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Tree and scrub species of the Treeline Ecotone in the Cairngorms National Park, Scotland

Andy Amphlett
Grantown on Spey, Scotland

Corresponding author: amphlett1958@gmail.com

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Abstract
Expansion of native woodland, in places up to a natural treeline with montane scrub above, is a priority within the Cairngorms National Park (CNP). Thirty native and six non-native tree and scrub species (phanerophytes and nano-phanerophytes) have records within the CNP treeline ecotone, defined as between 500 and 1000 m altitude. The altitudinal distribution (using a 25 m altitude interval) of the native species is analysed at monad (1 km grid square) precision. Results are displayed as the raw monad counts, monad counts calibrated to take account of altitudinal recording bias, and calibrated monad counts as a percentage of monads within the CNP. Summing the calibrated species monad counts in each altitude (25 m) class provides a combined measure of spatial and altitudinal frequency.

The same ten species occupy the top ten rank frequency positions in each of the altitudinal zones (forest line, treeline woodland and montane scrub). Therefore, across the whole treeline ecotone, we can expect woodland and scrub to comprise the same mix of species, though their proportions will vary, both altitudinally and geographically. *Juniperus communis* and *Sorbus aucuparia* are the two most widespread species in all three zones, *Pinus sylvestris* is in 4th or 5th place, while *Betula pubescens* is in 7th or 8th place.

In Norway there is typically a 'birch belt', in which *Betula pubescens* var. *pumila* (L.) Govaerts forms the highest treeline, above the altitudinal limit of *Pinus sylvestris*. It has recently been argued that an equivalent birch belt used to be present in Scotland, and should be a target for conservation interventions to restore it. The present analysis does not provide support for this view. While the low rank position of *B. pubescens* may reflect lack of seed sources and browsing pressure, that *P. sylvestris* occurs to very high altitudes, and comprises a higher percentage of the combined CNP calibrated taxon monad totals above 700 m than it does from 500-700 m strongly suggests that *B. pubescens* will not be able to form an exclusive 'birch belt' at elevations above the *P. sylvestris* altitudinal limit.

While *B. pubescens* var*. pumila* has not been confirmed as occurring in Scotland, introgression from *B. nana* into *B. pubescens* is widespread here, though only at a low level. The most parsimonious scenario that explains this is that during the post glacial period any highly introgressed *B. pubescens*, derived from tetraploid hybrids crossing with *B. pubescens,* rapidly crossed with 'ordinary' *B. pubescens*, hence diluting and dispersing the genetic contribution of *B. nana*. Within the CNP,

Mar Lodge NNR is the most likely location where future hybridisation and introgression of *B. nana* into *B. pubescens* will occur.

Keywords: forest line; scrub line; montane scrub; mountain birch; birch belt; introgression

Introduction

Expansion of native woodland, through natural regeneration and planting is a priority within the Cairngorms National Park (CNP) (Fig. 1). The Cairngorms National Park Partnership Plan 2022-27 includes amongst its aims, to *'Increase the amount of woodland in the National Park to support larger, more natural woodlands, expanding in places up to a natural treeline, providing connections across river catchments and around the central core of the mountains*'. (A2. Woodland expansion); and, *'Creating a more natural transition from woodland to montane scrub to upland heath*' (Policy A5), (CNPA, 2022). Cairngorms Connect http://cairngormsconnect.org.uk/ a partnership of four adjoining land owners, comprising 13% of the CNP area (Fig. 1), is committed to a 200-year vision to enhance and restore habitats, species and ecological processes, including by expanding woodland to its natural altitudinal limit, including high altitude sub-alpine scrub. The National Trust for Scotland's Mar Lodge NNR https://www.nts.org.uk/visit/places/mar-lodge-estate (Fig. 1), encompassing 6.5% of the CNP area, is also committed to expansion of native woodland upwards towards a natural treeline (NTS, 2012, 2022).

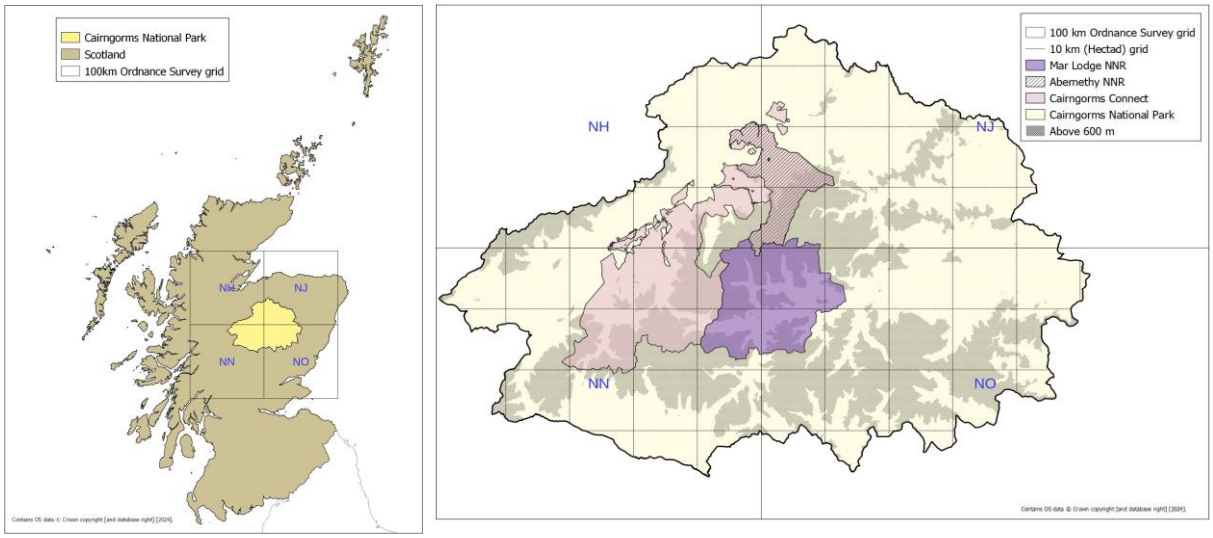

Figure 1. Cairngorms National Park location (left map). Abernethy and Mar Lodge NNRs, Cairngorms Connect, land above 600 m (right map)

In parts of the CNP there have been significant, rapid reductions in wild deer densities in support of these aims. Gullet *et al.* (2023) summarise deer reductions by culling over the last two decades in parts of the Cairngorms Connect project area. Glenmore & Inshriach Forests (Forestry and Land Scotland) from 34 deer km^{-2} in 2001 to 7.5 deer km^{-2} in 2019. Glen Feshie (Wildland) from >35 deer km^{-2} in 2000 to 2-5 deer km^{-2} in 2021 and Glen Tromie (Wildland), from 45 deer km^{-2} in 2003 to 1.9 deer km^{-2} in 2020. Rao (2017) summarises reductions of *Cervus elaphus* (red

deer) within a 12,487ha 'regeneration zone' within Mar Lodge NNR. From a high of 21.2 km^{-2} (prior to the start of a deer reduction programme in 1995) red deer density was reduced to *c.*8 km^{-2} in 2001 and then to 0.7 km^{-2} in 2016. From 2017 to 2023 red deer densities in this area have remained <1 km^{-2} (NTS unpublished data).

The Native Woodland Model (Towers *et al.*, 2004), predicts woodland types which could (hypothetically) develop under current climate and soil conditions, if there were no additional constraints. This would be described as *potential-natural* woodland, *sensu* Peterken (1981, 1996). The Native Woodland Model was used to predict potential habitats below and above 600 m altitude in the Cairngorms Connect project area (Amphlett, 2022). Below 600 m all terrestrial habitats are potentially capable of supporting some degree of tree and scrub cover, although 26% of that area is predicted to only support scattered trees and scrub. Above 600 m the model suggests 75% of terrestrial habitats could support some degree of tree and scrub cover, of which 58% would be scattered trees and scrub. It must be stressed that the model's outputs are entirely hypothetical predictions. The model assumes that the only constraints are soils and climate and it makes no allowance for availability of seed or impacts of wild or domestic herbivores.

The 'treeline ecotone'

Definitions used in this paper (Fig. 2) follow those adopted by Gilbert (2010). The '**treeline ecotone**' comprises '**treeline woodland**' and '**montane scrub**'.

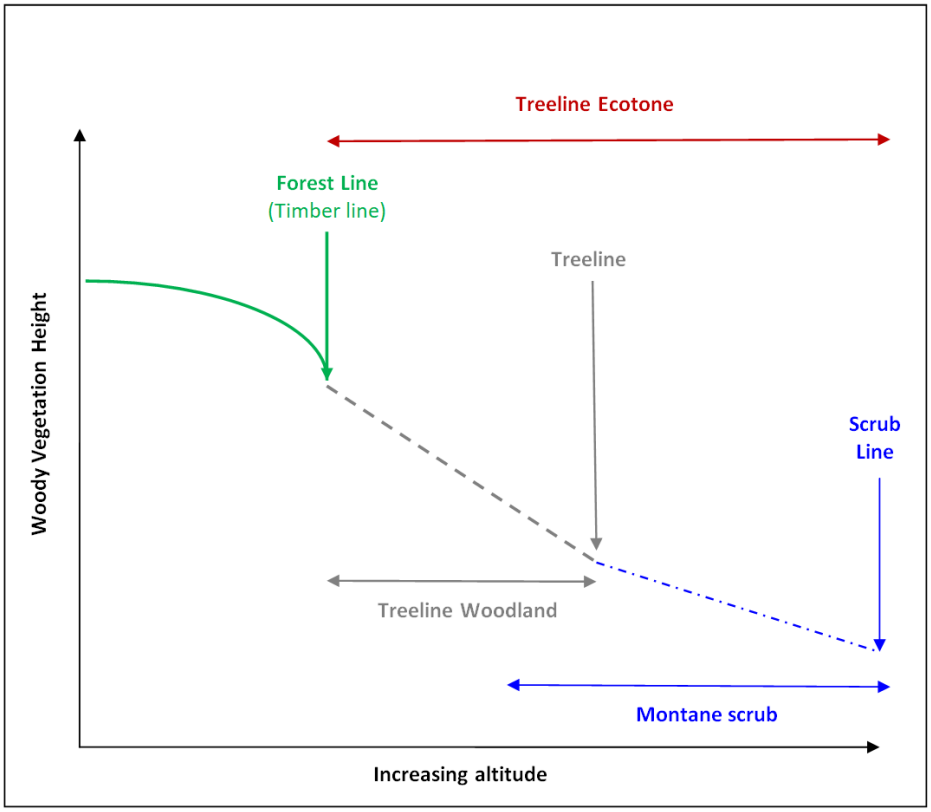

Figure 2. The Treeline Ecotone (Gilbert, 2010)

The lower altitudinal limit of treeline woodland is the '**forest line**' (also known as the 'timber line'), the altitudinal limit of erect tree growth above which trees

become wind-pruned and increasingly stunted. In the Cairngorms this change in growth form is most apparent in *Pinus sylvestris* (Scots pine). Trees growing above the forest line show a number of characteristic features including: 'flagging' (branches mainly found on the lee side of the trunk); presence of a low 'skirt' of branches, hugging the ground; twisted trunks and branches; and reduced height (Amphlett, 2022).

'**Treeline woodland**' comprises stunted trees above the forest line. The component tree species of treeline woodland are those present in the lower forest that can continue to grow in the adverse conditions at higher altitude. The upper limit of this zone (the '**treeline**') is usually defined as the altitude of the uppermost trees with a minimum height of 2 m.

'**Montane scrub**' comprises a variety of tall-shrub species, tolerant of the increasingly extreme climatic conditions, extending from a little below the treeline up to the scrub line. The tall-shrubs grow mixed with tree species at the lower edge, potentially as a nearly continuous canopy, but become increasingly broken into scattered clumps in mixture with dwarf-shrubs and graminoids at the upper edge. The '**scrub line**' is the potential altitudinal limit beyond which tall-shrub species cease to grow or are no more than occasional in montane (alpine) zone vegetation.

Field observations of *P. sylvestris* in the Rothiemurchus, Glenmore & Abernethy area of the north-west Cairngorms (Amphlett, 2003), demonstrated that the average forest line, on north-west to south facing slopes is at about 560-590 m altitude. However, on isolated hilltops, e.g. Carn na Chnuic (506 m) and Carn na Loinne (498 m), both in Abernethy NNR, the forest line can be lowered to just under 500 m.

Pears (1968) estimated the potential treeline in the Cairngorms to vary from 610 m in the most exposed locations to 685 m in reasonably sheltered sites. At Creag Fhiaclach, the most natural treeline in the UK (Shaw & Thompson, 2006) he found the treeline to be at 640 m. At this location the treeline has been ± stable for the last 1000 years (Nagy *et al.*, 2013). On south facing slopes of Meall a' Bhuachaille (NH9910), *P. sylvestris* scrub at a density of several hundred trees ha^{-1} extends above the forest line to at least 650 m, with greater than 100 ha^{-1} up to 690 m (Amphlett, 2022). The altitude of this developing treeline is in accord with Pears' earlier predictions.

Pears (1968) noted that the lower level of natural sub-alpine *Juniperus communis* (Juniper) scrub is a useful guide to the position of the natural treeline. This scrub community is especially frequent on the slopes above Loch Avon, in upper Strath Nethy & along the Lairig an Laoigh. Here, surveys by RSPB in 2001 and 2016/17 south of Ordnance Survey northing 05000, recorded *J. communis* in 622 out of 818 100 m grid cells between 680-900 m altitude. Here *Juniperus* is rare above 950 m altitude.

A range of indicative values can be given for the altitudes of the forest line, treeline and scrub line in the Cairngorms.

- Treeline woodland from the forest line at (500) - 560 - (590) m to the treeline at (610) - 650 - (690) m.
- Montane scrub from *c.*650 m to the scrub line at 950 - (1000) m, above which tall-shrub species cease to grow or are no more than occasional in montane (alpine) zone vegetation.

In this paper the treeline ecotone is defined as between 500 and 1000 m altitude.

Trees and shrubs of the treeline ecotone

A search was made on the BSBI Distribution Database (DDb) for records within or intersecting the CNP boundary, at grid reference precisions up to and including hectad, of all trees and woody shrubs (with their bud-bearing shoots in the air), >2 m tall (phanerophytes) and <2 m but >0.25 m tall (nano-phanerophytes) (Hill *et al.*, 2004). The initial search returned 148 taxa, of which 43 taxa had one or more records above 500 m altitude, based on the minimum altitude of the record grid references. Six native dwarf shrub species were excluded from further consideration: *Calluna vulgaris* (Heather), *Erica cinerea* (Bell Heather), *Erica tetralix* (Cross-leaved Heath), *Genista anglica* (Petty Whin), *Vaccinium myrtillus* (Blaeberry) and *Vaccinium uliginosum* (Bog Blaeberry), as well as *Lonicera periclymenum* (Honeysuckle). That left 30 native (Table 1) and 6 alien species (Appendix 1).

The number of unique occurrence grid references and unique 100 m grid squares were calculated for each taxon, at all altitudes and above 500 m, based on the minimum altitude within each record's grid reference square. Altitudes were calculated within the DDb, using the SRTM 90 m Digital Elevation Model https://www2.jpl.nasa.gov/srtm/coverage.html. Non-wild and planted occurrences (where noted in the DDb) were excluded, as were any doubtful records. Most records of recent conservation planting of montane *Salix* species are yet to be incorporated into the DDb, so are also excluded. If a centroid grid reference had been used, and the grid reference was at monad (1 km grid square) or better precision, the record was also excluded.

Table 1. Native phanerophytes (Ph) and nano-phanerophytes (Pn) recorded >500m altitude in the Cairngorms National Park. From the DDb January 2024.

Species	Unique grid references	Unique 100 m grid squares	% unique grid references >500 m	% unique 100 m grid references >500 m	Lifeform
Alnus glutinosa	960	558	0.3	0.5	Ph
Betula nana	1201	855	87.7	91.2	Pn
Betula pendula	1067	583	1.9	2.2	Ph
Betula pubescens	1647	948	10.8	11.8	Ph
Corylus avellana	508	259	2.0	2.7	Ph
Cytisus scoparius	1203	568	3.9	6.7	Pn
Fraxinus excelsior	381	161	0.3	0.0	Ph
Ilex aquifolium	174	92	0.6	1.1	Ph
Juniperus communis	7767	5379	57.3	53.3	Ph

Myrica gale	951	541	1.4	0.7	Pn
Pinus sylvestris	4793	3773	20.1	22.2	Ph
Populus tremula	1445	839	1.7	2.0	Ph
Prunus avium	208	59	1.9	5.1	Ph
Prunus padus	591	299	0.2	0.3	Ph
Rosa mollis agg.	165	40	2.4	7.5	Pn
Rosa spinosissima	43	20	4.7	15.0	Pn
Rubus idaeus	1042	429	3.0	3.3	Pn
Salix arbuscula	33	10	48.5	100.0	Pn
Salix aurita	1499	820	22.1	30.6	Pn
Salix caprea	709	361	6.9	8.0	Ph
Salix cinerea	584	263	4.3	4.2	Ph
Salix lanata	69	38	78.3	100.0	Pn
Salix lapponum	459	263	80.0	95.1	Pn
Salix myrsinifolia	192	63	34.4	69.8	Pn
Salix myrsinites	283	155	82.7	94.2	Pn
Salix phylicifolia	402	219	21.9	32.0	Ph
Salix repens	1151	546	17.4	25.6	Pn
Sorbus aucuparia	3513	2437	25.8	31.3	Ph
Sorbus rupicola	29	14	10.3	14.3	Ph
Ulex europaeus	667	274	0.6	1.5	Pn

In addition to the taxa listed in Table 1, 19 *Salix* (Willow) hybrids have been recorded above 500 m altitude. These are listed in Appendix 2. An example DDb query, used to create Table 1 and Appendix 1, is in Appendix 3.

Record grid reference precision varies from 1 m to 10 km. As the minimum altitude within grid reference squares is used in Table 1 and Appendix 1, low precision records of taxa typically found above the forest line may artificially reduce the reported number of unique occurrence grid references above 500 m. Comparison of the % unique grid references and the % unique 100 m grid references >500 m is therefore advised.

Distribution of records and altitudinal recording bias

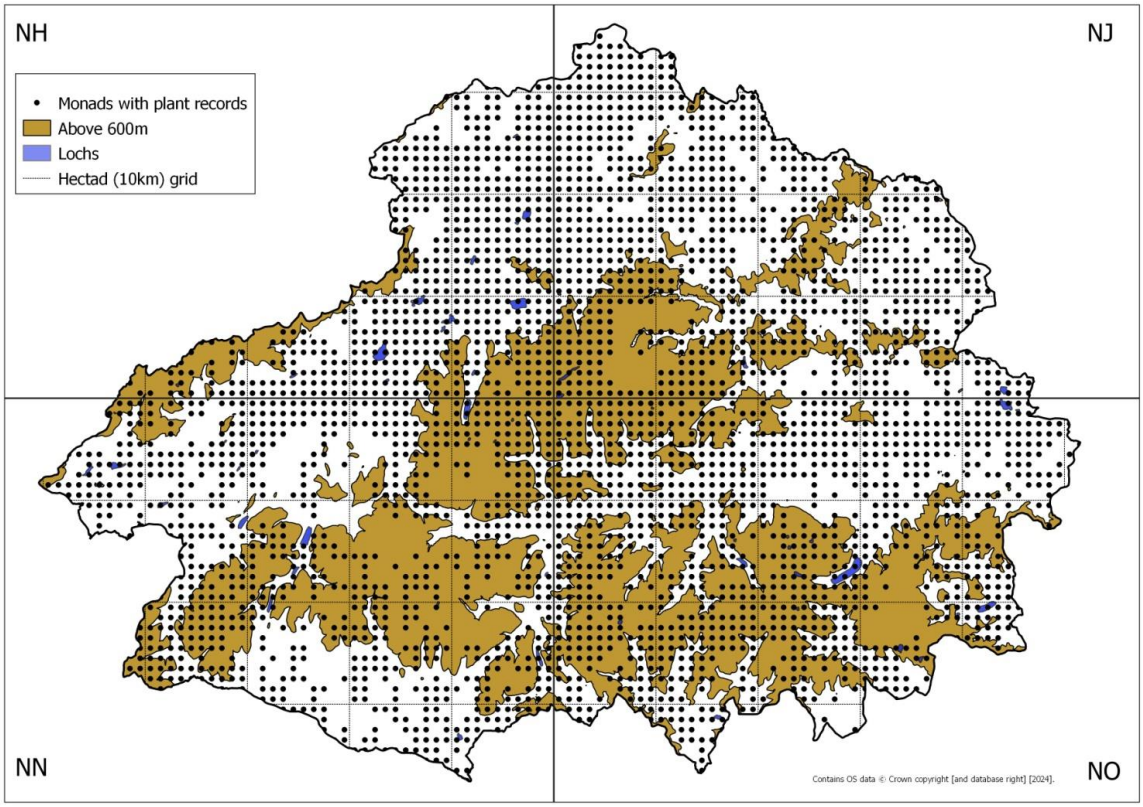

Figure 3. Monads within and intersecting the Cairngorms National Park boundary with plant records in the BSBI Distribution Database (DDb) at January 2024

4774 monads lie within or intersect the boundary of the CNP. Of these, 3273 (68.6%) have one of more plant records in the DDb (Fig. 3). There is a marked altitudinal bias in recording (Fig. 4).

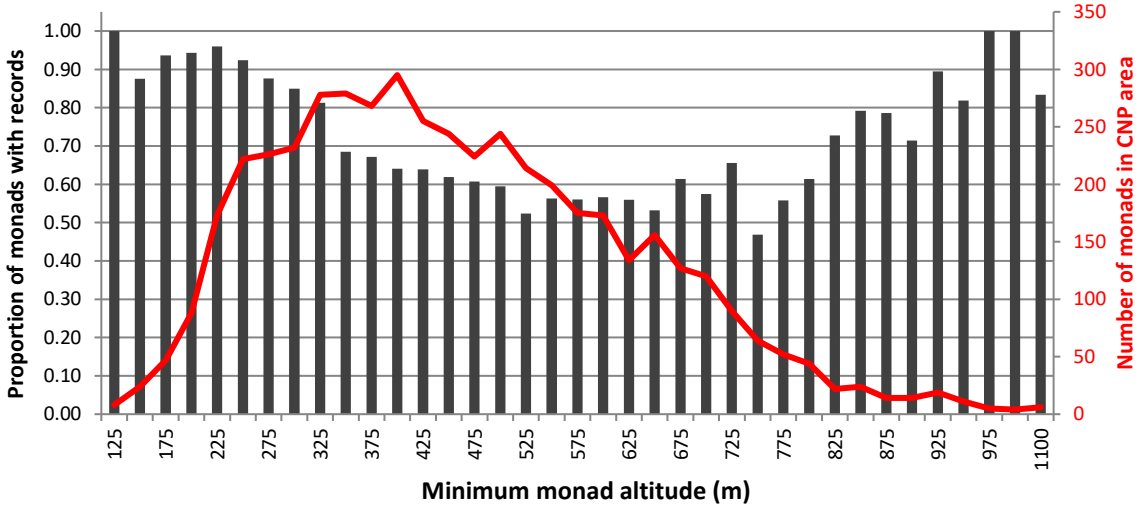

Figure 4. Proportion of Cairngorms National Park monads with plant records on the BSBI DDb at January 2024

Below 325 m, 88.6% of monads have records, and above 800 m, 80.6% of monads have records. In contrast, at intermediate altitudes, 325-800 m, only 60.4% of monads have records, and in altitude class 725-750 m only 46.9% of monads have records.

