28, https://www.miteco.gob.es/content/dam/miteco/es/biodiversidad/temas/espacios-protegidos/doc_manual_intp_habitat_ue_tcm30-207191.pdf, 2013.

Scott, D., Welch, D., Thurlow, M., and Elston, D. A.: Regeneration of Pinus sylvestris in a natural pinewood in NE Scotland following reduction in grazing by Cervus elaphus, Forest Ecology and Management, 130, 199-211, https://doi.org/10.1016/S0378-1127(99)00191-7, 2000.

Scottish Forestry: The Native VVoodland Survey of Scotland (NWSS), https://spatialdata.gov.scot/geonetwork/srv/api/records/BB223316-8746-4338-9056-5D9A2F0D2824, 2014.

Scottish Forestry: The Forestry Grant Scheme (FGS): https://www.forestry.gov.scot/available-funding-and-support, last access: 25/9/2025.

Scottish Government: Managing deer numbers for nature and climate: https://www.gov.scot/news/managing-deer-numbers-for-nature-and-climate/, last access: 26/03/2025.

Seaton, F., Wood, C., Hornigold, K., Kirby, K., Nichols, C., Jam, D., Dear, E., Kimberley, A., and Smart, S.: The increasing role of tree disease and decreasing influence of anthropogenic management over 50 years of woodland dynamics, Proceedings of the Royal Society B: Biological Sciences, 292, 20250554, https://royalsocietypublishing.org/doi/abs/10.1098/rspb.2025.0554, 2025.

Seaton, F. M., Robinson, D. A., Monteith, D., Lebron, I., Bürkner, P., Tomlinson, S., Emmett, B. A., and Smart, S. M.: Fifty years of reduction in sulphur deposition drives recovery in soil pH and plant communities, J. Ecol., 111, 464-478, https://doi.org/10.1111/1365-2745.14039, 2023.

Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M. J., Trotsiuk, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T. A., and Reyer, C. P. O.: Forest disturbances under climate change, Nature Climate Change, 7, 395-402, https://doi.org/10.1038/nclimate3303, 2017.

Slingo, J., Belcher, S., Scaife, A., McCarthy, M., Saulter, A., McBeath, K., Jenkins, A., Huntingford, C., Marsh, T., Hannaford, J., and Parry, S.: The recent storms and floods in the UK, Exeter, http://nora.nerc.ac.uk/id/eprint/505192/, 2014.

Smart, S. M. and Wood, C. M.: National Woodland Survey & Native Pine Survey Field Handbook, UK Centre for Ecology & Hydrology, Lancaster, 2021.

Smart, S. M., Walker, C., Sier, A. R. J., Seaton, F., Kirby, K. J., and Wood, C. M.: Fifty years of change across British broadleaved woodlands, UKCEH, Lancaster, 2024.

Smart, S. M., Bunce, R. G. H., Black, H. I. J., Ray, N., Bunce, F., Kirby, K., Watson, R., and Singleton, D.: Measuring long term ecological change in British woodlands (1971-2000). A pilot re-survey of 14 sites from the ITE/NCC 'Bunce 1971' woodland survey and two sites from the 1971 Native Pinewood survey. Volume 1, Peterborough English Nature. (English Nature Research Reports No 461a), 1-60 pp., 2001.

Smart, S. M., Wood, C. M., Seaton, F. M., McMullen, A., Ward, S. E., Ward, R., Routledge, G., Massey, K., Everard, A., Ross, L., Benskin, C. M. H., and Dodd, B. A.: Habitat, vegetation, tree and soil data from Native Pinewoods in Scotland, 2018-2022, NERC EDS Environmental Information Data Centre [dataset], https://doi.org/10.5285/5e268e86-4a4f-4112-bf2d-c3b0179c915c, 2023.

Steven, H. M. and Carlisle, A.: The native pinewoods of Scotland, Oliver & Boyd, Edinburgh, 1959.

Tayside Biodiversity Partnership: Tayside Biodiversity Action Plan: Woodland, Tayside Biodiversity Partnership, https://taysidebiodiversity.co.uk/wp-content/uploads/2015/01/Section2Woodland2.pdf, 2002.

UKCEH Countryside Survey: UKCEH Countryside Survey www.countrysidesurvey.org.uk, last access: 24/4/2026.

UK GEMINI: UK GEMINI, UK GEMINI https://www.agi.org.uk/groups/agi-gemini/, last access: 20/6/2025.

Wilson, B. and Puri, G.: A comparison of pinewood and moorland soils in the Abernethy Forest Reserve, Scotland, Global Ecology and Biogeography, 10, 291-303, https://doi.org/10.1046/j.1466-822X.2001.00226.x, 2001.

Wilson, R. Warmer and wetter: how climate change is impacting the Caledonian pine forest. Reforesting Scotland 68, 2023.

Wood, C. M. and Bunce, R. G. H.: Ecological survey of the native pinewoods of Scotland 1971, Earth Syst. Sci. Data, 8, 177-189, https://doi.org/10.5194/essd-8-177-2016, 2016.

Wood, C. M., Smart, S. M., and Bunce, R. G. H.: Woodland Survey of Great Britain 1971–2001, Earth Syst. Sci. Data, 7, 203-214, https://doi.org/10.5194/essd-7-203-2015, 2015.

Wood, C., Smart, S. M., Seaton, F., McMullen, A, Ward, S. E.. Hornigold, K., Nichols,C., Benskin. C.: Ecological change data from native Scottish pinewoods 1971 - 2022: Bunce pinewoods re-survey. figshare. Dataset. https://doi.org/10.6084/m9.figshare.34574874.v1, 2026.

Woth, K., Weisse, R., and von Storch, H.: Climate change and North Sea storm surge extremes: an ensemble study of storm surge extremes expected in a changed climate projected by four different regional climate models, Ocean Dynamics, 56, 3-15, https://doi.org/10.1007/s10236-005-0024-3, 2006.

Virginia Tree Care, Tree Age Calculator, https://virginiatreecare.com/tree-age-calculator/) last access: 11/3/2026

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