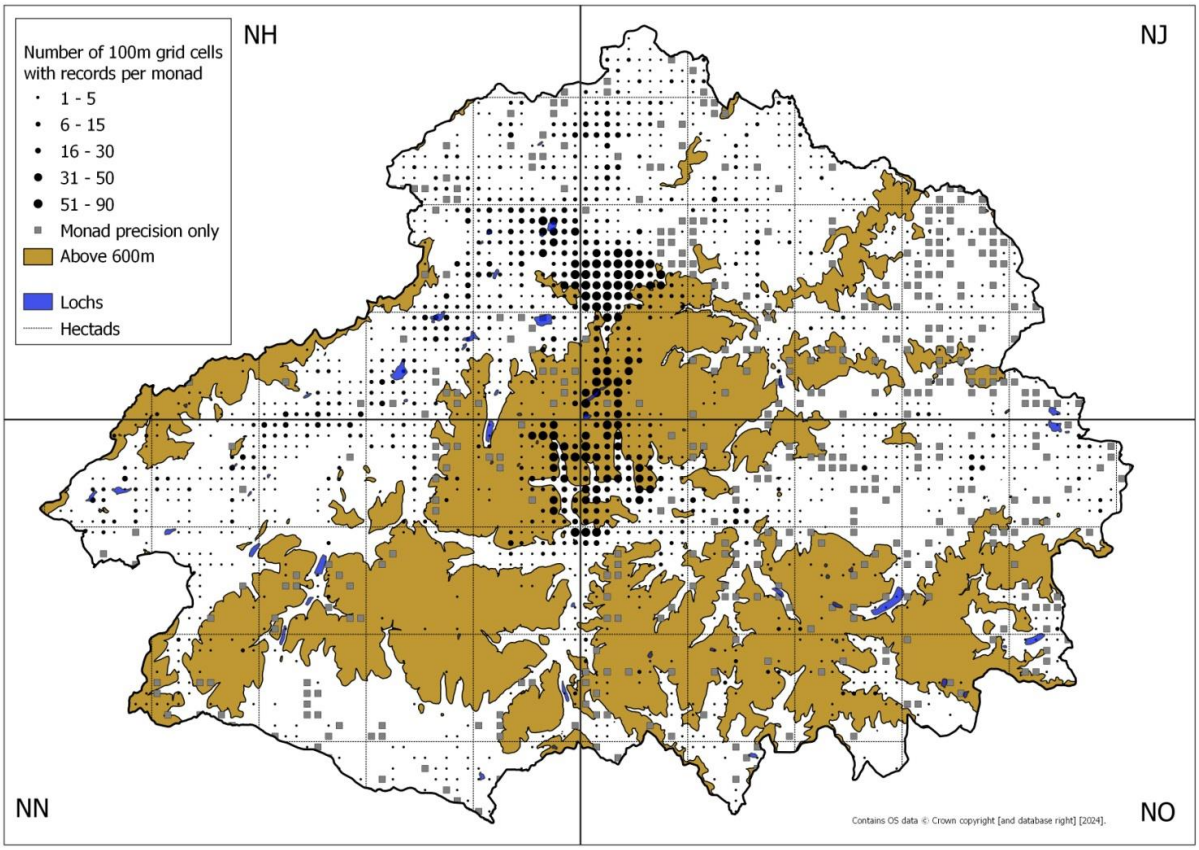

Figure 5. Number of 100 m grid cells per monad in the Cairngorms National Park, with records of any of 30 native phanerophyte and nano-phanerophyte species listed in Table 1

High precision records (100 m or better) of the 30 native species listed in Table 1, from above 500 m altitude, are heavily biased to the Abernethy and Mar Lodge National Nature Reserves (Fig. 5), where detailed systematic transect surveys of natural regeneration have been undertaken.

Native phanerophytes and nano-phanerophytes with records >500 m in the Cairngorms National Park

A chart (Fig. 6-38) for each of the 30 native species analysed shows:

- The number of monads with one or more records per 25 m altitude height class. The x axis labels are the upper limits of the 25 m altitude bands.
- The calibrated number of monads with one or more records in each 25 m altitude height class. The calibration factor (CF) used was calculated for each 25 m altitude height class; CF = 1 / (number of monads with records of any vascular plant taxon / total monads in CNP). Mean CF = 1.44 (range 1.0-2.13). The calibrated monad values indicate how many monads would be expected to contain a species if all monads in the CNP had been recorded

with the same average survey effort as the recorded monads (Fig. 3). It does not indicate the total number of monads occupied by each species, which is unknown. Other potential biases, e.g. increased visibility of seedlings / saplings at higher altitude with lower sward height, are not accounted for.

- The calibrated number of monads as a percentage of the total number of CNP monads per 25 m altitude height class.

Excluding those species with less than four monad occurrences, brief accompanying text gives details of the percentage of the calibrated monad total and the percentage occupied 100 m grid cells that are at >500 m minimum grid square altitude. The maximum altitude recorded in the CNP is also given. The national (GB) status where applicable is given for each species: red list (above Least Concern), nationally rare and nationally scarce.

Alnus glutinosa (Alder)

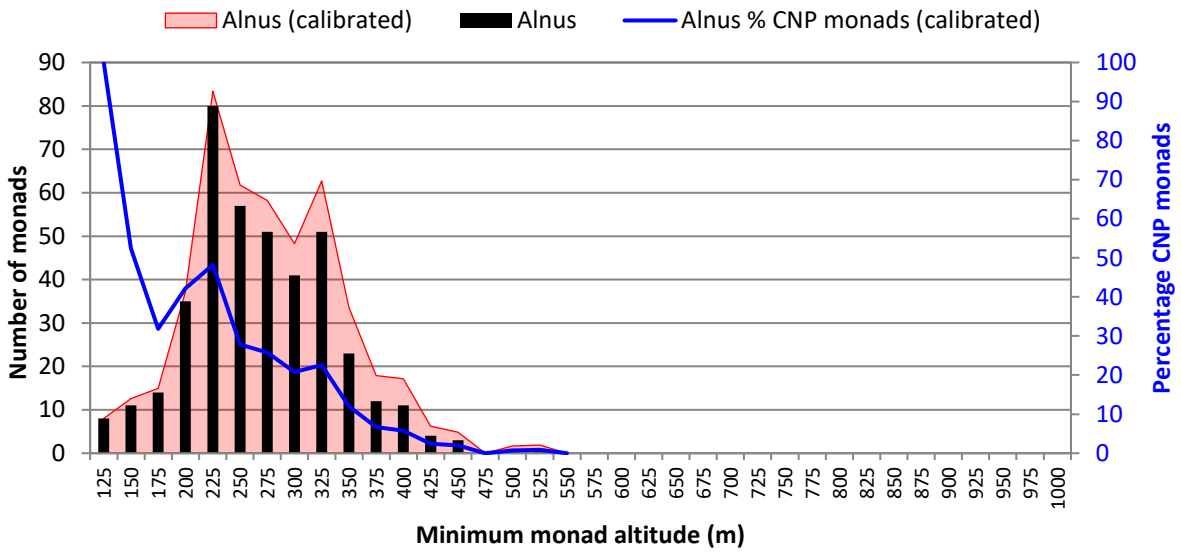

Figure 6. *Alnus glutinosa*

In the CNP 0.4% of monads (calibrated) and 0.5% of 100 m grid cells with *A. glutinosa* have minimum altitudes above 500 m. The only records at >500 m altitude are three records in monad NO0397 (Mar Lodge NNR: Glen Derry), the highest at 527 m. *Alnus glutinosa* has also been planted in monad NJ0011 (Abernethy NNR) at a maximum 547 m, and at one location in monad NO1479 (Cairnwell Burn) at a minimum altitude of 512 m.

McVean and Ratcliffe (1962) noted that *A. glutinosa* did not set 'good seed' at that time above 900-1000 ft (275-305 m), and therefore moribund alderwoods above that altitude were "*doomed irrespective of any changes in land management which might allow the growth of seedlings*". The CNP records indicate a reduction in frequency of *A. glutinosa* above 325 m, but with 17.7% of monads (calibrated) with minimum altitude above that elevation.

***Betula nana* (Dwarf Birch)** Nationally Scarce

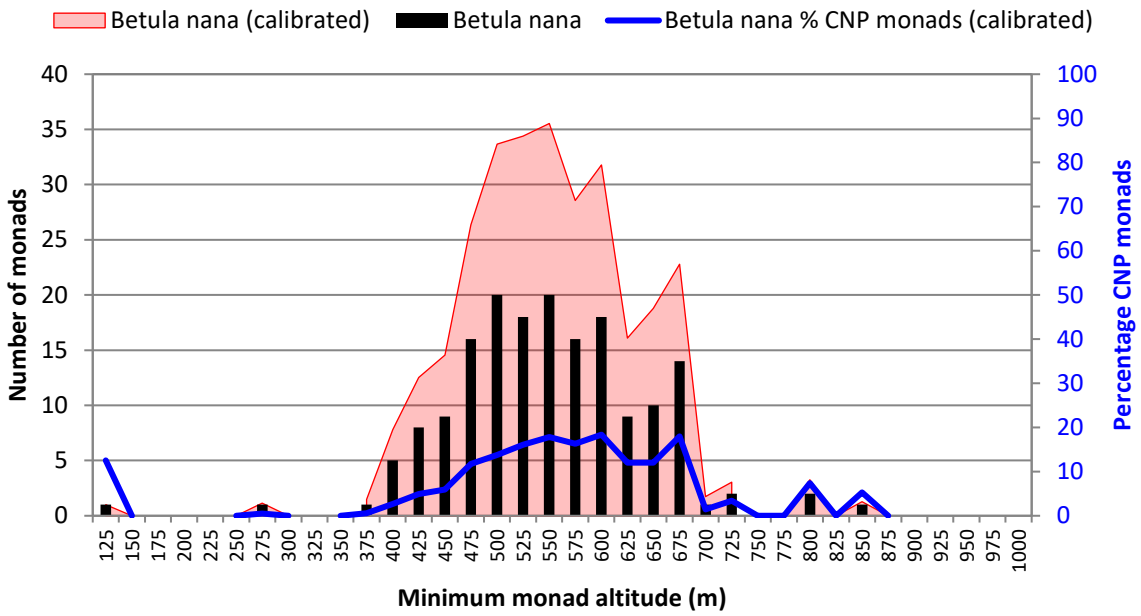

Figure 7. *Betula nana*

All locations of *B. nana* within the CNP are >400 m, and 67% of monads (calibrated) and 91% of occupied 100 m grid cells have minimum altitudes above 500 m. There is one monad (NN9062) record in the height class 100-125 m, but the location is Craig Fonvuick, just outwith the CNP boundary, which has a maximum height of 413 m. The highest altitude record is on Craig Derry (Mar Lodge NNR, NO048979) at 860 m.

The largest and most extensive populations are at Mar Lodge NNR, where the species is recorded from 600 100 m grid cells in 89 monads. These populations extend into upper Glen Feshie forming what may be the largest continuous population of *B. nana* in Scotland (S. Rao, pers. comm.). At Abernethy NNR it is recorded in 167 100 m grid cells in 19 monads.

Typically associated with flat or gently sloping blanket bog, it may have been restricted to this habitat in Great Britain by historical land management e.g. burning or overgrazing (Watts & Dines, 2023). At the head of Loch Muick (NO2681 *etc*.) it grows among *Calluna* heath and granite block scree, including areas of shallow mineral soil rather than its more usual habitat of M19 *Calluna vulgaris* - *Eriophorum vaginatum* blanket mire (Rodwell *et al*., 1991, MacKenzie, 2000). At Mar Lodge NNR, following reduction in grazing and browsing pressure, *B. nana* is now noted in much drier heath areas, growing to 1 m tall (S. Rao, pers. comm.).

The known altitudinal range of *B. nana* in the CNP almost entirely spans the least well recorded altitudes, hence the marked difference between observed and calibrated monad totals. It may be significantly under-recorded.

Betula pendula (Silver Birch)

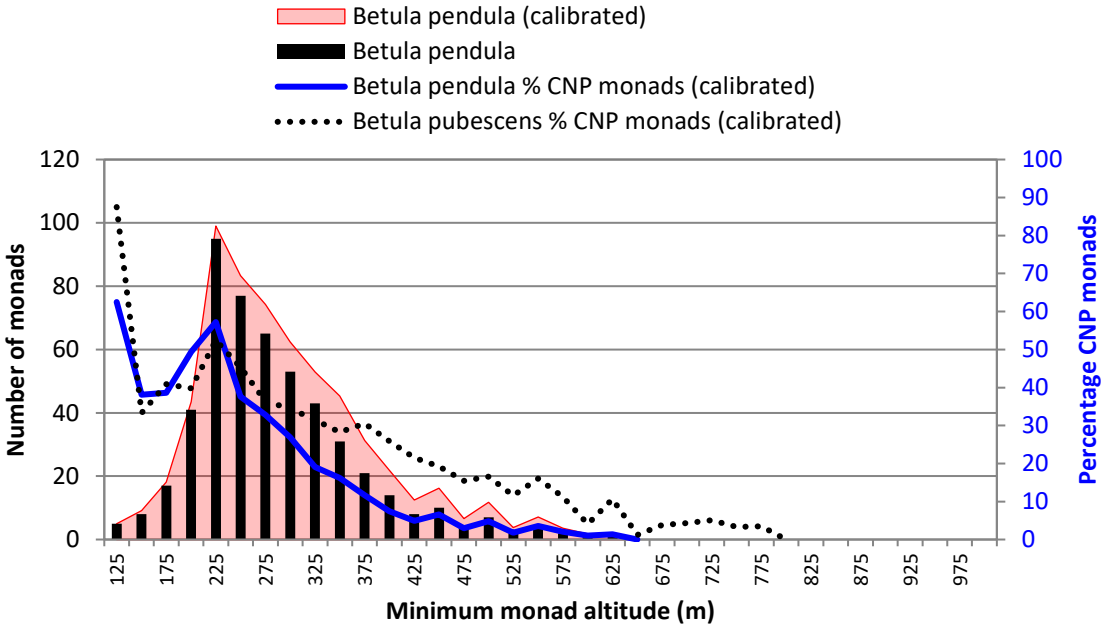

Figure 8. *Betula pendula*

Forbes and Kenworthy (1973) did not record *B. pendula* above 1300 ft (*c.*400 m) on Deeside, and Worrell & Malcolm (1998) commented that *B. pendula* is not usually found above 350 m in the Highlands, and reaches this height only in sheltered inland locations.

In the CNP 3.0% of monads (calibrated) and 2.2% of 100 m grid cells with *B. pendula* have minimum altitudes above 500 m. A small tree was recorded at NN981972 at 575 m (Lairig Ghru, Mar Lodge NNR), and a single browsed sapling was found at NO004965 at 821 m (Sron Riach, Mar Lodge NNR).

Wang *et al.* (2014) demonstrated a morphological continuum between the leaf shapes of *B. pendula* and *B. pubescens* and that this is inherent to the species, and hybridisation is not its major cause. In the zone of leaf morphology overlap between the two species, identifications using leaf shape had an error rate of more than 10 percent. It is likely that some records of *B. pendula* in the chart above were misidentified.

Betula pubescens (dotted line Fig. 8) is more frequent above 225 m than *B. pendula*, and its range extends to higher altitude. Forbes and Kenworthy (1973) found that on Deeside the switch in dominance of the two *Betula* species occurred at 1000 ft (*c.*300 m).

Betula pubescens (Downy Birch)

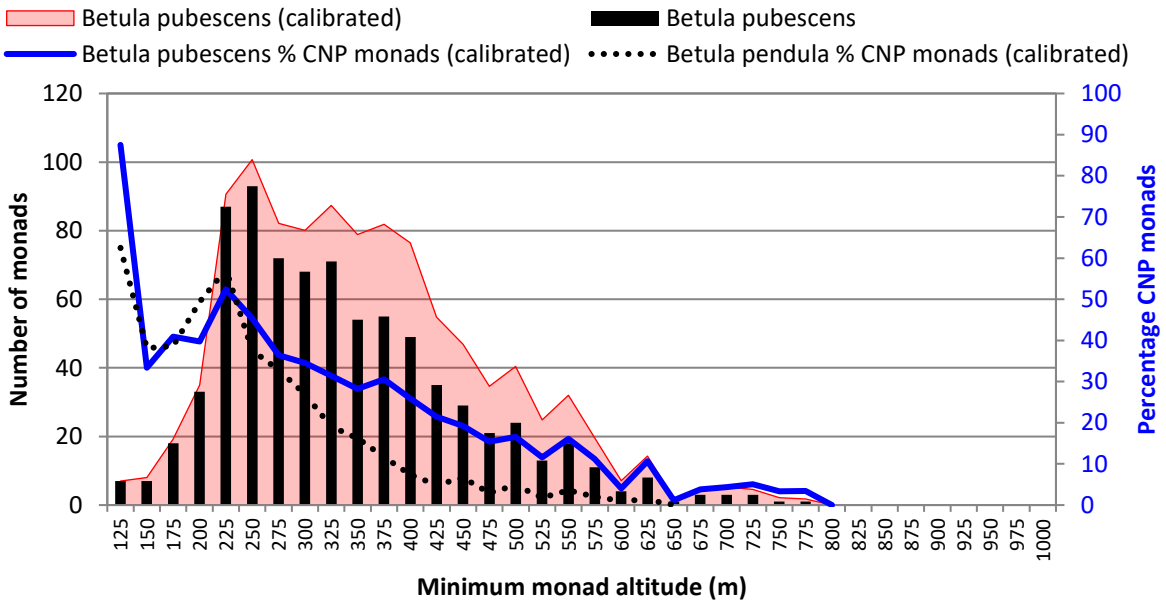

Figure 9. *Betula pubescens*

Records of both *B. pubescens* subsp. / var. *pubescens* (typically found at lower altitudes) and *B. pubescens* var. *fragrans* Ashburner & McAll. are included here. The latter is the characteristic small-leaved upland birch in the Highlands of Scotland. See Amphlett (2021) for discussion of the taxonomy and naming of *Betula*.

In the CNP 11.3% of monads (calibrated) and 11.8% of 100 m grid cells with *B. pubescens* have minimum altitudes above 500 m. *Betula pubescens* is more frequent above 225 m than *B. pendula* (dotted line in Fig. 9) and its range extends to higher altitude. There is an exceptional record at 1015 m at NJ012059 (north of Cnap Coire na Spreidhe), presumably a seedling or small sapling, with another 10 localities with minimum altitudes above 700 m.

Corylus avellana (Hazel)

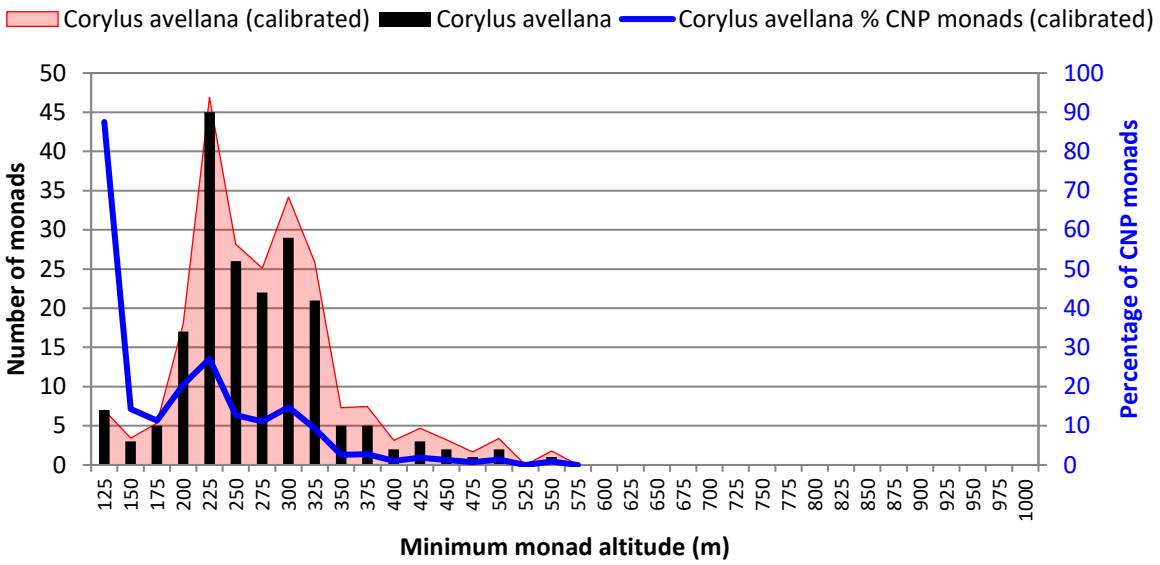

Figure 10. ***Corylus avellana***

In the CNP 0.8% of monads (calibrated) and 2.7% of 100 m grid cells with *C. avellana* have minimum altitudes above 500 m. The highest record is at NO309755 (Coire of Bonhard) at minimum 717 m. This record dates from 1982 (pre-GPS) and the site description "Various stunted trees (1 hazel, 1 holly, 2 aspen, 3 *Salix caprea*, several rowans, 3 larch and broom) scattered over rocks" suggests the site may have been the 100 m grid square immediately to the south, which has a minimum altitude of 645 m. At NJ015087 (Abernethy NNR: Stac na h-Iolaire) a single bush was recorded on the crag, at a minimum 640 m.

Cytisus scoparius (Broom)

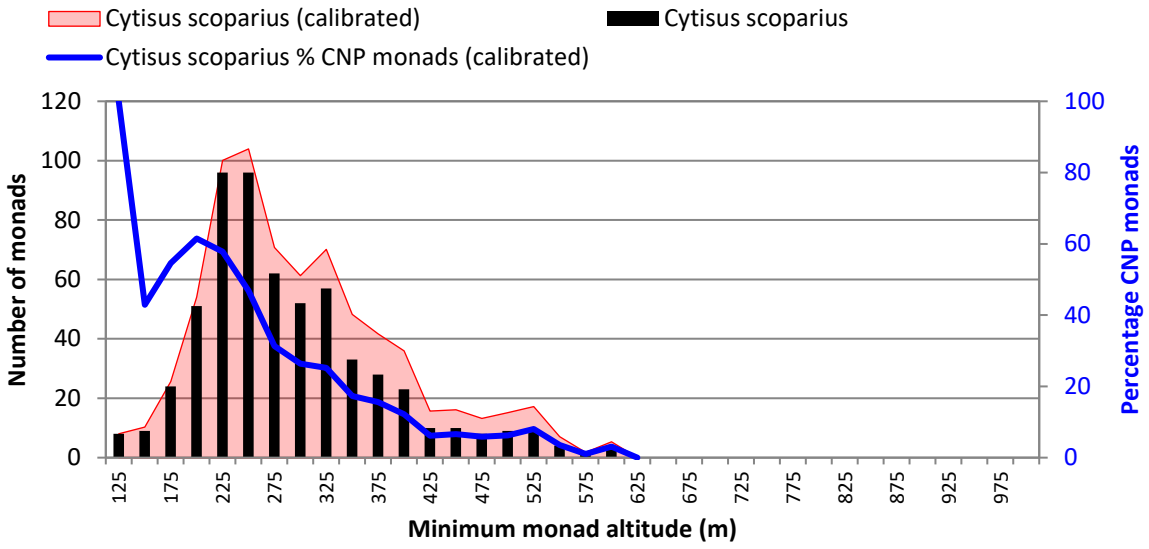

Figure 11. *Cytisus scoparius*

In the CNP 4.4% of monads (calibrated) and 6.7% of 100 m grid cells with *C. scoparius* have minimum altitudes above 500 m. The highest record is at NO309755 (Coire of Bonhard) at minimum 717 m. This record dates from 1982 (pre-GPS) and the site description (see under *Corylus avellana*) suggests the site may have been the 100 m grid square immediately to the south, which has a minimum altitude of 645 m. There is one other record from >700 m, at NJ035080 (Abernethy NNR: Choire Dhuibh), minimum 711 m.

Fraxinus excelsior (Ash)

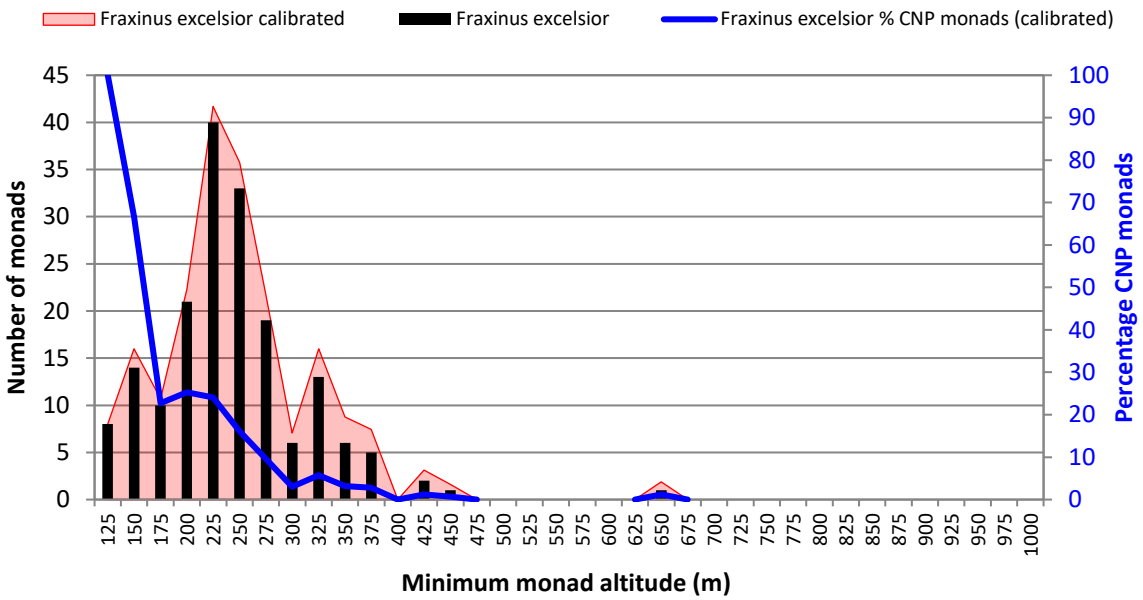

Figure 12. ***Fraxinus excelsior***

There is a single record >500 m, at NO3475 (Loch Brandy), minimum altitude 631 m. The next highest are four records between 450-500 m, including one at 460 m (West Dunandhu), a veteran tree by a ruin. While the Loch Brandy record is at an atypically high altitude for the CNP area, the DDb has 13 other records of *F. excelsior* from >500 m elsewhere in Scotland and in Wales.

Ilex aquifolium (Holly)

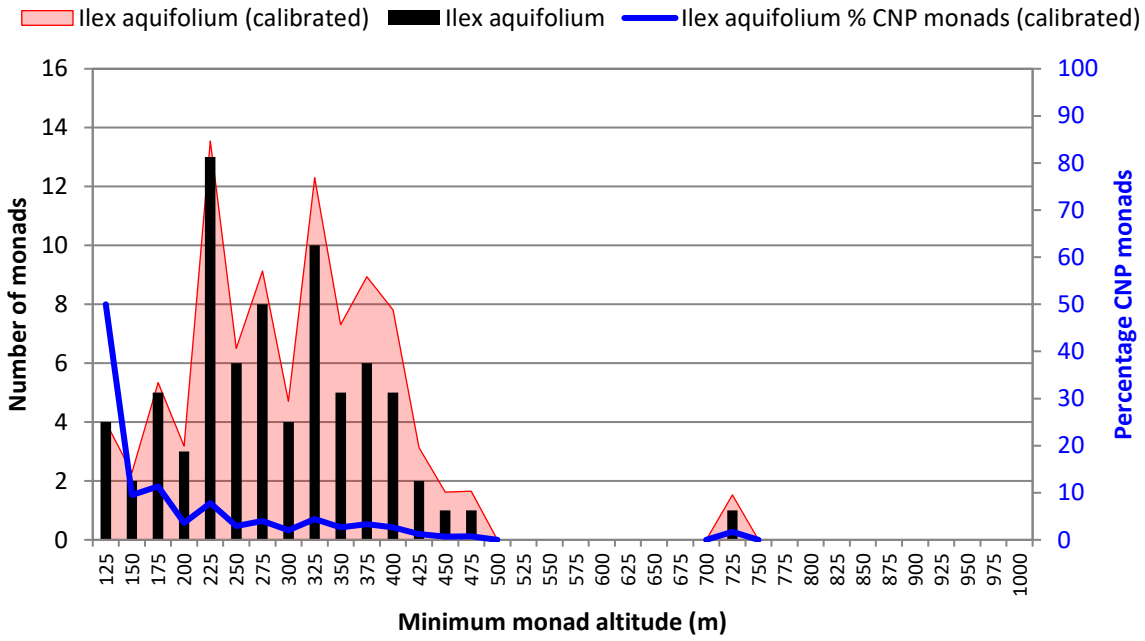

Figure 13. ***Ilex aquifolium***

The only CNP record from >500 m is at NO309755 (Coire of Bonhard) at minimum 717 m. This record dates from 1982 (pre-GPS) and the site description (see under *Corylus avellana*) suggests the site may have been the 100 m grid square immediately to the south, which has a minimum altitude of 645 m. The next highest are nine CNP records from 450-500 m. Elsewhere in Scotland, England and Wales there are 12 records from >500 m.

Juniperus communis (Juniper)

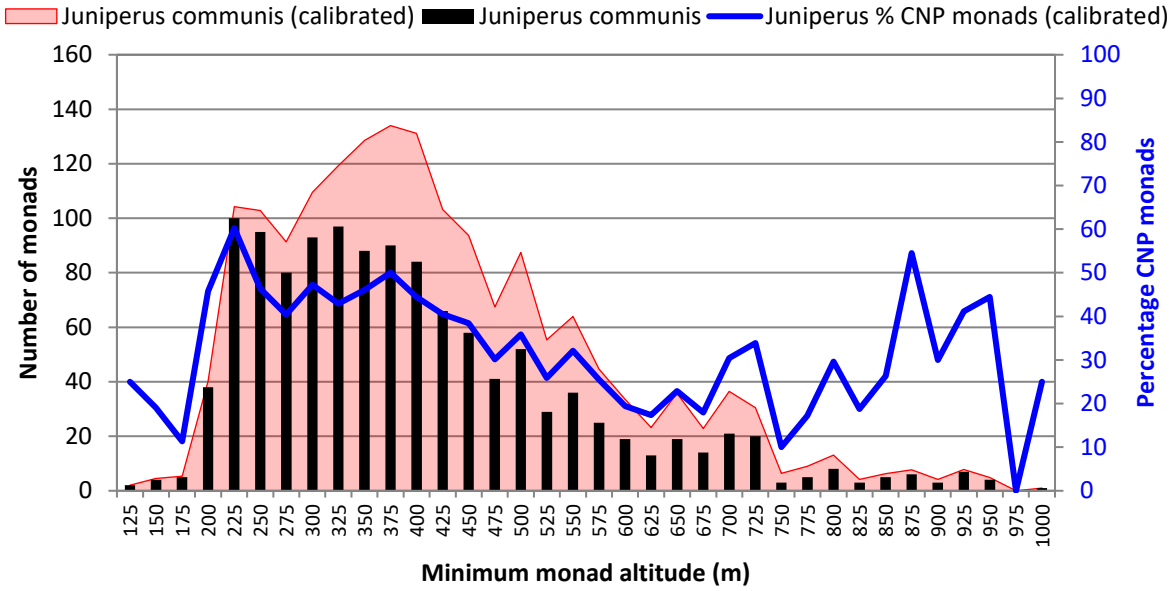

Figure 14. *Juniperus communis*

All lower altitude *Juniperus communis* in the CNP are subsp. *communis*. On exposed high-altitude sites, some plants are referable to subsp. *nana*, though these plants are not of as extreme a form as typical plants in the north-west Highlands. Most bushes above the treeline are of an intermediate form, and Pears (1968) noted that the lower level of natural sub-alpine *J. communis* scrub is a useful guide to the position of the natural treeline.

This is the most widespread (>500 m) of the species analysed (at monad scale). In the CNP 23.7% of monads (calibrated) and 53.3% of 100 m grid cells with *J. communis* have minimum altitudes above 500 m. The 100 m (or better) precision records are heavily biased towards the Abernethy and Mar Lodge NNRs, where detailed surveys have been undertaken. Between 325 and 1000 m *J. communis* is the most frequent of the species analysed, in 20 out of 27 height classes (25 m). A small bush at NN99719823 (1195 m) (Mar Lodge NNR: SE of Ben Macdui) is the highest recorded altitude for this species in Great Britain.

Myrica gale (Bog-myrtle)

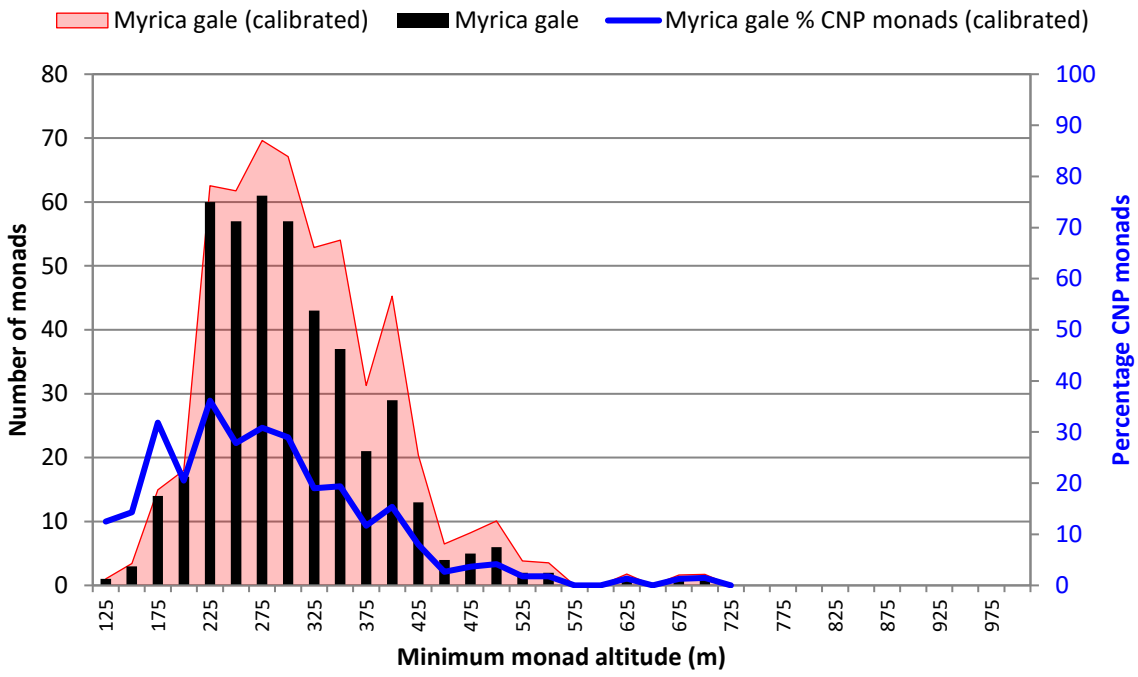

Figure 15. *Myrica gale*

In the CNP 2.3% of monads (calibrated) and 0.7% of 100m grid cells with *M. gale* have minimum altitudes above 500 m. The DDb has 13 CNP records >500 m, of which four are from >600 m, though these latter records perhaps require confirmation. The highest altitude recent record is at minimum 576 m (Mar Lodge NNR: Coire an t-Seilich) in tetrad NN98M.

***Pinus sylvestris* (Scots Pine)** Nationally Scarce (as a native)

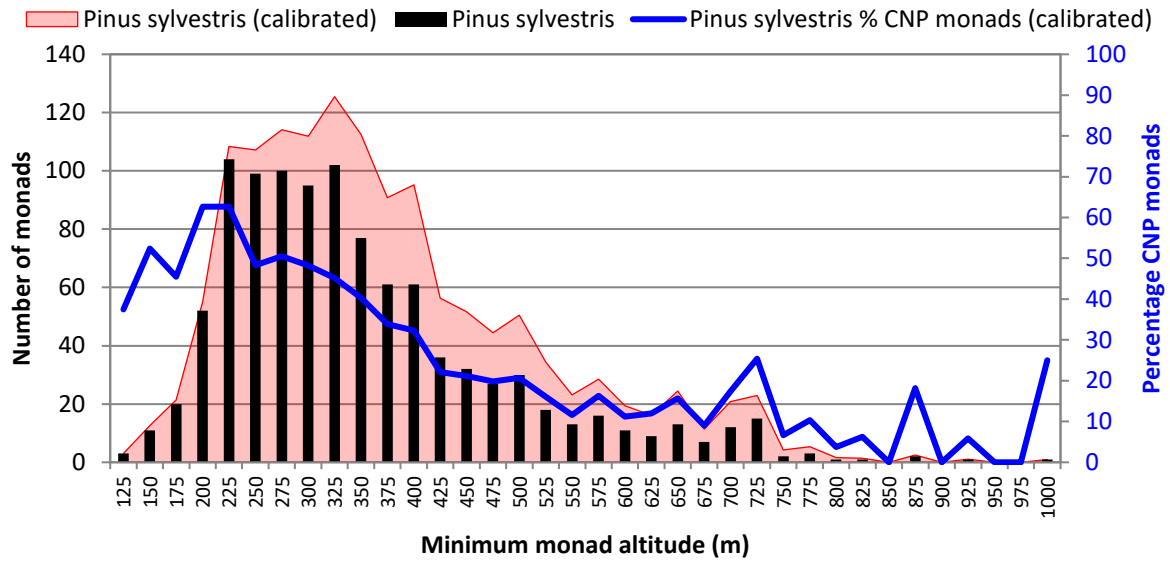

Figure 16. *Pinus sylvestris*

This is the third most widespread (>500 m) of the species analysed (at monad scale), after *Juniperus communis* and *Sorbus aucuparia*. In the CNP 15.8% of monads (calibrated) and 22.2% of 100 m grid cells with *P. sylvestris* have minimum altitudes above 500 m. Monad frequency shows a decline >725 m, but small saplings and seedlings are occasional to very high altitude. The highest record is at 1159 m (Mar Lodge NNR: SE of Ben Macdui) at NN99589813. A 60 cm tall sapling was also found at 1130 m (Abernethy NNR: Garbh Uisge Mor) at NN99629972.

Populus tremula (Aspen)

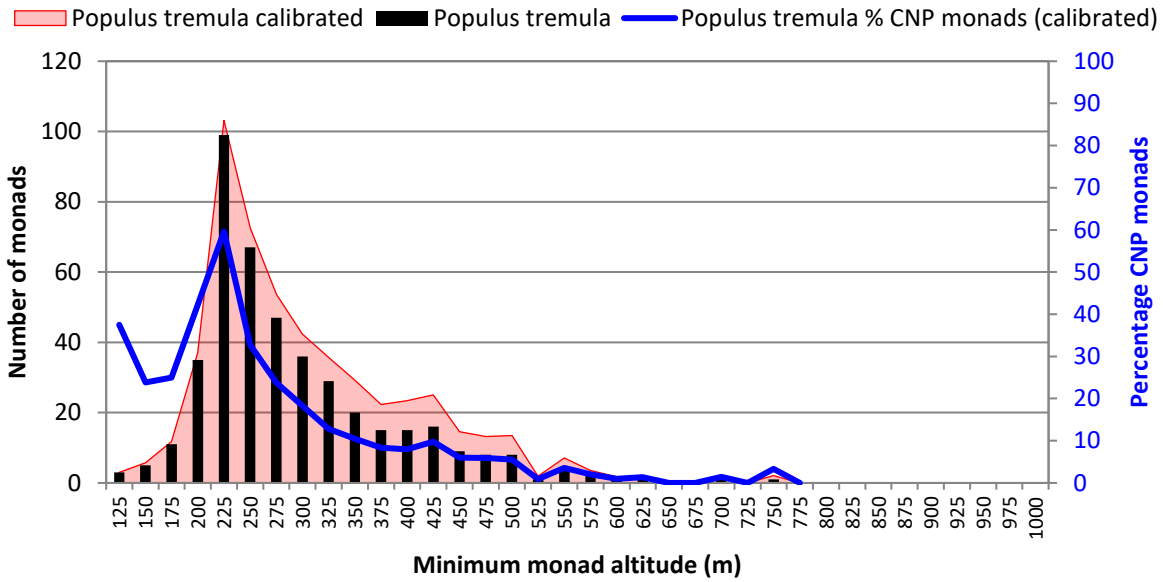

Figure 17. *Populus tremula*

In the CNP 3.8% of monads (calibrated) and 2.0% of 100 m grid cells with *P. tremula* have minimum altitudes above 500 m. The highest reported records are at minimum 739 m (Gaick, NN7884) and at NO309755 (Coire of Bonhard) at minimum 717 m. This record dates from 1982 (pre-GPS) and the site description (see under *Corylus avellana*) suggests the site may have been the 100 m grid square immediately to the south, which has a minimum altitude of 645 m. The highest recent record (described as a seedling) is at minimum 695 m (Clach a' Cleirich, NO113990).

Prunus avium (Wild Cherry)

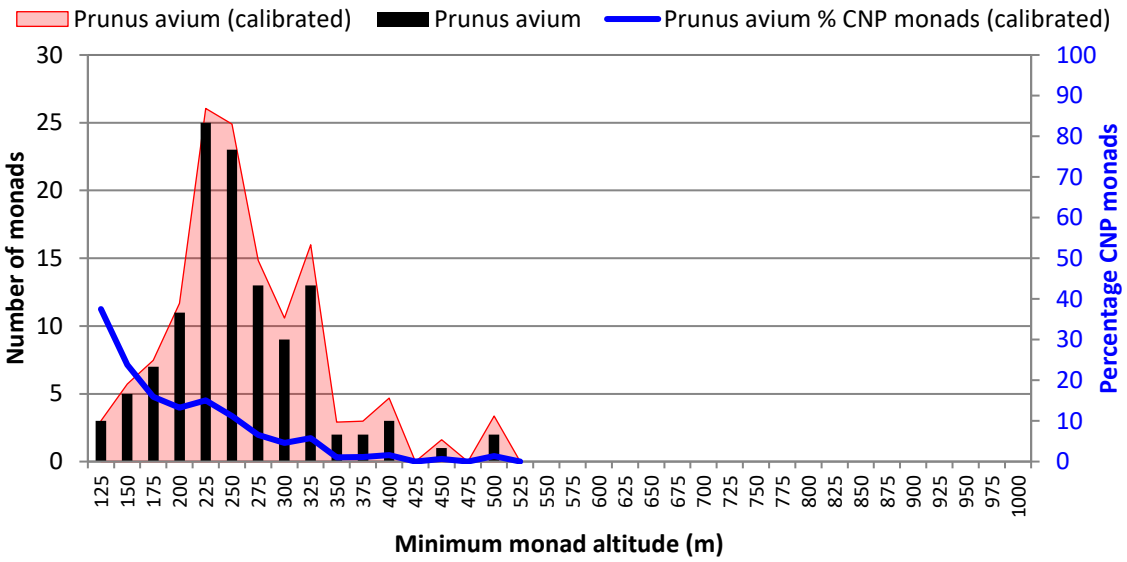

Figure 18. ***Prunus avium***

There are only three CNP records >500 m. The highest, a seedling at minimum 638 m, was at NH981116 (Abernethy NNR: SE of Creagan Gorm). In Corrie Fee, at NO24407506, there is a record at 611 m. At Fealar, NO008798, there is a record at minimum 551 m in the gorge.

Prunus padus (Bird Cherry)

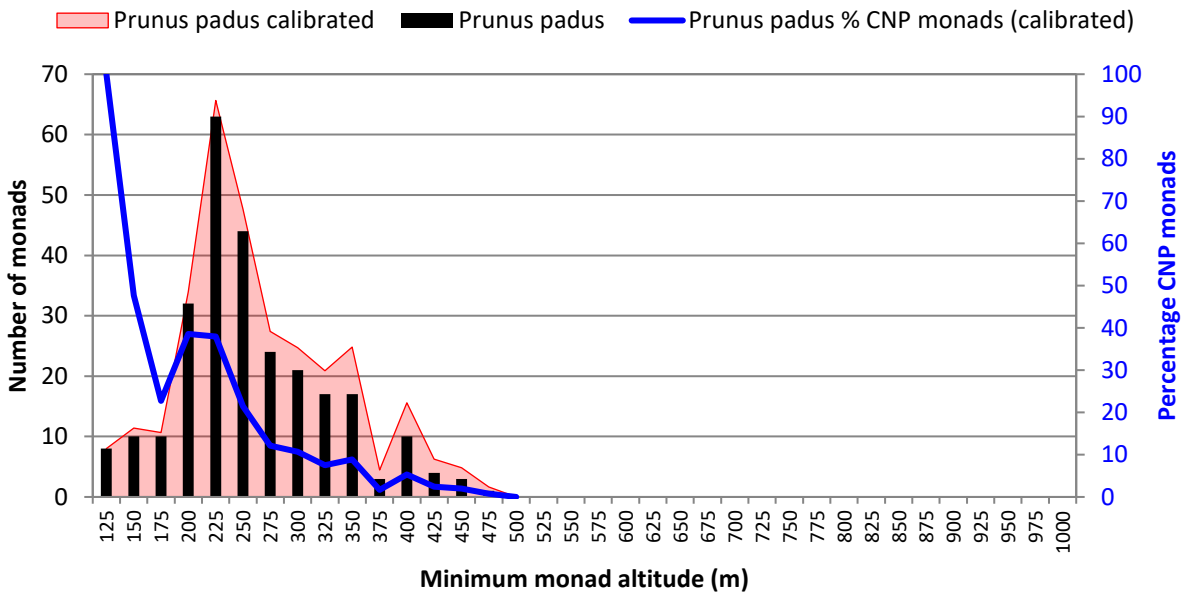

Figure 19. ***Prunus padus***

There is only a single CNP record >500 m, at NO296826 (Creag Bhiorach, Glen Muick) at minimum 563 m. The grid reference may refer to a slightly wider area, but the record is likely to be at >500 m. There are no other records >500 m in Scotland, but there are seven records in the north of England.

Rosa mollis agg. (Soft Downy-rose)

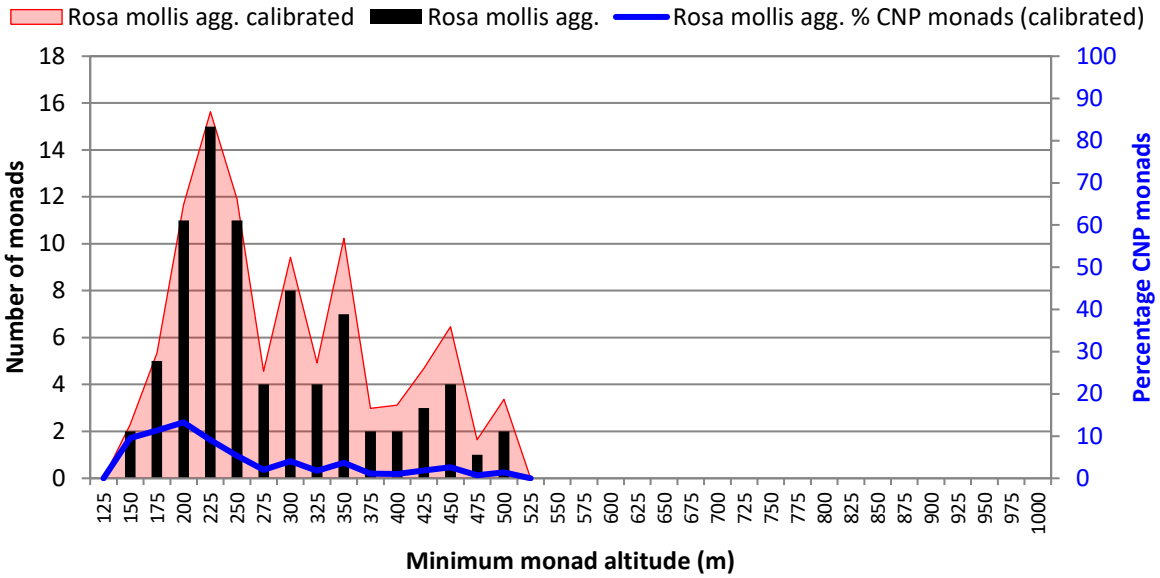

Figure 20. *Rosa mollis* agg.

This aggregate taxon includes records of *R. mollis*, *R. sherardii* and their hybrid, *R.* x *perthensis*. There are only two CNP records >500 m, both of the aggregate taxon; at minimum 585 m (Corrie Fee, NO249756) and at minimum 551 m (Fealar, NO008798). The only other records from >500 m in Great Britain are at Black Darren, Herefordshire (SO2929) where *R.mollis* s.s. grows between *c.*520-550 m. The highest record in the CNP of *Rosa sherardii* is at minimum 490 m at NO0693 (Mar Lodge NNR: Clais Fhearnaig).

Rosa spinosissima (Burnet Rose)

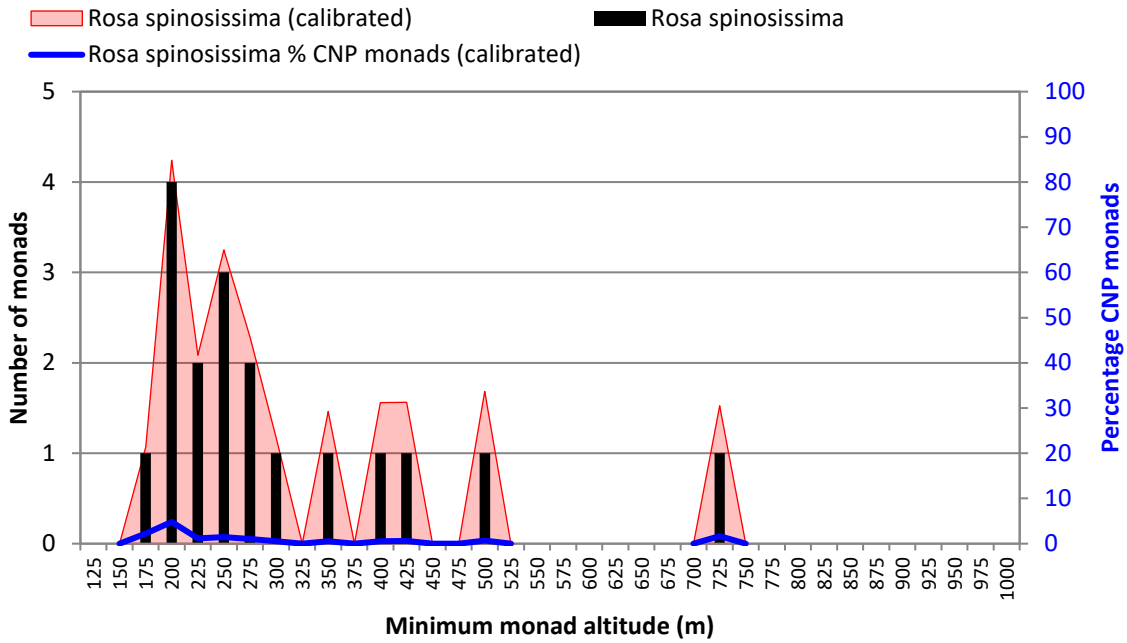

Figure 21. ***Rosa spinosissima***

A strongly suckering deciduous shrub, most frequently found on stabilized coastal sand dunes, where it often forms extensive patches; inland it occurs on less acidic heathland and in chalk and limestone grassland and scrub (Maskew, 2023). In the CNP there are both native and alien cultivar populations of *R. spinosissima*.

There are only two CNP records >500 m, both native. One at 740 m (Abernethy NNR: NW side of Loch Avon, NJ012024) is the highest population in Great Britain. The other at *c.*500 m (Mar Lodge NNR: Clais Fhearnaig, NO065930). In GB there a further eight sites >500 m (in Scotland, Wales and England) the highest of which is at 566 m (Tarren-yr-esgob, SO238315).

Rubus idaeus (Raspberry)

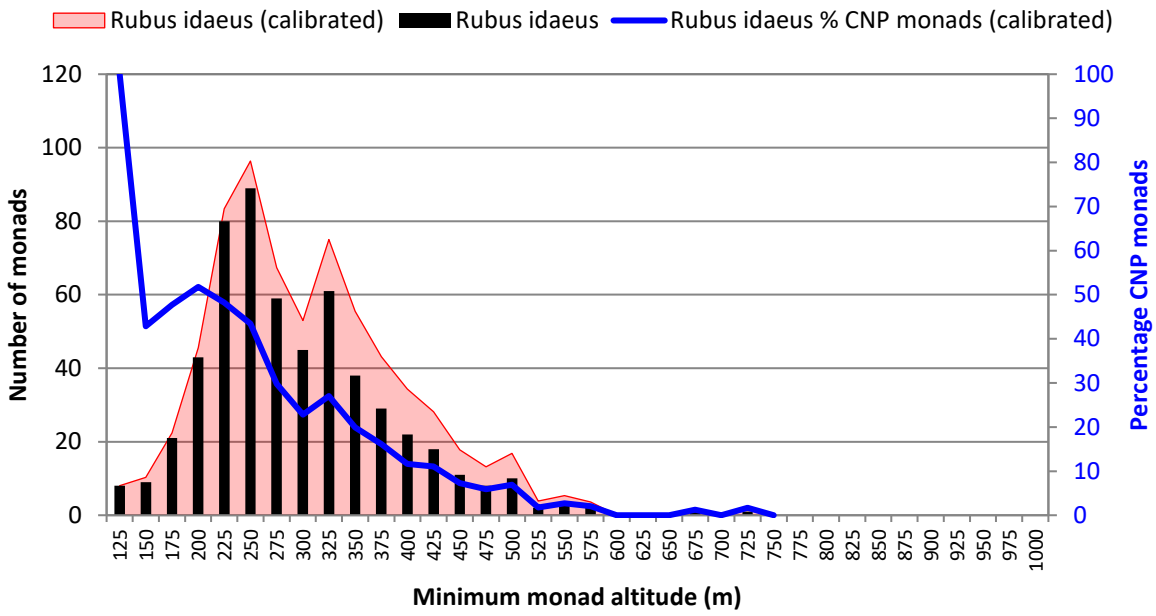

Figure 22. *Rubus idaeus*

In the uplands, this species grows on the drier ledges of basic crags and ravines, and below base-rich cliffs. It tends to tolerate all but the most nutrient poor and acidic soils, and spreads by bird-dispersed fruit, and by suckering, often forming thickets (McCosh & Aspey, 2023).

In the CNP 2.3% of monads (calibrated) and 3.3% of 100 m grid cells with *R. idaeus* have minimum altitudes above 500 m. The species reaches 790 m at NN95789039 (Mar Lodge NNR: Beinn Bhrotain (S. of)).

***Salix arbuscula* (Mountain Willow)** Nationally Scarce

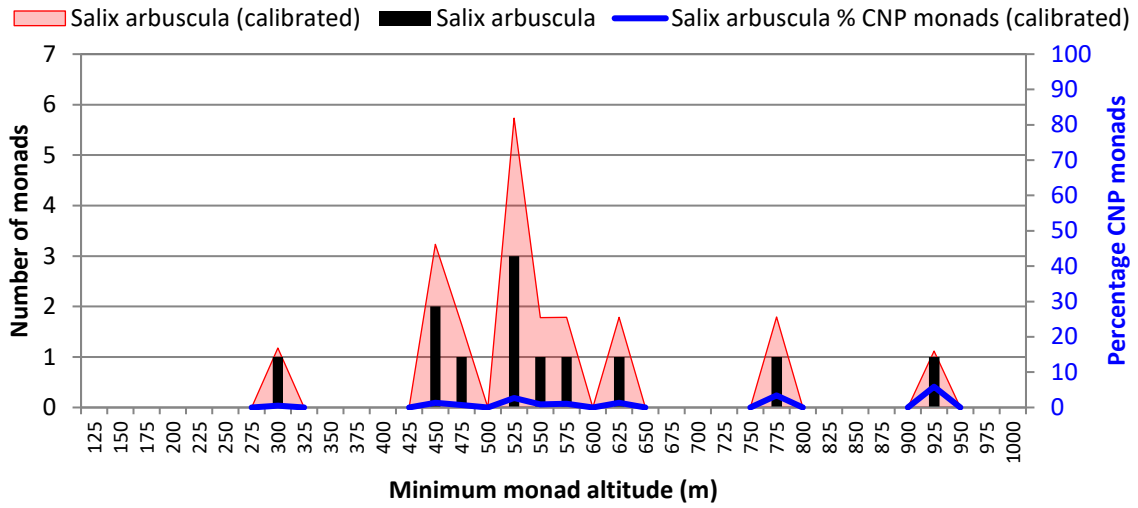

Figure 23. *Salix arbuscula*

A montane shrub of moist or wet base-rich substrates in flushes, on streamsides and on rock ledges. It can also grow on upland slopes of damp calcareous grassland. It is rarely found below 600 m (Watts & Hutchinson, 2023a). In the CNP 69.8% of monads (calibrated) and 100% of 100 m grid cells with reported records of *S. arbuscula* have minimum altitudes above 500 m. The species is reported from minimum 904 m at Sgor an Lochan Uaine (NN9597).

In the CNP *S. arbuscula* is recorded in 12 monads, however, the only confirmed records are of two bushes in NO143762 at 548 m (south of the Glenshee ski area). Doubts have been raised about other CNP records, which may be misidentifications for other montane *Salix* species or hybrids. The core of this species range in Scotland is in Breadalbane, Perthshire.

Salix aurita (Eared Willow)

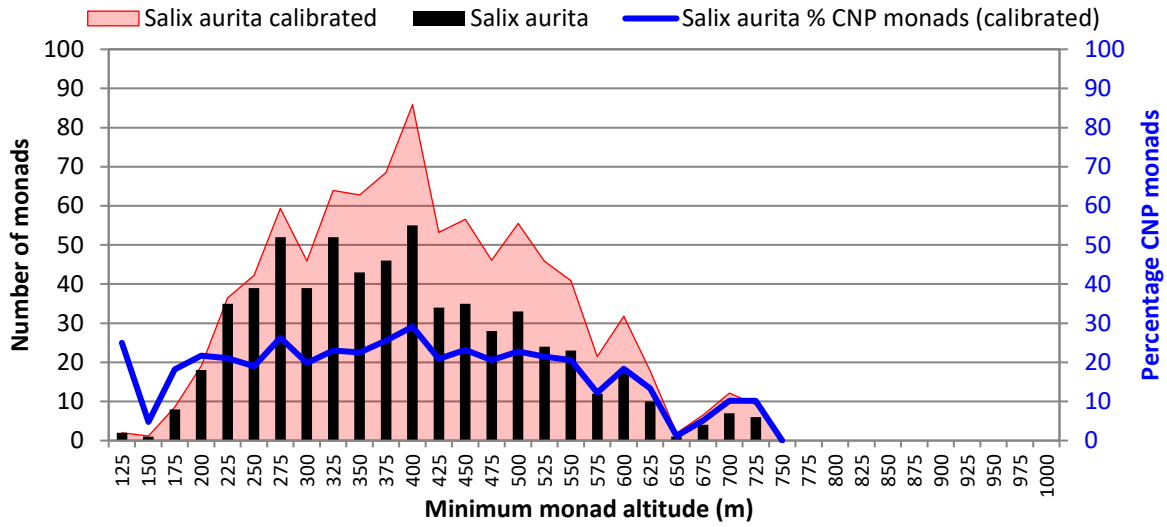

Figure 24. *Salix aurita*

This is the fifth most widespread (>500 m) of the species analysed (at monad scale). In the CNP 21.0% of monads (calibrated) and 30.6% of 100 m grid cells with *S. aurita* have minimum altitudes above 500 m. The highest record is at NJ002013, 880 m (Abernethy NNR: below Castlegates Gully).

It is likely that some records of *S. aurita* refer to the hybrid *S. aurita x cinerea = S. x multinervis*, which is common in the CNP area. Because not all recorders are familiar with *S. x multinervis*, the altitudinal distribution of CNP records of the hybrid *c.f.* its parent species is shown in Fig. 25 below, based on records at 100 m precision or better, by two recorders familiar with the taxa (A. Amphlett & I.P. Green). Given the reduction in sample sizes, the chart uses 3 altitude class (75 m) moving averages to better reveal the altitudinal distribution of the taxa.

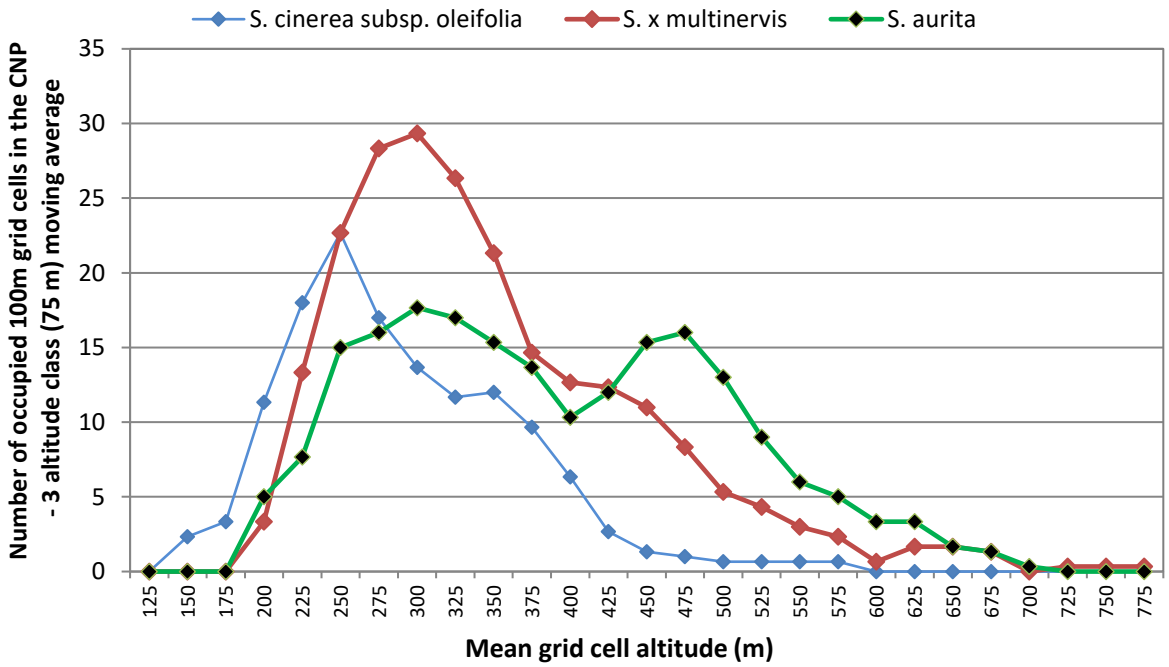

Figure 25. *Salix cinerea, S.* x *multinervis* and *S. aurita*

Median altitude of the records for the three taxa are: *S. cinerea* (264 m); *S.* x *multinervis* (317 m); *S. aurita* (360 m). The highest record for the hybrid in Great Britain is 730 m at NJ025032 (Abernethy NNR: outflow of Loch Avon). It is likely that some of the lower altitude records of *S. aurita* actually refer to the hybrid, which (Fig. 25) is more frequent that *S. aurita* between 200-425 m.

***Salix caprea* (Goat Willow)** Nationally Scarce (subsp. *sphacelata* only)

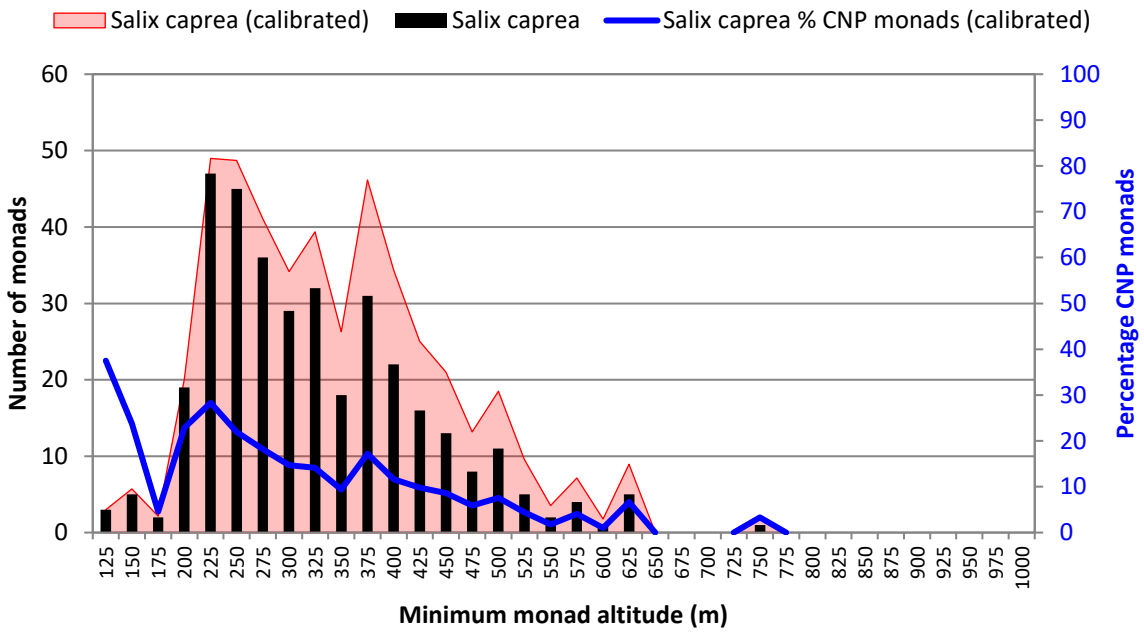

Figure 26. *Salix caprea*

Records include both *S. caprea* subsp. *caprea* and subsp. *sphacelata*, although 87% of CNP records are not assigned to a subspecies. In the CNP 7.2% of monads (calibrated) and 8.0% of 100 m grid cells with *S. caprea* have minimum altitudes above 500 m. The highest record is at minimum 730 m, in monad NN9598, at *c.*NN958984 (Mar Lodge NNR: Sgor an Lochain Uaine, NE ridge). The highest record of subsp. *sphacelata* is at minimum *c.*620 m, at NH601002 (SE of Red Burn, Glen Markie).

In the CNP the subspecies appear to represent the two extremes of variation within the species. Trees and bushes referable to subsp. *caprea* as described by Meikle (1984) are uncommon, being restricted to low altitude sites, and here sometimes planted. Most *S. caprea* in the CNP are perhaps best considered to be intermediate between the subspecies. The most extreme '*sphacelata*' type trees appear to be uncommon; particularly fine examples grow alongside the Red Burn, in upper Glen Markie.

Salix cinerea subsp. *oleifolia* (Rusty Willow)

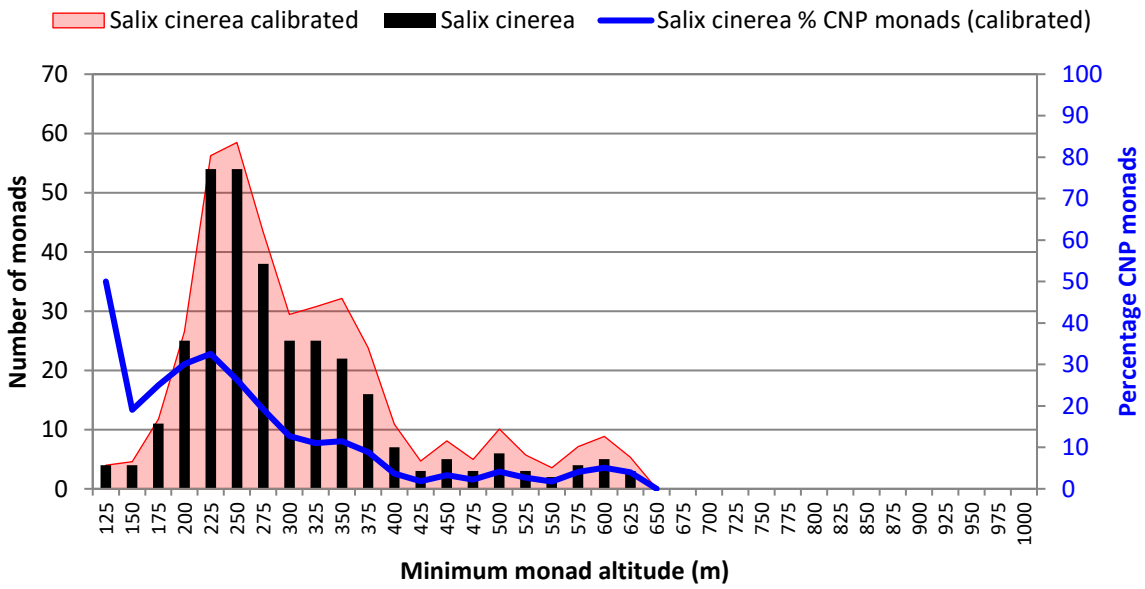

Figure 27. *Salix cinerea*

In Great Britain, there are two subspecies of *S. cinerea*. In the CNP subsp. *oleifolia* is overwhelmingly the commonest, there being only a single record of subsp. *cinerea*. The chart can therefore be taken to refer to subsp. *oleifolia*. This taxon was previously recognised at species rank in Britain, as *S. atrocinera* (Clapham *et al.*, 1952) and still is in some European accounts, e.g. Elven and Fremstad (2018).

In the CNP 7.8% of monads (calibrated) and 4.2% of 100 m grid cells with *S. cinerea* have minimum altitudes above 500 m. The highest record is at NO065770 at 688 m (Glas Tulaichean: Glas Choire Bheag).

***Salix lanata* (Woolly Willow)** Vulnerable - Nationally Rare

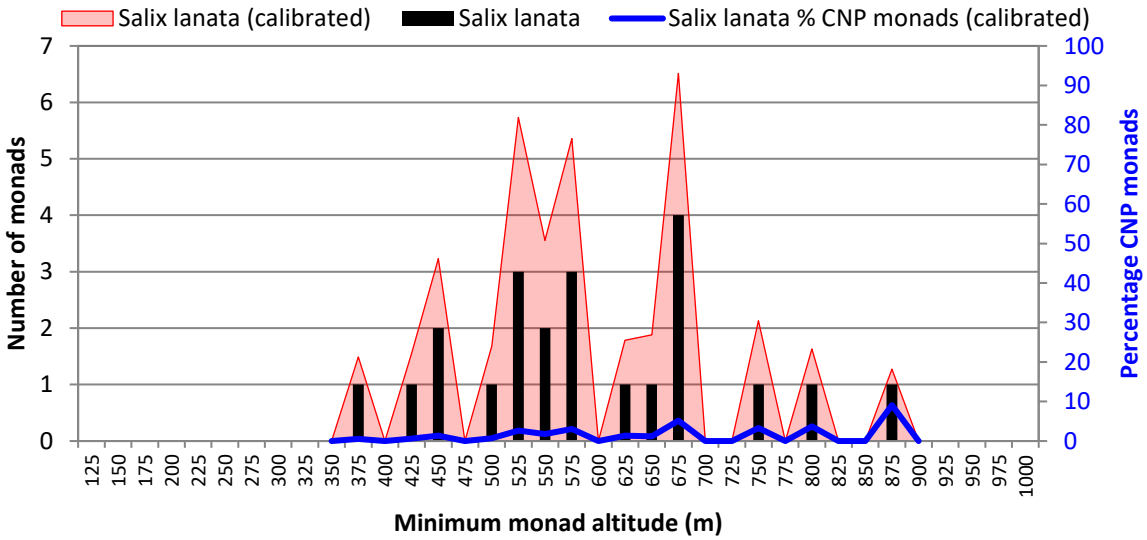

Figure 28. *Salix lanata*

As a native plant, strictly montane. In the CNP 78.9% of monads (calibrated) and 100% of 100 m grid cells with *S. lanata* have minimum altitudes above 500 m. The highest localised record is at NO05397663 at 930 m (Glas Tulaichean).

***Salix lapponum* (Downy Willow)** Vulnerable - Nationally Scarce

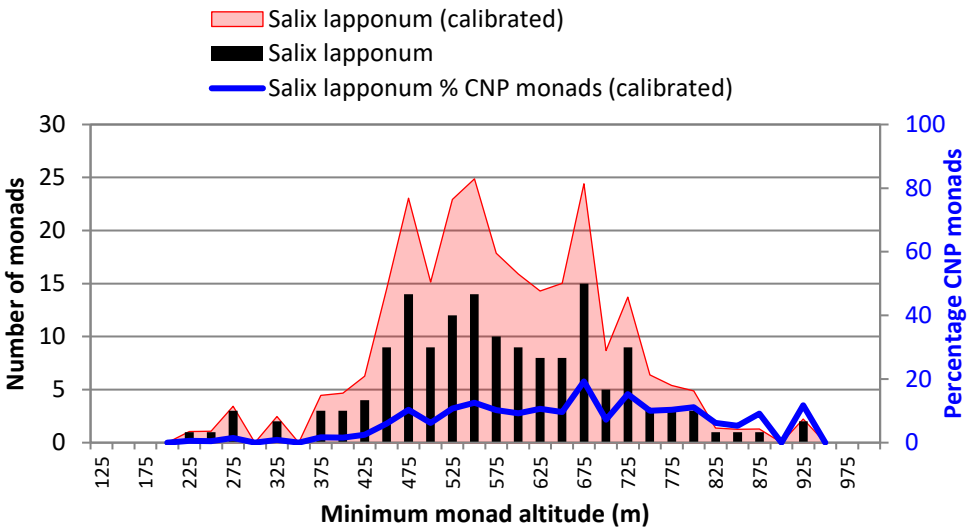

Figure 29. *Salix lapponum*

In the CNP 70.3% of monads (calibrated) and 95.1% of 100 m grid cells with *S. lapponum* have minimum altitudes above 500 m. The highest record is at NN95709790 at *c.*1000 m (Mar Lodge NNR: Coire an Lochain Uaine). The lowest localised record is at NN764715 at 330 m (Dalnamein, NE of), though it may grow at a slightly lower altitude by the Edendon Water (NN7170). Of note are three very large bushes at 450 m at NN62987628 (Drumochter Pass, just west of A9), (Fig. 30).

Figure 30. *Salix lapponum*, Drumochter Pass

There is another huge bush at 374 m at NN63948316 (River Truim: N. of the Wade Bridge), which may be lost when the A9 road is dualled.

Following a recent genetic study (Finger *et al.*, 2023) planting of *S. lapponum* to reinforce existing populations with new, unrelated individuals, as well as creating new stepping-stone populations is being undertaken in the Abernethy and Mar Lodge NNRs.

Salix myrsinifolia (Dark-leaved Willow)

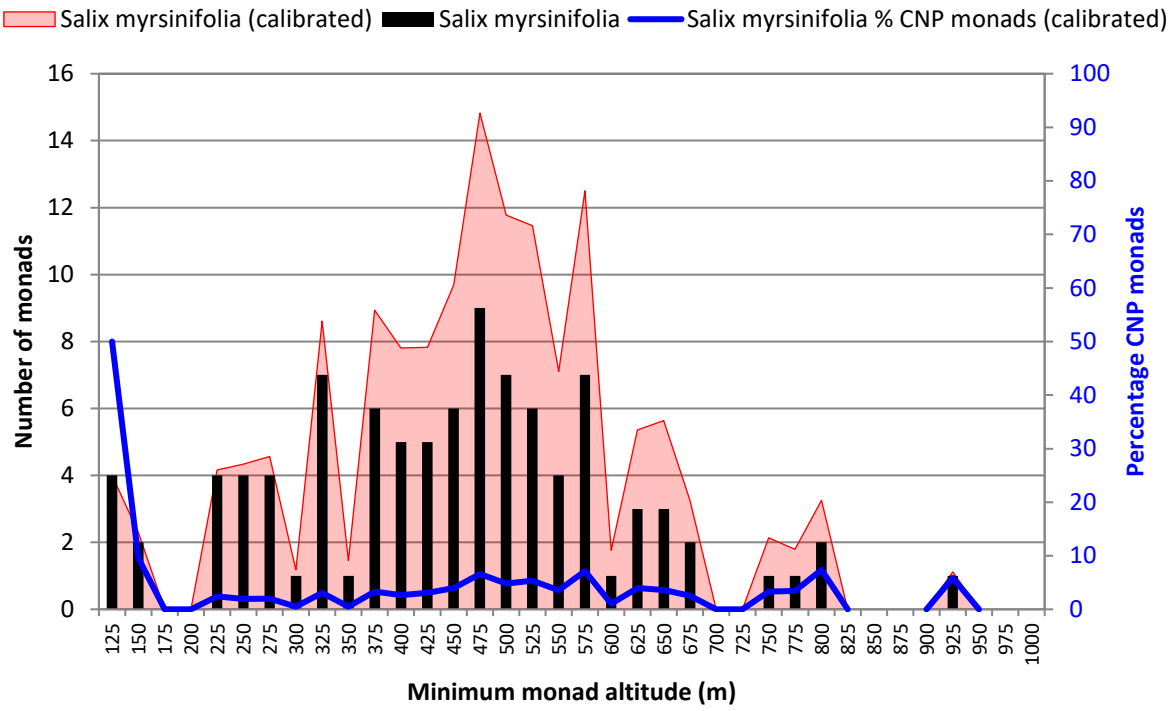

Figure 31. *Salix myrsinifolia*

In the CNP 36.8% of monads (calibrated) and 69.8% of 100 m grid cells with *S. myrsinifolia* have minimum altitudes above 500 m. The highest record is at minimum 904 m at NN9597 (Mar Lodge NNR: Coire Lochan Uaine). This species has an exceptionally wide altitudinal range; the lowest altitude record in the CNP is at NN91136280 at 110 m (Killiecrankie, beside the River Garry).

Six hybrids involving *S. myrsinifolia* have been recorded in the CNP, of these *S. myrsinifolia x phylicifolia* = *S. x tetrapla* is the most frequent. In montane areas this is considered "*the most common and most perplexing willow hybrid, completely linking the two parent species and often making their identification virtually impossible*" (Watts & Hutchinson, 2023b). It is possible that some records of *S. myrsinifolia* and *S. phylicifolia* actually refer to this hybrid.

***Salix myrsinites* (Whortle-leaved Willow)** Endangered - Nationally Scarce

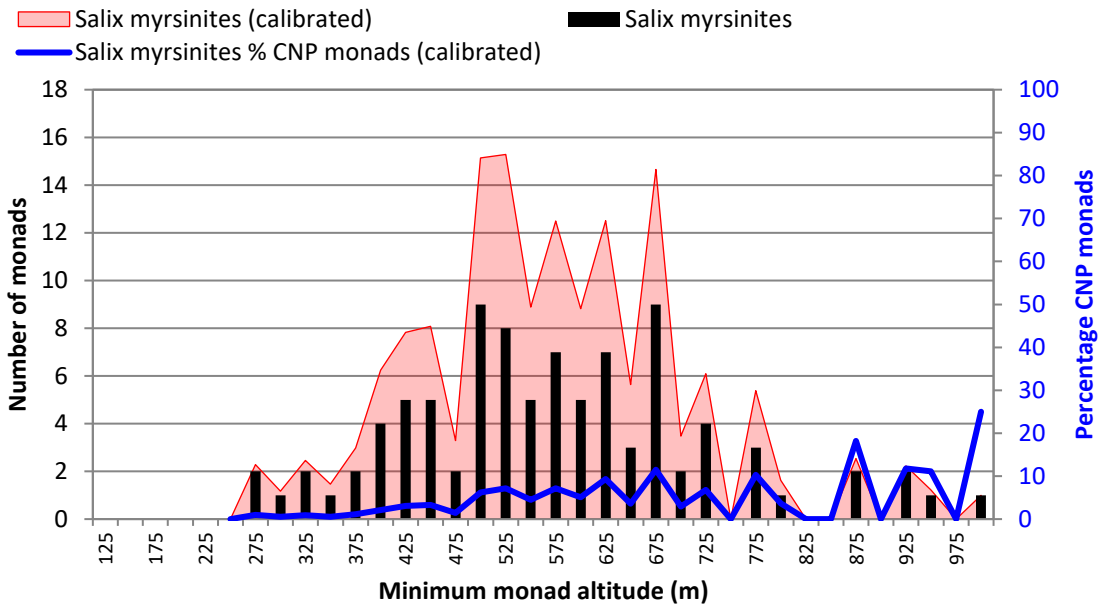

Figure 32. *Salix myrsinites*

In the CNP 66.7% of monads (calibrated) and 94.2% of 100 m grid cells with *S. myrsinites* have minimum altitudes above 500 m. The highest record is at just over 1000 m at NN956978 and NN957979 (Mar Lodge NNR: Coire an Lochain Uaine, Cairn Toul). This species is usually found on moist or wet, base-rich substrates on Scottish mountains, but it can tolerate a moderate range of geology and soil types (Watts and Hutchinson, 2023c). In some of the CNP sites it grows on granite with few if any indicators of base enrichment.

Salix phylicifolia (Tea-leaved Willow)

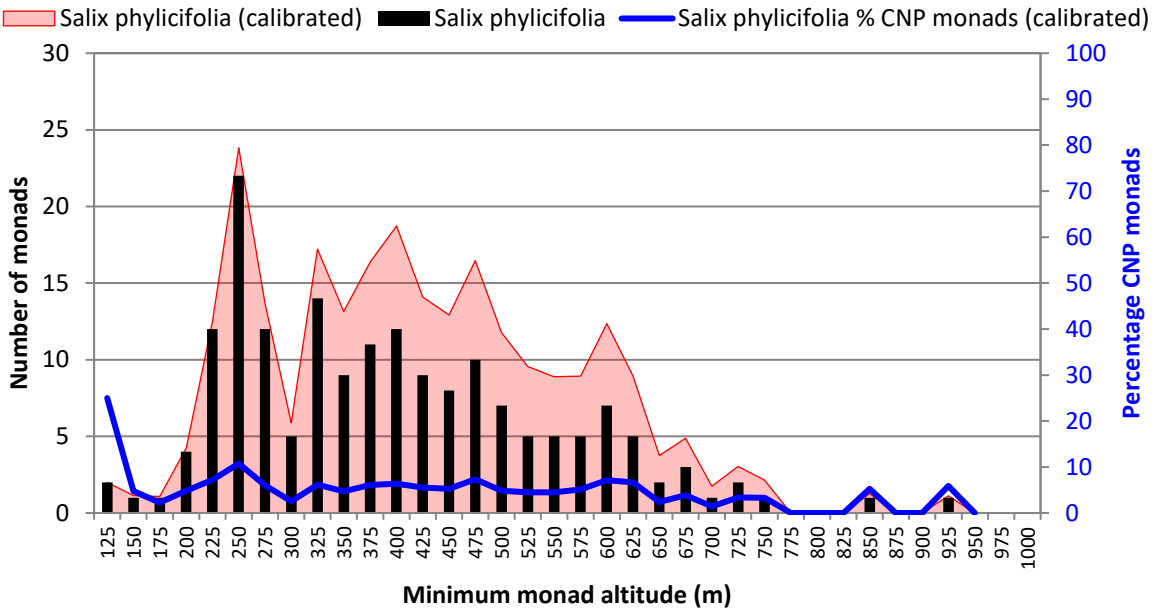

Figure 33. *Salix phylicifolia*

In the CNP 26.5% of monads (calibrated) and 32.0% of 100 m grid cells with *S. phylicifolia* have minimum altitudes above 500 m. The highest record is at 1020 m at NN956979 (Mar Lodge NNR: Coire an Lochain Uaine, Cairn Toul). This species has an exceptionally wide altitudinal range; the lowest altitude record in the CNP is at 120 m at NN893639 (Aldclune Island, River Garry).

Unless recorders carefully check that the leaf underside is completely glabrous, sparsely hairy forms of the hybrid *S. myrsinifolia x phylicifolia* = *S. x tetrapla* may be mistaken for this species. See *S. myrsinifolia* account.

Salix repens (Creeping Willow)

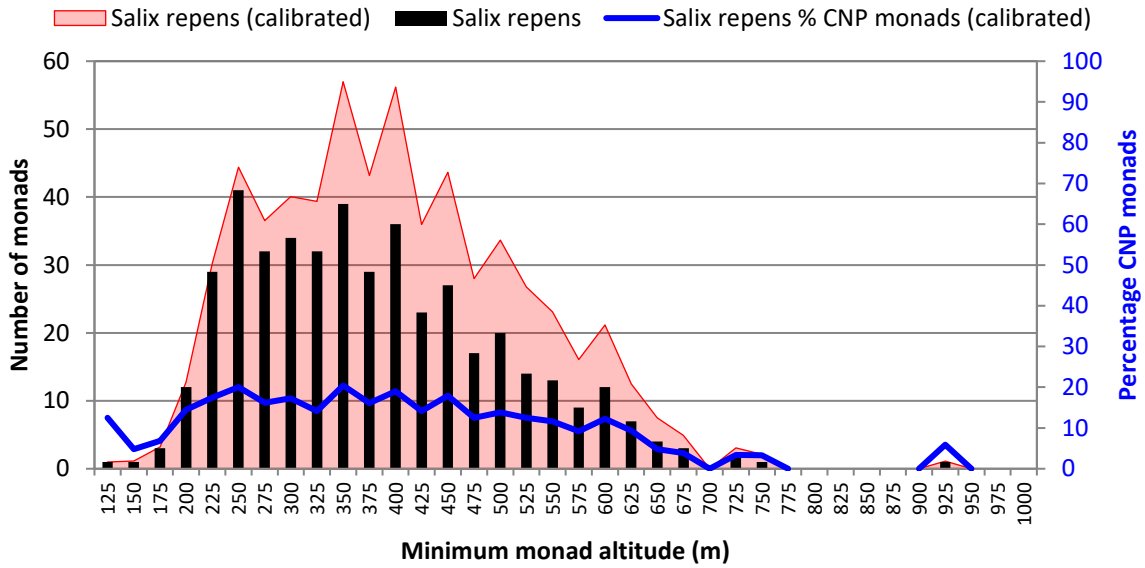

Figure 34. *Salix repens*

In the CNP 18.9% of monads (calibrated) and 25.6% of 100 m grid cells with *S. repens* have minimum altitudes above 500 m. The highest record is at minimum 918 m at NJ0000 (Loch Etchachan area), however the record lacks details. There is another record at minimum 897 m at NO093966 (Bruach Mhor, Beinn a'Bhuird).

All *Salix* species combined

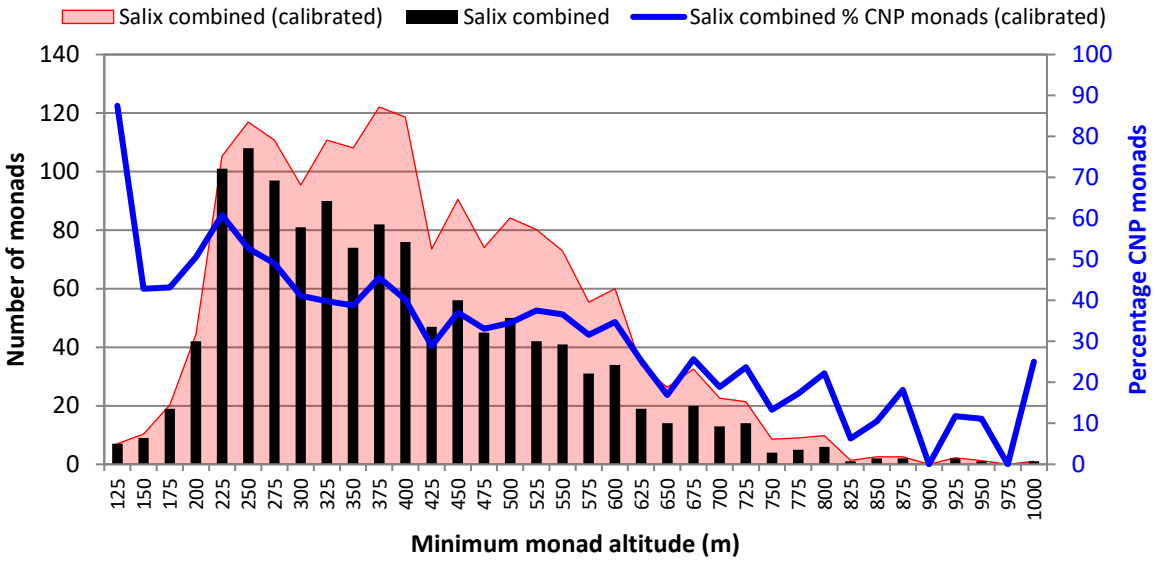

Chart includes records of *Salix arbuscula, aurita, caprea, cinerea, lanata, lapponum, myrsinifolia, myrsinites, phylicifolia* and *repens*

Figure 35. All *Salix* species

In combination, the ten *Salix* species show a ± linear downward trend in percentage calibrated monad occupancy with altitude. However, the individual species show widely different altitudinal trends; see Figs. 40 and 41 and discussion in the 'Between species comparisons' section below.

Sorbus aucuparia (Rowan)

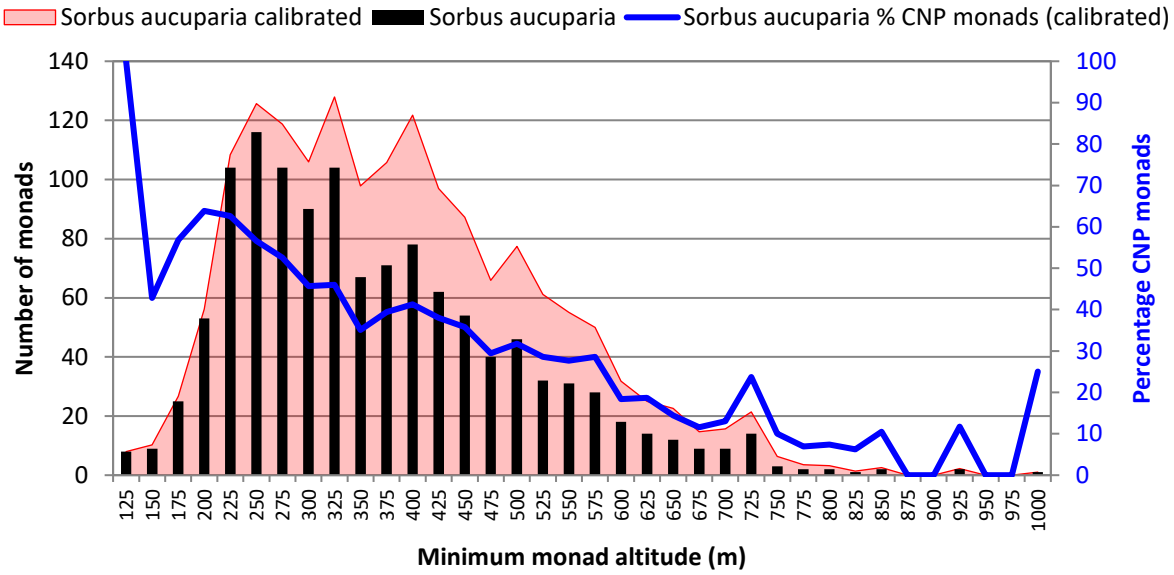

Figure 36. ***Sorbus aucuparia***

In the CNP 19.2% of monads (calibrated) and 31.3% of 100 m grid cells with *S. aucuparia* have minimum altitudes above 500 m. The highest record is at 1093 m at NJ00210051 (Abernethy NNR: Garbh Uisge Mor (E. of)). This is the second most widespread (>500 m) of the species analysed (at monad scale).

***Sorbus rupicola* (Rock Whitebeam)** Nationally Scarce

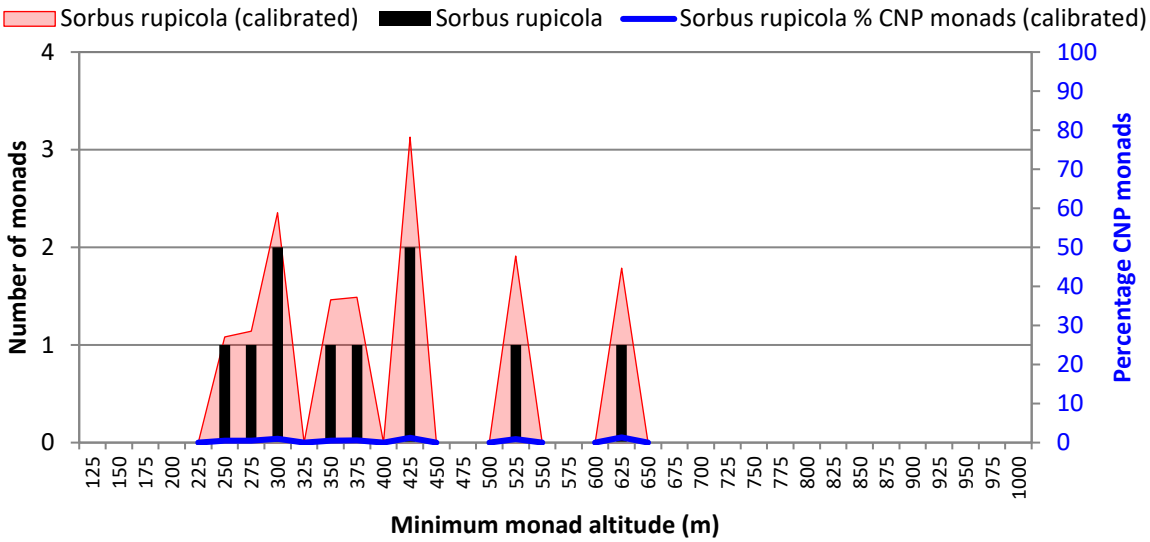

Figure 37. *Sorbus rupicola*

In the CNP 25.8% of monads (calibrated) and 14.3% of 100 m grid cells with *S. rupicola* have minimum altitudes above 500 m. The highest record is at minimum 650 m at NH602009 (Red Burn, Glen Markie). A rare species in the CNP, only recorded at four locations post-1999.

Ulex europaeus (Gorse)

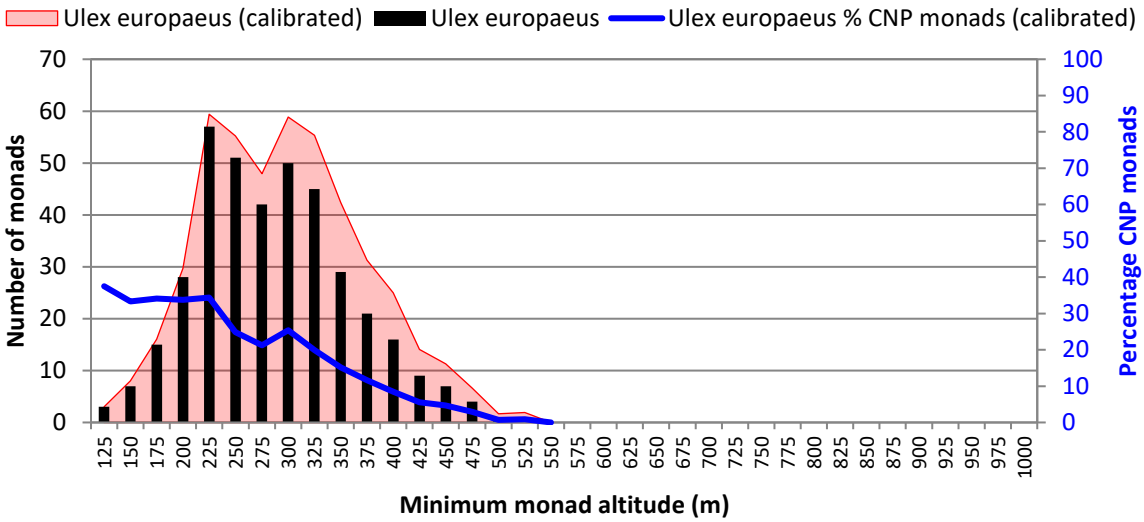

Figure 38. *Ulex europaeus*

In the CNP 0.4% of monads (calibrated) and 1.5% of 100 m grid cells with *U. europaeus* have minimum altitudes above 500 m. The highest record is at minimum 580 m at NJ252113 (Hill of Allargue (N. of): A939).

Summary of native phanerophytes and nano-phanerophytes with records >500 m in the Cairngorms National Park

Of the 30 native species with records >500 m in the CNP (Table 2), only 16 species occur with >5% of their calibrated monad totals above that altitude. A further five species have 2-5% of calibrated monad above 500 m. Nine species have <1% of calibrated monad totals or have <4 individual records above 500 m.

Table 2. Percentage calibrated monads and percentage 100 m grid cells with records >500 m (species highlighted in green are the 10 most frequent species (combined CNP calibrated taxon monad totals)

Species	% monads (calibrated) >500 m	% 100 m grid cells > 500 m
Salix lanata	78.9	100.0
Salix lapponum	70.3	95.1
Salix arbuscula	69.8	100.0
Betula nana	67.0	91
Salix myrsinites	66.7	94.2
Salix myrsinifolia	36.8	69.8
Salix phylicifolia	26.5	32.0
Sorbus rupicola	25.8	14.3
Juniperus communis	23.7	53.3
Salix aurita	21.0	30.6
Sorbus aucuparia	19.2	31.3
Salix repens	18.9	25.6
Pinus sylvestris	15.8	22.2
Betula pubescens	11.3	11.8
Salix cinerea	7.8	4.2
Salix caprea	7.2	8.0
Cytisus scoparius	4.4	6.7
Populus tremula	3.8	2.0
Betula pendula	3.0	2.2
Rubus idaeus	2.3	3.3
Myrica gale	2.3	0.7
Corylus avellana	0.8	2.7
Ulex europaeus	0.4	1.5
Alnus glutinosa	0.4	0.5
Prunus avium	Three records >500 m	
Rosa mollis agg.	Two records >500 m	
Rosa spinosissima	Two records >500 m	
Fraxinus excelsior	One record >500 m	
Ilex aquifolium	One record >500 m	
Prunus padus	One record >500 m	

Between species comparisons

The calibrated monad totals in each 25 m altitude class, as a percentage of the total monads in that altitude class in the whole CNP, are plotted using 3 altitude class (75 m) moving averages. The mean value is plotted offset by one altitude class, so the mean for the altitude range 100-125 to 150-175 m, is plotted in the 125-150 m class interval.

29 of the native species are plotted in the following five charts. *Sorbus rupicola* is excluded as there are too few records to be easily visible. *Betula pendula* and *B. pubescens* (combined) and *Salix* (all species combined) are also plotted. Species are grouped in individual charts to make interpretation easier. *Salix* species are in two charts, the species groups having different altitudinal distributions.

In Fig. 39, *Juniperus* is unique in having a bimodal frequency distribution, with peaks at low and high altitudes. *Betula nana* is also unique in being most frequent at mid-altitudes, with a peak at or below the forest line. *Pinus sylvestris* shows a small subsidiary peak just above the potential treeline. Shorter, wind-clipped vegetation at this altitude may provide favourable conditions for establishment of saplings. *Pinus sylvestris* is consistently more frequent at all altitudes above 125 m than *Betula pubescens*. Combining records of *B. pendula* and *B. pubescens* increases the *Betula* monad frequency below the treeline, especially at low elevations, but makes no difference above the treeline.

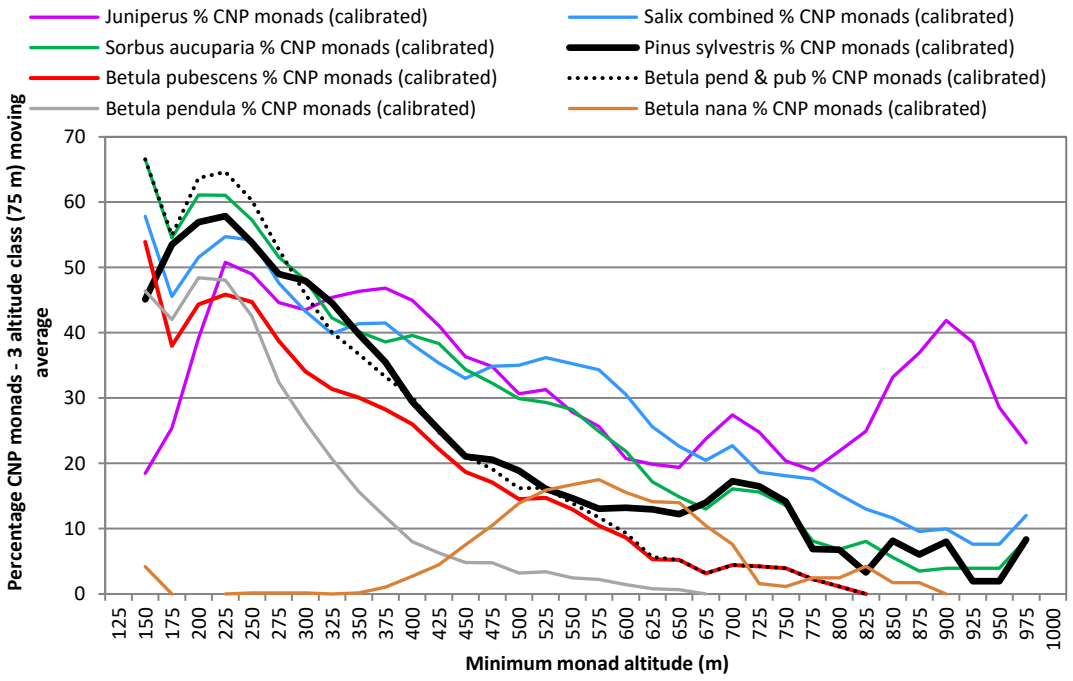

Figure 39. Percentage Cairngorms National Park calibrated monad totals - 3 altitude class (75 m) moving averages

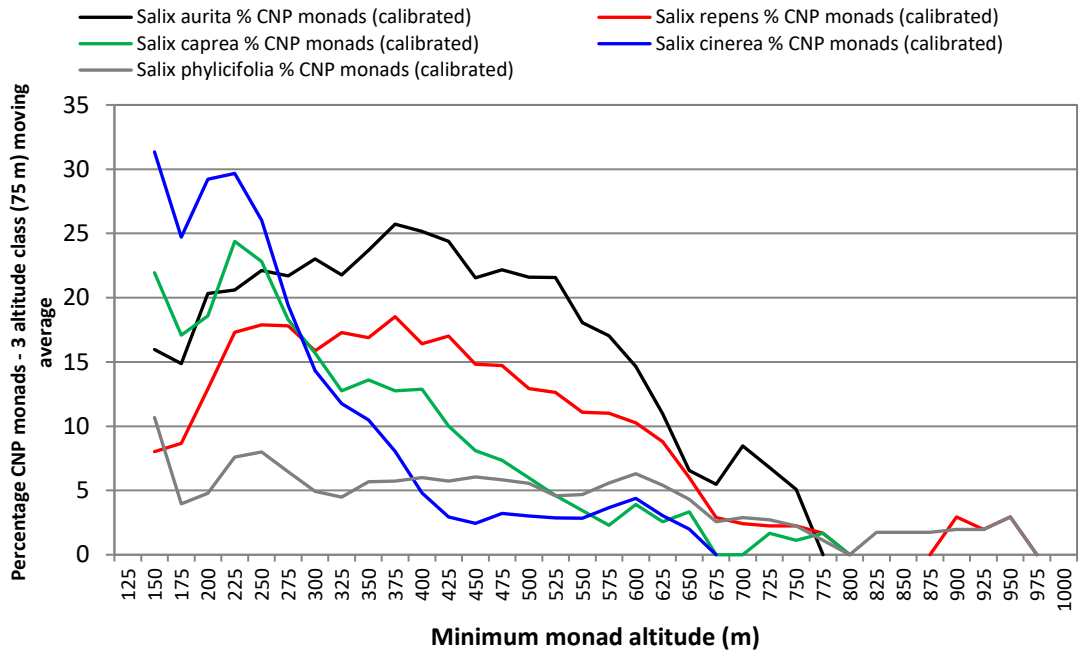

Figure 40. Percentage Cairngorms National Park calibrated monad totals - 3 altitude class (75 m) moving averages

Four of the five Salix species in Fig. 40 all have peak calibrated monad frequency at low to mid elevations, well below the treeline. *Salix phylicifolia* is distinctive in having a very flat frequency distribution, from the lowest elevations to the treeline, declining above that level.

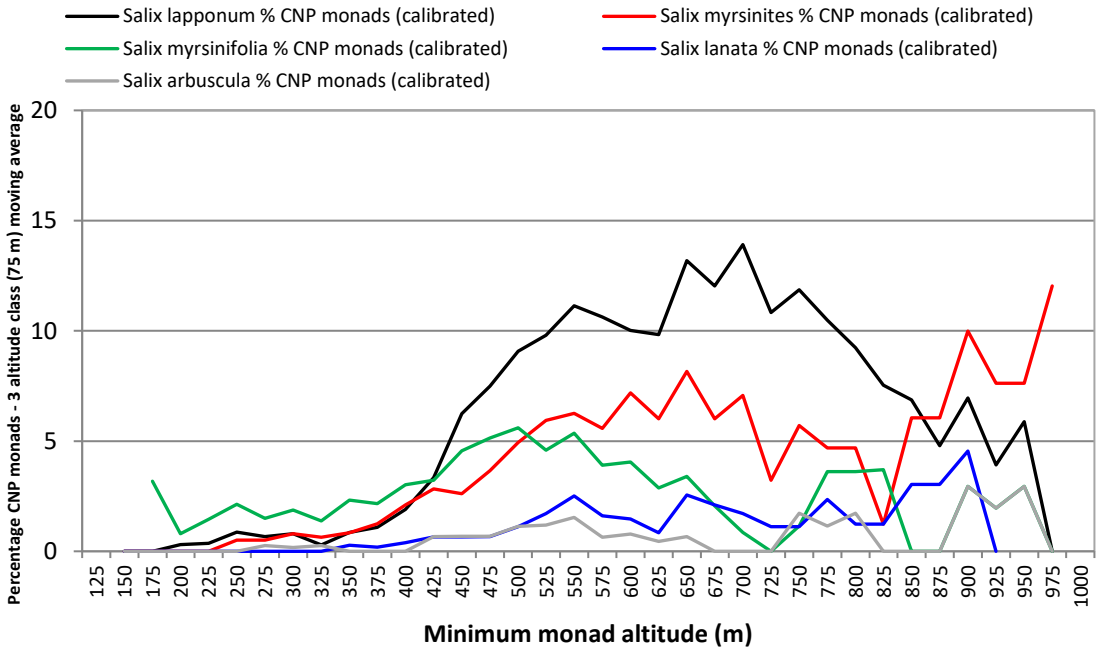

Figure 41. Percentage Cairngorms National Park calibrated monad totals - 3 altitude class (75 m) moving averages

The five *Salix* in Fig. 41 all have peak calibrated monad frequencies above or near the treeline.

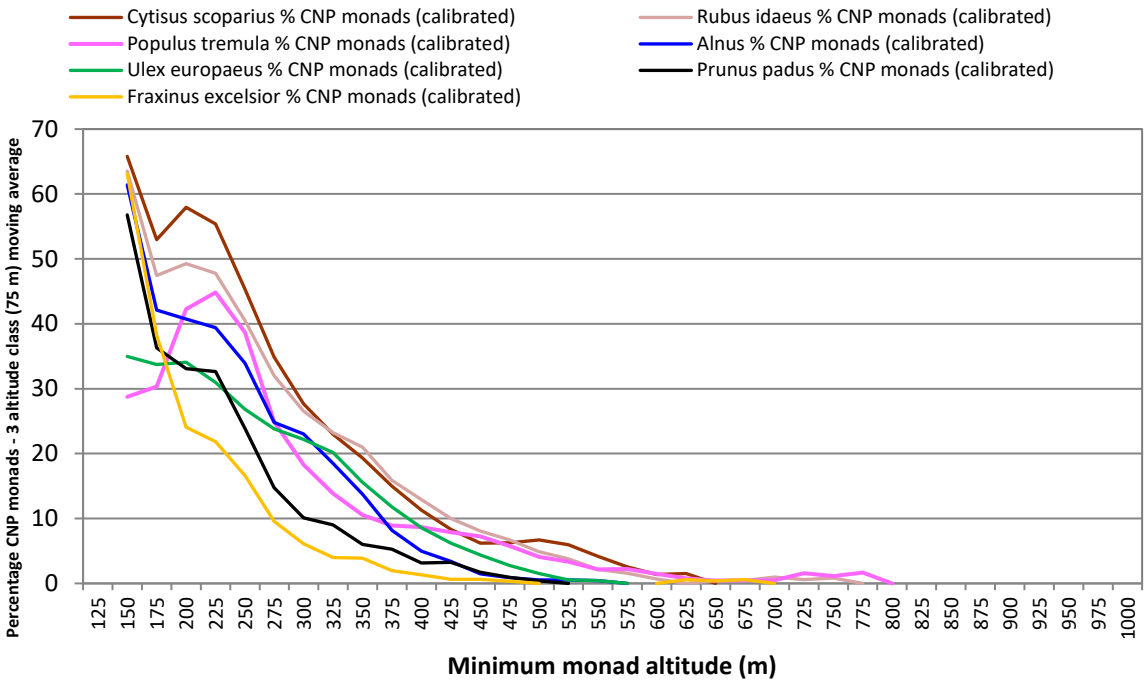

Figure 42. Percentage Cairngorms National Park calibrated monad totals - 3 altitude class (75 m) moving averages

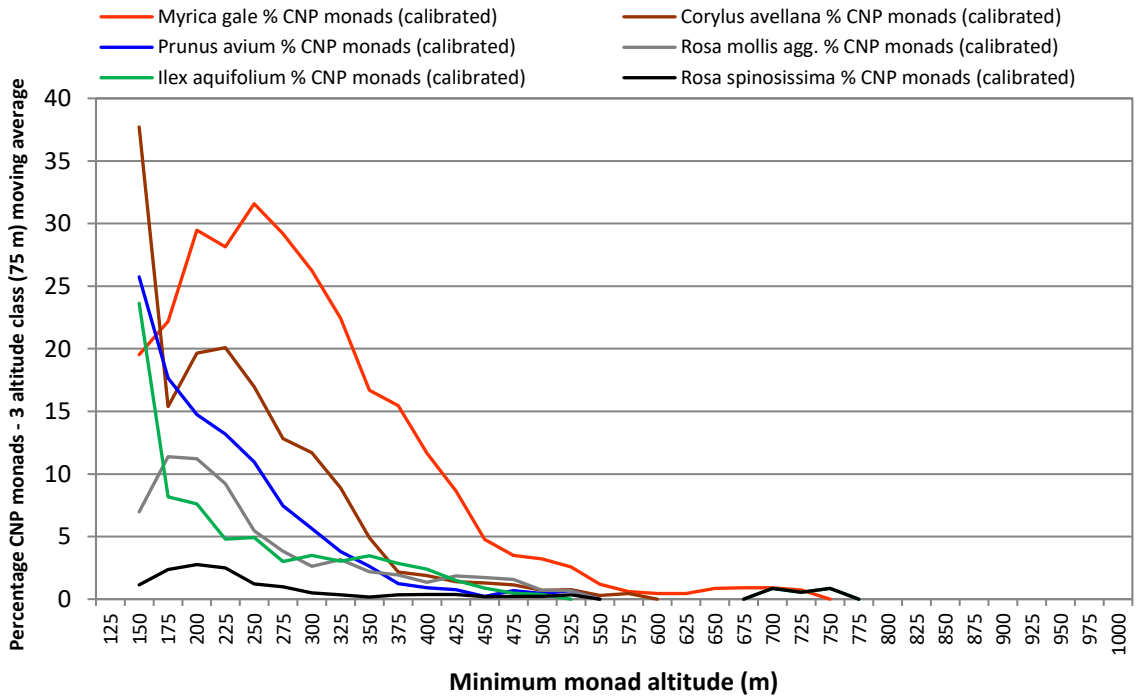

Figure 43. Percentage Cairngorms National Park calibrated monad totals - 3 altitude class (75 m) moving averages

These 13 species (Fig. 42 and 43) have peak calibrated monad frequencies at low elevation, and their frequency declines very rapidly with altitude. They are only exceptionally recorded above the treeline, e.g. *Cytisus scoparius* and *Populus tremula*.

Calibrated taxon monad totals

Summing the calibrated monad count in each altitude (25 m) class for each species provides a combined measure of spatial and altitudinal frequency. Figures 44-46 display these values for the three non-overlapping altitudinal ranges, 500-600 m (the upper forest zone to the Forest line), 600-700 m (Treeline woodland) and >700 m (Montane scrub). In reality, these zones overlap, their altitudinal limits determined by local exposure.

Pinus sylvestris and *Betula pubescens* are highlighted as their relative frequencies are referred to in the Discussion section.

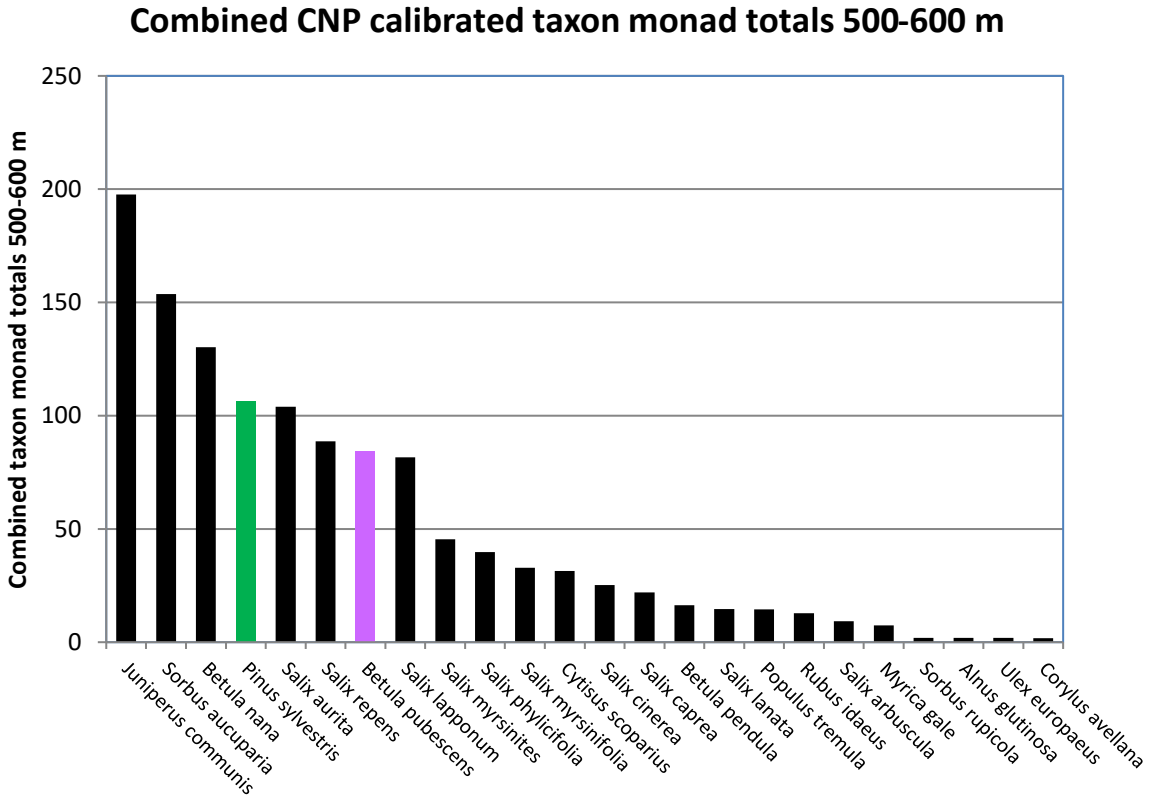

Figure 44. Calibrated monad totals, 500-600 m (upper forest zone to the Forest line)

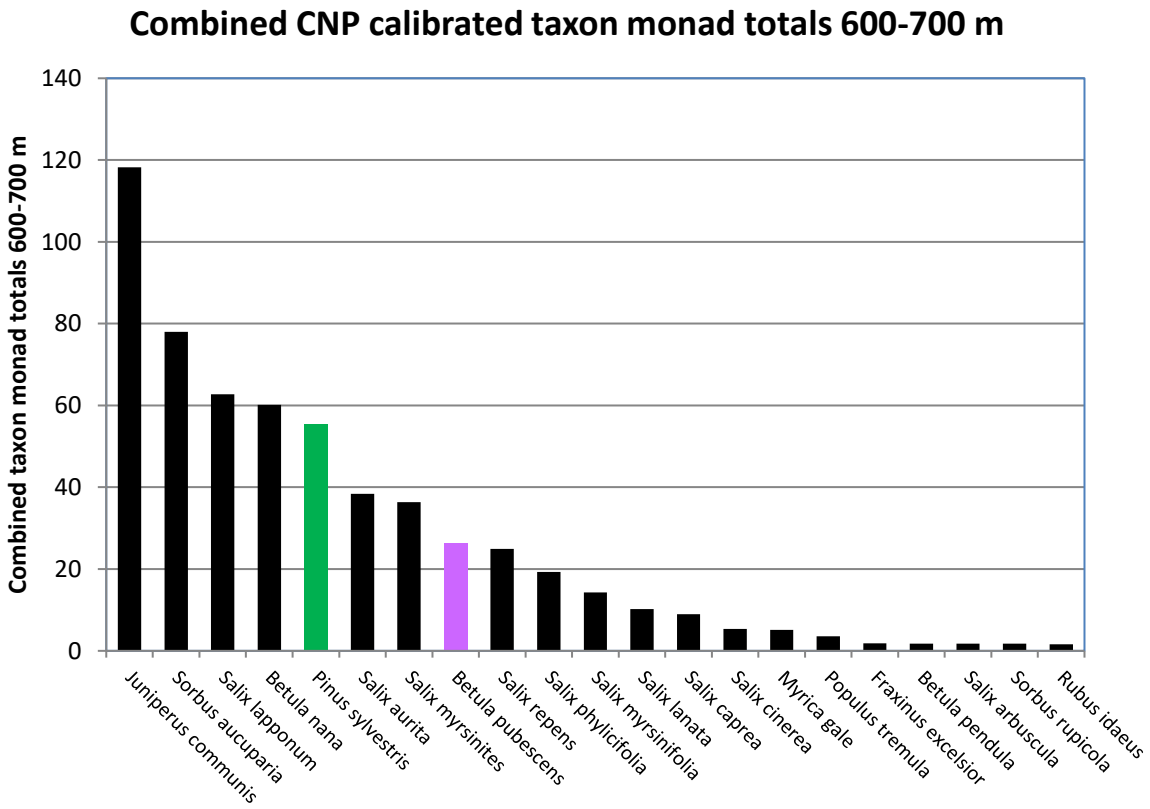

Figure 45. Calibrated monad totals, 600-700 m (Treeline woodland)

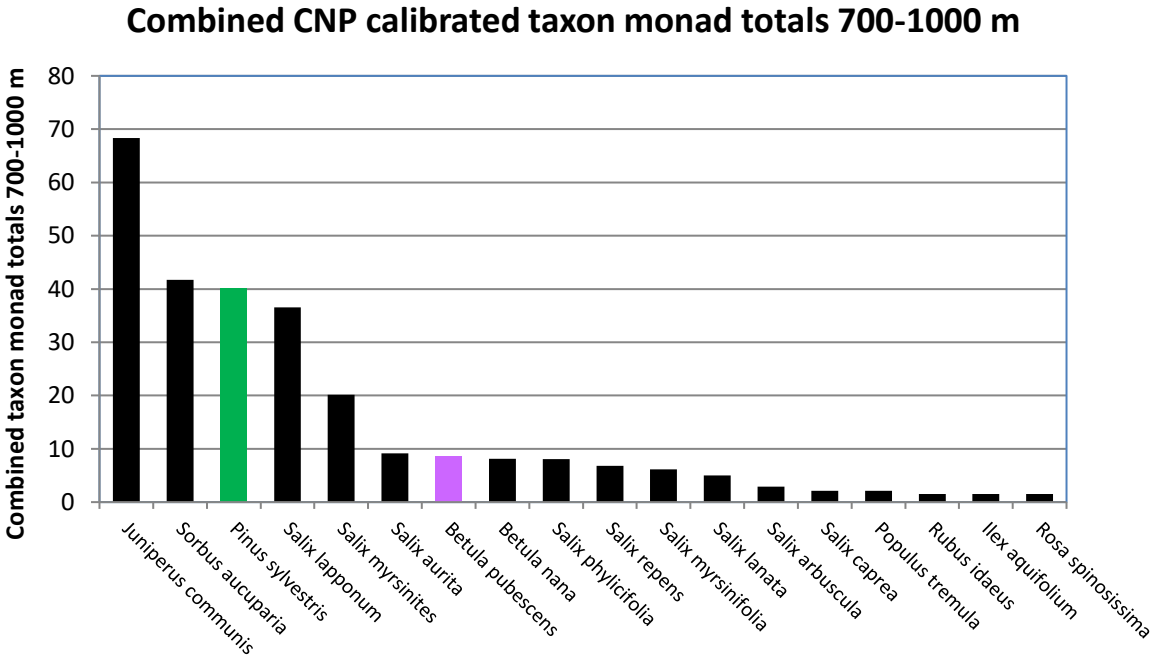

Figure 46. Calibrated monad totals, 700-1000 m (Montane scrub)

The ten most frequent species in the three altitudinal zones are listed in Table 3 and displayed in Fig. 47. The table and cell colours are an aid to interpretation.

Table 3. Ten most frequent species (combined CNP calibrated taxon monad totals) in three altitudinal zones in the Cairngorms National Park

	Minimum monad altitude (m)		
	≤Forest Line	Treeline Woodland	Montane Scrub
Rank	500-600 m	600-700 m	700-1000 m
1	*Juniperus communis*	*Juniperus communis*	*Juniperus communis*
2	*Sorbus aucuparia*	*Sorbus aucuparia*	*Sorbus aucuparia*
3	*Betula nana*	*Salix lapponum*	*Pinus sylvestris*
4	*Pinus sylvestris*	*Betula nana*	*Salix lapponum*
5	*Salix aurita*	*Pinus sylvestris*	*Salix myrsinites*
6	*Salix repens*	*Salix aurita*	*Salix aurita*
7	*Betula pubescens*	*Salix myrsinites*	*Betula pubescens*
8	*Salix lapponum*	*Betula pubescens*	*Betula nana*
9	*Salix myrsinites*	*Salix repens*	*Salix phylicifolia*
10	*Salix phylicifolia*	*Salix phylicifolia*	*Salix repens*

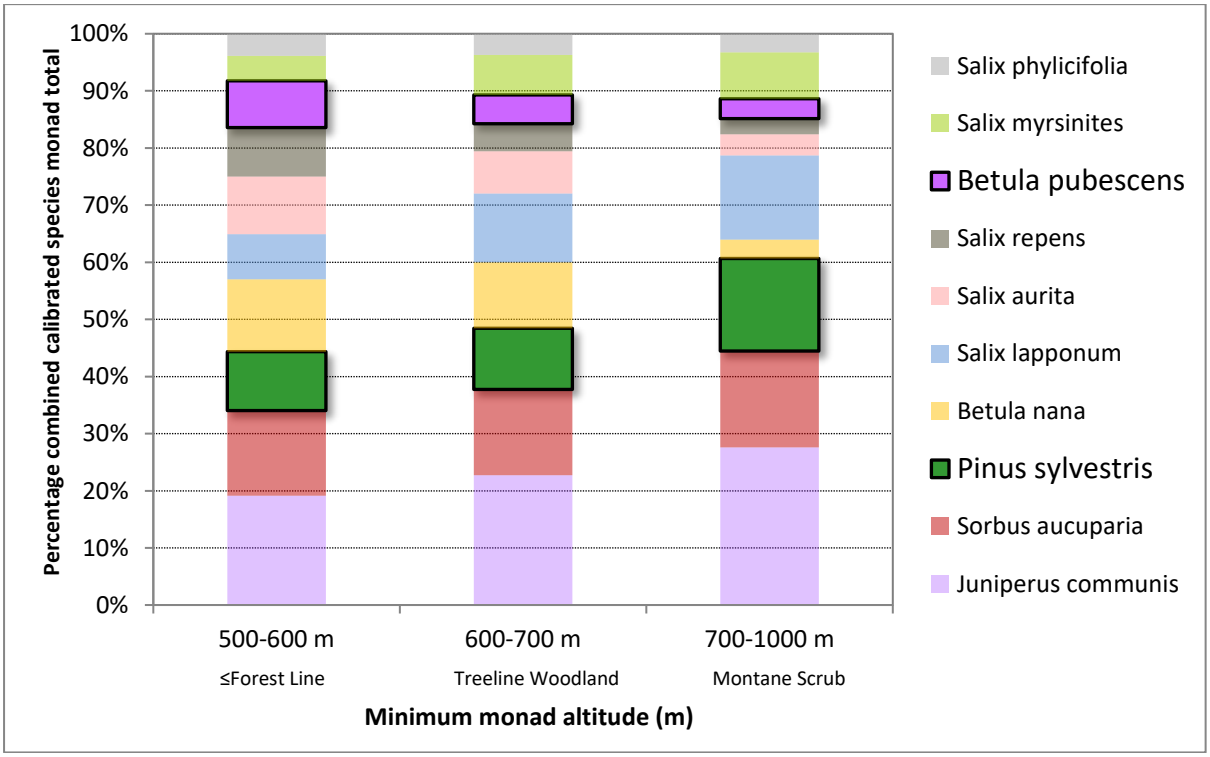

Figure 47. Ten most frequent species (combined CNP calibrated taxon monad totals) in three altitudinal zones in the Cairngorms National Park

Discussion

The current distribution, spatial frequency and abundance of native tree and scrub species within the treeline ecotone of the CNP are well below their *potential-natural* extent. These species were reduced by, and are still limited by, land management practices including browsing and grazing by wild and domestic herbivores and by muirburn. Tree and scrub populations within the CNP treeline ecotone continue to also be limited by remoteness of many areas from sources of wind dispersed seed, and the small population sizes of remnant *Salix* populations limits recovery, with skewed sex-ratios, evidence of inbreeding and possible inbreeding depression (Finger *et al*., 2023).

This paper has analysed occurrence records across the whole CNP of all native tree and scrub species found above the potential forest line. While all these species are understood to be below their *potential-natural* abundance levels, their altitudinal distribution, and to a lesser degree their spatial frequency, here expressed as calibrated counts of monads, are considered to be reliable indicators of the species composition of a possible future, more natural transition from the forest line, through treeline woodland and montane scrub, to the montane (alpine) zone.

The same ten species (Table 3, Fig. 47) occupy the top ten rank frequency positions in each of the altitudinal zones (forest line, treeline woodland and montane scrub). Therefore, across the whole altitudinal range of the treeline ecotone we can expect woodland and scrub to comprise a similar mix of species, though their proportions will vary, both altitudinally and geographically. Currently *Juniperus communis* and *Sorbus aucuparia* are the two most widespread species in all three zones, *Pinus sylvestris* is in 4th or 5th place, while *Betula pubescens* is in 7th or 8th place.

However, there is evidence that the broadleaf component of the native pinewoods in the CNP has been much reduced from the *original-natural* forest, *sensu* Peterken (1981, 1996). For example, Pratt (2006a, 2006b) reconstructed the most likely percentage land cover of different woodland types and of open space for 6400, 4260 and 2150 BP (Before Present; based on dated tephra layers), over a 15 x 15 km area, centred on Abernethy Forest. In summary, this study showed that the combined area of mixed *Pinus sylvestris* – broadleaf woodland and broadleaf woodland (as a percentage of the total woodland area), varied between 20 and 37% over a 4250-year period, prior to 2150 BP. Currently the figure is only *c*.5%.

The current spatial distribution and abundance of mature seed-bearing broadleaf trees is likely to be a significant determining factor of the current distribution and frequency of these species in the treeline ecotone. This will change over time and we may see a shift in relative abundance of species at higher altitudes.

Of the 30 native tree and scrub species recorded >500 m, only 16 species occur with >5% of their calibrated monad totals above that altitude. Of the remainder, four species (*Alnus glutinosa*, *Prunus padus*, *Rosa mollis* agg. and *Ulex europaeus*) have no records above 600 m, and it is doubtful that any of these occur within the treeline ecotone. Three tree species (*Fraxinus excelsior*, *Ilex aquifolium* and *Prunus avium*) have only one to three records above 600 m, and their potential as components of treeline woodland is marginal at best. *Populus tremula*, though currently having only 3.8% of its calibrated monad total >500 m, does have the

potential to be a more significant component of treeline woodland, especially through vegetative spread.

In recent years, land managers in the CNP who are working towards expanding woodland to its natural altitudinal limit, including high altitude sub-alpine scrub, have looked to areas in south-west Norway, which have a similar climate and geology to the Cairngorms, as a model of how CNP upland habitats might develop. Since the late 19th century, and especially over the last 80 years, there has been very rapid expansion of native woodland here, and development of a natural treeline (Halley, 2011, 2021, undated).

A distinctive feature of the Scandinavian mountain range (Scandes) is that *Betula pubescens*, in Scandinavian literature named subsp. *czerepanovii* (Orlova) Hämet-Ahti*,* or subsp. *tortuosa* (Ledeb.) Nyman, and commonly referred to as 'mountain birch', forms the treeline in almost all areas (Jonsell, 2004). This 'birch belt' forms a zone with an elevational range of 50 to 300 m (Kullman & Öberg, 2009) above the altitudinal limits of *Picea abies* (Norway Spruce) and *Pinus sylvestris*. However, in their central Swedish study area, Kullman & Öberg found that *Pinus* or *Picea* can grow to higher elevation than *Betula* in the southern and most continental and snow-poor parts of their study area.

The recent *Betula* monograph (Ashburner & McAllister, 2013) recognised this taxon, but renamed it as *B. pubescens var. pumila* (L.) Govaerts, as Linnaeus (1745) had used the name *pumila* (meaning dwarf, diminutive, low, or stunted) at variety level (of *B. alba* L.) in his Flora Suecica.

Recently it has been asserted that in Scotland "*the loss (of the 'birch belt') has been so complete, for so long, that many are unaware that it was ever there, covering hundreds of square kilometres of the Highlands and Southern Uplands between about 650 and 900 m*" (Halley, 2021), and this view has gained currency amongst conservation practitioners and advocates. For example, after seeing the landscapes in south-west Norway, a (Cairngorms Connect) group was asked to describe what Scotland's landscapes in the future could look like. ... "*If you were to scan a hillside from base to summit, you would see pines – young and ancient – merging seamlessly into the bright, airy birch belt*" (Cairngorms Connect, undated). Finger *et al*. (2023) in their paper on conservation genetics of montane willow populations in Scotland suggested that results from their study "*will inform restoration work in Scotland aiming to create continuous woodland habitats from pinewoods at lower altitudes through to higher altitude downy birch woodlands merging with montane willows*" and, "*the birch belt is a habitat that has been almost completely obliterated; lost from our landscapes for so long that it has faded from our cultural memory*" (The Scottish Rewilding Alliance, 2024). The Mountain Birch Project (Reforesting Scotland, undated) states "*The mountain birch was once widespread across our hills, as it is now in Norway, growing above the height of the pinewoods and below the height of the montane scrub and open heaths. ... The mountain birch itself seems to have something about it that allows it to grow at these high altitudes, between 600-850 m roughly, that the lower ground downy birch doesn't have*".

This idea of a missing birch belt in Scotland, and in the CNP in particular, has gained traction with little evidential support, beyond the existence of this habitat in Scandinavia. Attempting to ground these claims in evidence, or at least in well-founded hypotheses, is reminiscent of the efforts previously required to counter

some of the more historically inaccurate versions of Scottish woodland history (Smout, 1997, 2014).

The ratios of calibrated monad totals of *B. pubescens* to *P. sylvestris* in the three zones (Table 3, Fig. 47) are 1:1.27, 1:2.11 and 1:4.73. In the CNP *P. sylvestris* becomes, relative to *B. pubescens*, more frequent with increasing altitude. *Pinus sylvestris* is also consistently more frequent in all 25 m altitude classes above 125 m than *B. pubescens* (Fig. 39). While the low rank position of *B. pubescens* may well reflect lack of seed sources (Pratt, 2006b) and browsing pressure, the fact that *P. sylvestris* occurs to very high altitudes, and comprises a higher percentage of the combined CNP calibrated taxon monad totals above 700 m than it does from 500-700 m strongly suggests that *B. pubescens* is unlikely to form an exclusive birch belt at elevations above the *P. sylvestris* altitudinal limit. That, of course, does not exclude the possibility (even likelihood) that *B. pubescens* will have the potential to be a significant component of treeline woodland in the CNP. Indeed, on soils of higher base status, *B. pubescens* could potentially be the dominant treeline species (Gimingham, 2002).

This contrast between the CNP and Scandinavia should perhaps not be a surprise as the 'mountain birch' taxon of Scandinavia, Iceland and northern Russia is a different taxon to the *B. pubescens* found in upland areas of the CNP and other parts of Highland Scotland. This difference was only finally clarified by Ashburner & McAllister (2013), and see Amphlett (2021) for additional discussion. The northern 'mountain birch' *B. pubescens* var. *pumila* is derived through adaptive selection of northern forms of *B. pubescens* and introgression from *B. nana*. These trees show obvious morphological intermediary with *B. nana*, *e.g.* in leaf size and shape, and fruit and female catkin scale shape. They are often low growing, multi-stemmed, with stems growing from the tree base, with stout twigs and ± erect fruiting catkins. In contrast, *B. pubescens* var *fragrans*, a British and possibly Irish endemic, is a thin twigged, partially pendulous tree, which has no obvious morphological signs of introgression from *B. nana*. Much of the confusion, in Great Britain at least, resulted from the adoption of the name subsp. *tortuosa* for the small-leaved British upland tree by Stace (1991, 2019), the same name used in the Scandinavian literature for their 'mountain birch'.

Elkington (1968) undertook a morphometric study of *B. nana* and *B. pubescens* in NW Iceland. He observed that *B. nana* (diploid) was relatively uniform in morphology, while the variable populations seem to be centred upon *B. pubescens* (tetraploid). The latter formed dense thickets up to 2-3 m high, and would now be named var. *pumila*. Earlier work (Löve & Löve, 1956) had found that elsewhere in Iceland, the majority of plants they considered to be hybrid were tetraploids (2n = 56, i.e. they were *B. pubescens*) with only a few being triploids (2n = 42). Elkington concluded that gene flow was likely to be uni-directional from diploid to tetraploid, and that the most likely mechanism would be through the fertilization of *Betula pubescens* female gametes by unreduced *B. nana* pollen (F1 hybrids). Gene flow may alternatively be via partially fertile hybrids (triploids), through the production of unreduced eggs, which are then fertilized by normal haploid *B. nana* pollen (F2 hybrids).

This uni-directional introgression from *B. nana* into *B. pubescens* has recently been demonstrated to be widespread in Great Britain, but only at a very low level (Zohren *et al.*, 2016), (Fig. 48).

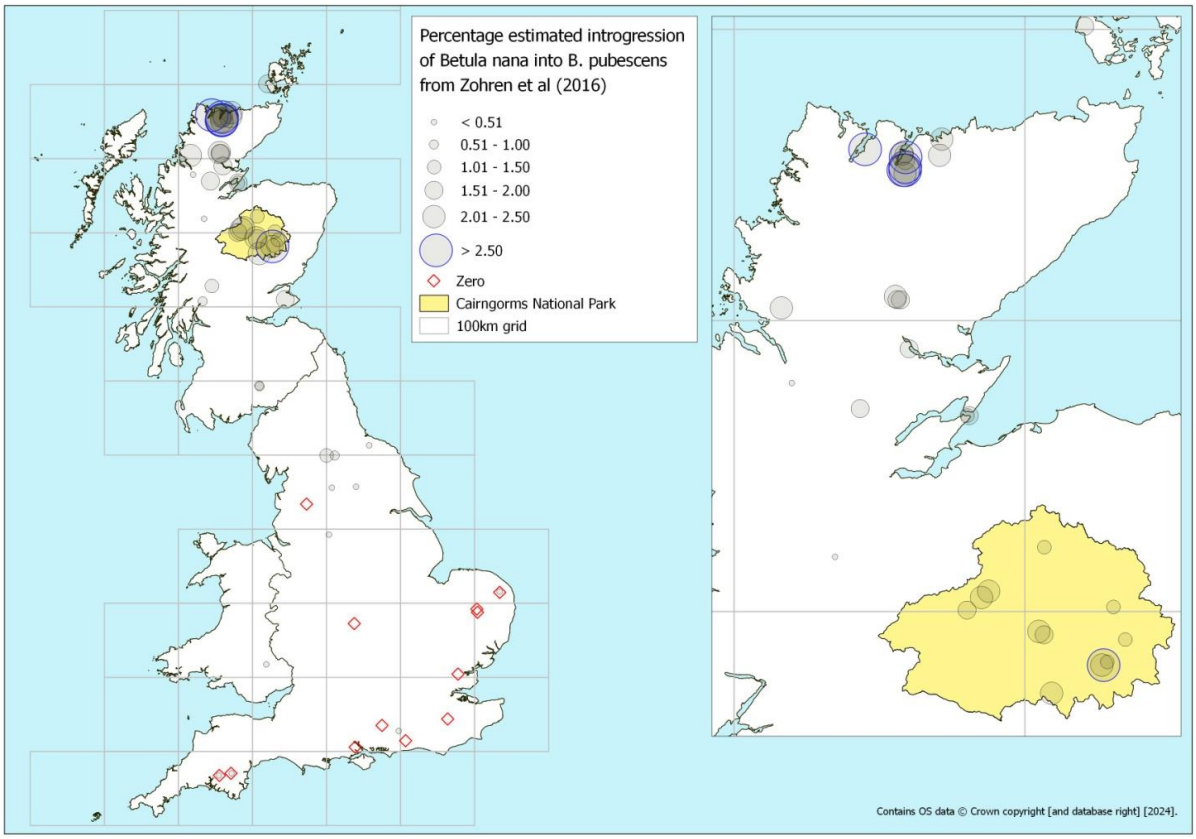

Figure 48. Percentage introgression of *Betula nana* into *B. pubescens*. From Zohren *et al*. (2016) supplementary information Table S1

This study detected an introgression gradient from south to north across the length of Britain; extremely low in the south (a legacy of the early post-glacial distribution of *B. nana*), but higher to the north. The authors concluded that "*a zone of hybridization between B. nana and B. pubescens moved northwards through the UK since the last glacial maximum, leaving behind a footprint of introgressed genes in the genome of B. pubescens*". In Scotland, Zohren *et al*. sampled *B. pubescens* at 39 unique locations, and found evidence of introgression from *B. nana* at all of them; mean 1.83%, range 0.10-3.07%.

The most parsimonious scenario that explains the findings of Zohren *et al*. is that during the post glacial period any highly introgressed *B. pubescens*, derived from tetraploid hybrids crossing with *B. pubescens,* rapidly crossed with 'ordinary' *B. pubescens*, hence diluting and dispersing the genetic contribution of *B. nana*. *Betula pubescens* is an out-breeding species (possibly obligate) and introgression was frequent enough for molecular evidence of *B. nana* to disperse widely through the whole *B. pubescens* population.

The alternative scenario that highly introgressed *B. pubescens* referable to var. *pumila* was, at some point in the current post glacial period, found in Scotland but has been lost, is possible. Evidence for its former existence here now only occurs through the molecular evidence of wider introgression that Zohren *et al*. found.

For a self-sustaining population of var. *pumila* to become established, the trees would have to be reproductively isolated from 'ordinary' *B. pubescens*. This isolation

might be provided by differing flowering times, *e.g.* at different altitudes, or by differing habitats or distributions.

No conclusive examples of var. *pumila* have been found to date in Scotland. The most plausible examples are specimens collected by Marshall and referred to in Druce (1905) and Marshall (1901, 1914) and discussed in Amphlett (2021). These putative examples of var. *pumila* and other examples of *B. pubescens* obviously introgressed from *B. nana* are from a wide range of altitudes (10-750 m). Localised records of the hybrid *Betula x intermedia* (*B. nana x pubescens*) in the DDb are from *c.*70-660 m altitude.

The altitude distribution of records of *B. nana* with high precision grid references (100 m or better) in the CNP is shown in Fig. 49.

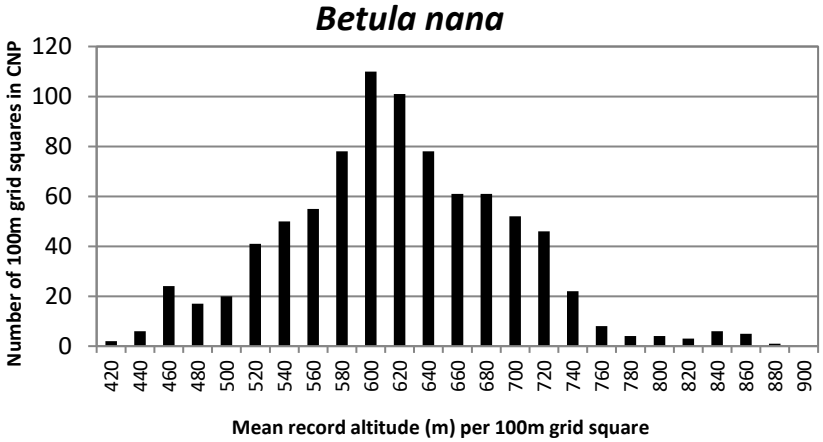

Figure 49. High precision (100 m or better) *Betula nana* records in the Cairngorms National Park (n=1097)

The peak frequency of records is in the range 580-620 m, and 69% of occupied 100 m grid squares are in the range 560-720 m, from the potential forest line, to slightly above the potential treeline. Across the Highlands of Scotland, *B. nana* occurs at the highest altitudes in the CNP (Fig. 50).

Betula nana is recorded from 964 monads in Britain, with the majority of records in the Highlands of Scotland. Of these, in only 154 monads (16%) is *B. pubescens* also recorded, of which 30 monads (19.5%) are in the CNP. Of these CNP monads, 13 are within the Mar Lodge NNR, almost entirely within that part of the NNR where NTS are maintaining very low deer densities (Rao, 2017).

Within the CNP, Mar Lodge NNR is the most likely location where future hybridisation and introgression of *B. nana* into *B. pubescens* will occur. Because of the altitudinal distribution of *B. nana* in the CNP (Fig. 49), it is possible that introgressed forms of *B. pubescens* might be better adapted to grow at slightly higher elevation than var. *fragrans*. However, *B. nana* occurs at much lower altitudes further north in Scotland (Fig. 50).

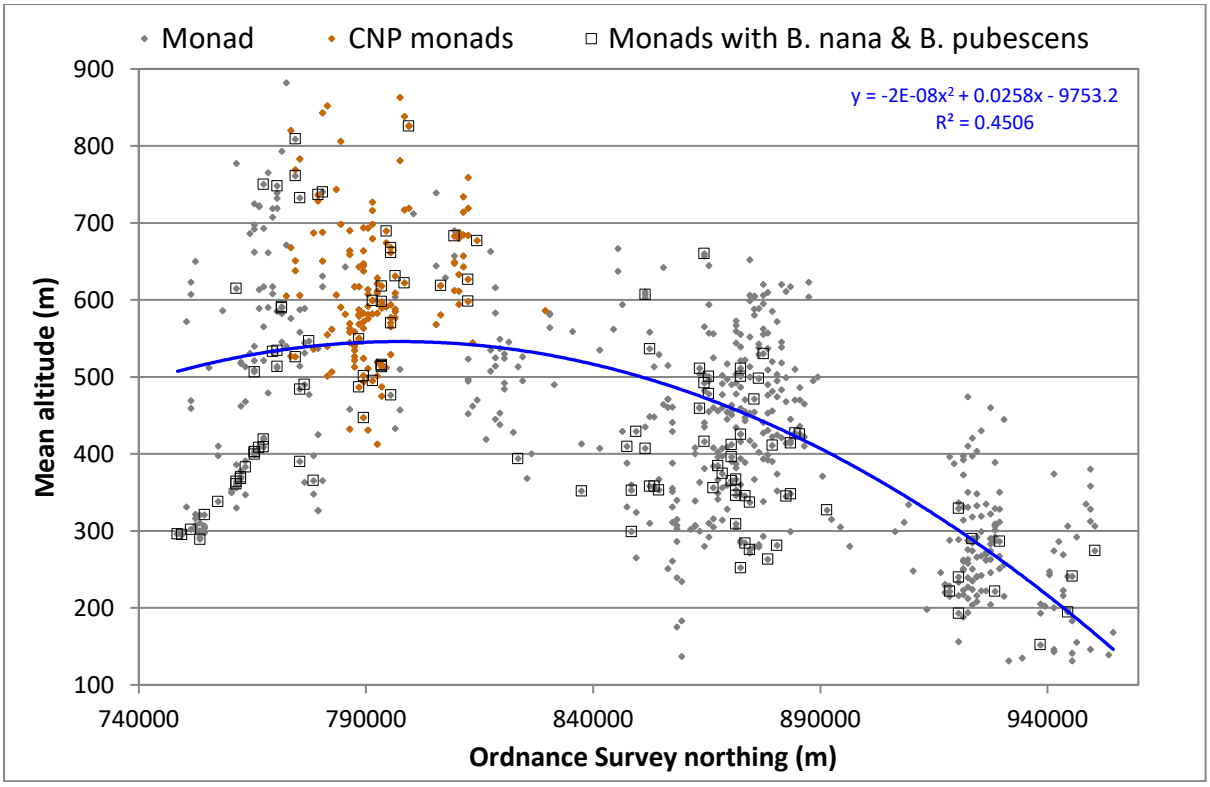

Figure 50. *Betula nana*. Mean altitude of records at 100 m precision (or better) per monad. Rannoch Moor (Scotland) northwards. Monads in Cairngorms National Park and with *Betula pubescens* co-occurring indicated

Evidence of the former existence of an introgressed form of *B. pubescens* as a significant component of treeline woodland and montane scrub zones in the CNP is currently absent. Analysis of peat and sediment cores from small basins and lochans within the treeline woodland and montane scrub zones, looking for vegetation macrofossils, could provide the necessary evidence (Birks & Birks, 2000; Birks, 2003; Gaillard & Birks, 2013). There are numerous small lochans above 700 m that might provide suitable sampling sites.

Targeted searches of *Betula* stands in monads where *B. nana* and *B. pubescens* co-occur (Fig. 50), looking for the hybrid *Betula x intermedia* and introgressed *B. pubescens* would also be worthwhile. Identifications should be based on the full range of available identification features, including fruits and female catkin scales.

As well as different *B. pubescens* taxa, the CNP and south-west Norway have differences in their compliment of native *Salix* and other tree taxa. In the CNP *S. cinerea* is represented by subsp. *oleifolia*, which is common (Fig. 27). This taxon is unknown as a native in Scandinavia (Jonsell, 2000), and is absent from Norway. In south-west Norway and much of the rest of Scandinavia, *S. cinerea* is represented by subsp. *cinerea*, which has only a single CNP record. South-west Norway also has a number of additional *Salix* taxa, entirely absent from Great Britain, most notably *S. glauca*, which is an important constituent of the 'grey willow' thickets in treeline woodland and montane scrub zones in Norway (Elven & Fremstad, 2018). *Alnus incana* (grey alder) is non-native in Britain, where it was only introduced in 1780, and was not recorded from the wild until 1922 (Dines & Pearman, 2023). In the CNP there is a single record of one tree above 500 m, where it was most probably

planted or accidentally introduced. In Norway, where it is native, its altitudinal limit is between that of *P. sylvestris* and *B. pubescens* (Kullman, 2013). *Picea abies* (Norway spruce), alien in Britain, grows close to the treeline in Scandinavia.

In Norway, the observed forest line rises to almost 1300 m a.s.l. in south-central Norway (Bryn & Potthoff, 2018) at the same latitude as Shetland. Here the mountains reach a maximum of 2,469 m at Galdhøpiggen, the highest mountain in Norway and Scandinavia. In Norway and Sweden, Odland (2015) demonstrated that while latitude explained most (70.9%) of the forest line height variation, the altitude of the nearest mountain summit explained an additional 18.1%. Where the mountains are lower (approximately 1000 m higher than the measured local treeline) the treeline elevation is reduced substantially and climatically determined forest lines will probably not have been reached. In addition to its relatively maritime location, the core mountain area of the CNP is simply too low, and too limited in extent, for the treeline to reach the altitude that might be expected from latitude alone.

Treelines are considered to be sensitive indicators of climate change, and Pears (1968, 1970) showed that during the post-glacial climatic optimum, the treeline in the Cairngorms was at 790 m. Appendix 4 lists eight native and four alien phanerophytes and nano-phanerophytes with maximum altitude (based on minimum altitude of grid reference square) in the range 450-500 m in the CNP. These include species with wind as well as bird and mammal dispersed seeds and fruits, and as the climate warms, might extend their altitudinal range into the currently defined treeline ecotone.

Conclusion

The analyses presented here have clarified the species composition of developing treeline woodland and montane scrub in the CNP. However, the relative frequency of the individual species may change as these habitats develop. The analyses also highlight those species whose altitudinal limits are just above or just below the forest line, and as the climate changes some of these may become established above that level. The distribution and abundance of the non-native *P. sitchensis* within the treeline ecotone is incompletely known, probably a gross underestimate, and likely to become a management problem where the aim is to develop a natural transition from forest to treeline and montane scrub.

Whether or not a 'birch belt' above the altitudinal limit of *Pinus sylvestris* is a missing element of the treeline ecotone in the CNP is currently unknown, but evidence presented here strongly suggests that *B. pubescens* is unlikely to form an exclusive birch belt at elevations above the *P. sylvestris* altitudinal limit. The potential altitudinal limit of *B. pubescens* var. *fragrans* is also unknown, as is whether or not highly introgressed examples of *B. pubescens*, perhaps referable to var. *pumila*, occurred in the past, or still occur in the CNP or elsewhere in Scotland.

Within the core of the CNP five adjoining landowners have reduced deer numbers to sufficiently low densities to allow expansion of native tree and scrub species. However most of these reductions have happened only recently (the last two decades), and there needs to be an ongoing commitment to maintaining low deer densities here, to enable a more natural transition from forest to scrub line to develop.

There is sometimes a conservation case to intervene by planting, e.g. of *Salix* species to reinforce existing populations with new, unrelated individuals, and to create new stepping-stone populations between remnant stands of a species. Similarly, the creation of new seed sources in locations remote from existing populations may be warranted. However, where nature conservation is the management priority, a strong case can be argued that interventions, such as planting, should be the minimum to achieve conservation objectives, and no more than that.

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Appendix 1

Alien phanerophytes and nano-phanerophytes recorded >500 m altitude in the Cairngorms National Park. From the BSBI DDb January 2024

Species	Unique grid references	Unique 100 m grid squares	% unique grid references >500 m	% unique 100 m grid references >500 m	Lifeform
Alnus incana	21	11	4.76	9.1	Ph
Berberis vulgaris	24	11	4.2	9.1	Pn
Larix decidua	326	110	3.07	5.5	Ph
Larix x *marschlinsii*	41	20	9.76	20.0	Ph
*Picea sitchensis**	612	447	21.9	28.4	Ph
Pinus contorta	175	121	1.14	1.7	Ph
Sorbus aria agg.	95	32	2.11	6.3	Ph

*See Fig. 51 below.

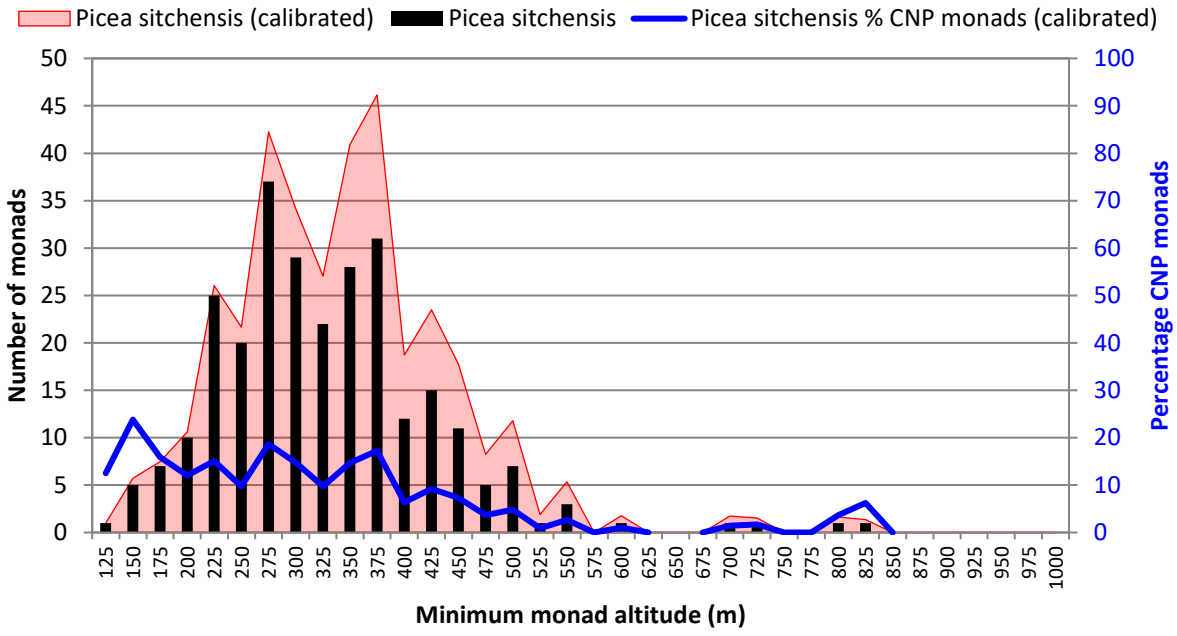


Figure 51. ***Picea sitchensis***

Picea sitchensis (Sitka Spruce) is the most widespread non-native tree (or scrub) species found above 500 m in the CNP. However, examination of the distribution of records in the DDb suggests it is grossly under-recorded. There is a marked concentration of records in Abernethy NNR where it was recorded in the course of detailed transect surveys of tree regeneration. The highest altitude record in the DDb is at 1050 m at NH99490118 (Abernethy NNR: Feithe Buidhe, S. of), but has recently (Walker & Harding, 2024) been found at 1210 m on Braeriach.

Appendix 2

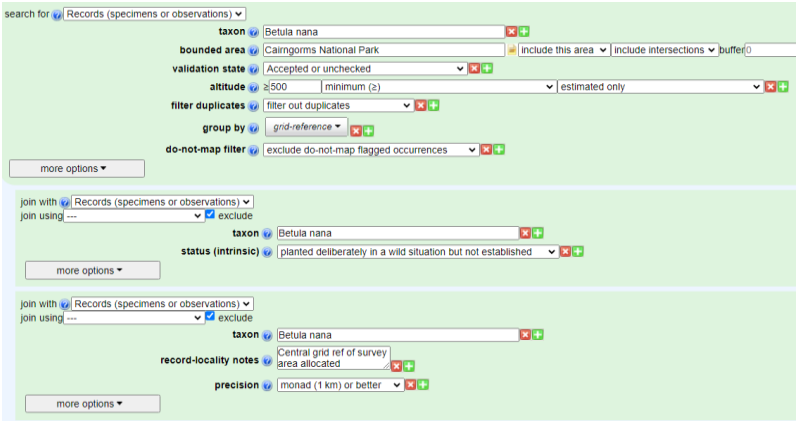
Native *Salix* hybrids recorded >500 m altitude in the Cairngorms National Park. From the BSBI DDb January 2024

Species	Unique grid references	Unique 100 m grid squares	% unique grid references >500 m	% unique 100 m grid references >500 m
Salix aurita x *cinerea = S.* x *multinervis*	329	233	4.3	5.6
Salix aurita x *herbacea = S. x margarita*	5	-	20.0	-
Salix aurita x *lapponum = S.* x *obtusifolia*	16	2	31.3	100.0
Salix aurita x *lapponum* x *herbacea*	2	-	50.0	-
Salix aurita x *myrsinifolia = S.* x *coriacea*	7	3	14.3	33.3
Salix aurita x *repens = S.* x *ambigua*	45	6	8.9	0.0
Salix caprea x l*apponum = S. x canescens*	6	1	33.3	100.0
Salix caprea x *repens = S.* x *laschiana*	4	-	25.0	-
Salix cinerea x *myrsinifolia = S.* x *puberula*	4	2	25.0	50.0
Salix cinerea x *repens = S.* x *subsericea*	3	2	33.3	50.0
Salix herbacea x *lanata = S.* x *sadleri*	10	1	20.0	100.0
Salix herbacea x *lapponum = S.* x *sobrina*	14	1	14.3	100.0
Salix herbacea x repens = S. x *cernua*	9	1	22.2	100.0
Salix lapponum x *lanata*	5	1	40.0	100.0
Salix myrsinifolia x *lapponum*	1	-	100.0	-
Salix myrsinifolia x	15	2	46.7	100.0

myrsinites = S. x *punctata*				
Salix myrsinifolia x *myrsinites* x *phylicifolia = S.* x *blyttiana*	5	-	20.0	-
Salix myrsinifolia x *phylicifolia = S. x tetrapla*	52	27	28.9	40.7
Salix myrsinites x *herbacea*	4	-	25.0	-

Appendix 3

Example of DDb query used to calculate values for Tables 1 and 2.



https://database.bsbi.org/search.php#retrievesaved=0.xyags&query=ccda9b80989a708b57b138f663334feb

Appendix 4

Phanerophytes and nano-phanerophytes with maximum altitude (based on minimum altitude of grid reference square) in the range 450-500 m in the Cairngorms National Park. From the BSBI DDb January 2024

Native in CNP
Crataegus monogyna (Hawthorn)
Ribes rubrum (Red Currant)
Ribes spicatum (Downy Currant)
Rosa canina agg. (Dog-rose)
Rubus fruticosus agg. (Bramble)
Salix purpurea (Purple Willow)
Sambucus nigra (Elder)
Ulmus glabra (Wych Elm)

Alien in CNP
Acer pseudoplatanus (Sycamore)
Fagus sylvatica (Beech)
Picea abies (Norway Spruce)
Pinus contorta (Lodgepole Pine)