Caledonian Pinewoods

Findings from the Caledonian Pinewood Recovery Project

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Appendix 1

Health and resilience concepts

Trees for Life

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1. Health and resilience definitions

For the purposes of this project, the following definitions of Caledonian Pinewood health and resilience were developed and used:

- Healthy Caledonian Pinewoods have capacity to support the full range and abundance of associated wildlife.
- Resilient Caledonian Pinewoods can recover after disturbance and sustain their health during change.

2. Associated wildlife

Healthy Caledonian Pinewoods have capacity to support the full range and abundance of associated wildlife. Associated wildlife includes generalist species also found in other habitats, specialist species restricted or almost restricted to Caledonian Pinewood and other old-growth woodlands, and keystone species that have important impacts on capacity of the habitat to support other species. Species associated with Caledonian Pinewood and their habitat requirements are considered for different groups of organisms in this section.

2.1. Fungi

Caledonian Pinewoods can support rich fungal assemblages and are particularly important for declining tooth fungi in the genera *Bankera*, *Hydnellum*, *Phellodon* and *Sarcodon* (Holden 2008). The main habitats for fungi are soil, dead branches and trees, decay features in living trees, and living plants. In soil, most species are mycorrhizal (form associations with plant roots to exchange water and minerals for sugars) or litter decomposers. Mycorrhizal species include those that form ectomycorrhizae (usually associated with trees), arbuscular mycorrhizae (associated with most other plants), and ericoid mycorrhizae (associated with ericoid shrubs like Blaeberry and heathers). Mycorrhizal relationships can be species specific, and so mycorrhizal fungi richness is expected to scale with plant richness. Additionally, some mycorrhizae are associated with different tree growth stages.

Fungi can degrade lignin, and as such many species are deadwood specialists and associated with the decomposition of dead branches and trees. Further specialism takes place according to the decomposition stage, with different assemblages present in recently dead wood (mostly short-lived ascomycetes transferred by bark beetles), initial to intermediate wood decay (mostly polypores), advanced wood decay (mostly saprotrophic agarics), and final wood degradation (mostly mycorrhizae) (Stokland *et al*. 2012). Some species are specialists of burnt deadwood (Summers 2018) or fallen pine bones (Niemelä *et al*. 2002). Decay features in living trees such as hollowing and open wounds can support specialist fungal assemblages, including heart-rot and sugar fungi respectively. Heart-rot fungi can be species or genera specific, such as *Phellilnis pini* on pines, while sugar fungi (including yeasts and sapstain fungi) are usually confined to broadleaved trees as conifers produce sticky resins that close wounds quickly (Stokland *et al*. 2012).

Some fungi have specialised to develop on living plants and often have specific hosts (eg. rust fungi).

2.2. Lichens

434 epiphytic lichen taxa have been recorded from native pinewood in Scotland, with 219 species recorded from Scots pine bark or lignum and 18 species confined to Caledonian Pinewood (Coppins

& Coppins 2006). Groups of lichen species form communities that often grow together on tree surfaces according to bark chemistry, habitat longevity and continuity, light availability, exposure, competitive relationships, and other factors. Key lichen communities in Caledonian Pinewood include:

- The Pseudovernion and Parmelion, which typically grow on mature to old trees with acidic bark such as Scots pine, birch, and alder.
- Lignicolous lichens that grow on exposed wood, particularly standing dead Scots pines that have shed their bark (pine bones).
- The Graphidion, which comprises around 30 species in Caledonian Pinewood that typically grow in the smooth living bark of rowan, hazel and holly
- The Lobarion, which includes around 25 species in Caledonian Pinewood that typically grow on mature to old trees with neutral to basic bark, such as rowan, oak, willow, aspen and hazel (Coppins & Coppins 2006)

Lignicolous lichen communities are especially rich in species found primarily in Caledonian Pinewood (Mason *et al*. 2004). There is regional variation in community composition and distribution (Coppins & Coppins 2006), and one species is endemic to old Scots pine forests in the temperate/boreal rainforest zone in North West Europe (*Melaspilea lentiginosula*, Jordal *et al*. 2017). Many lichens are dispersal limited and associated with old growth Caledonian Pinewood.

2.3. Plants

Caledonian Pinewoods are typically found on podzols capped with mor humus or shallow peat, although some areas occur on brown podzolic soils or brown earths (Rodwell 1991), or deep peats. These acidic soils generally give rise to plant communities dominated by calcifugous species (plants that preferentially grow in acidic soils), many of which are also found in mires and heaths. Plant community composition is also heavily influenced by long-term browsing and grazing pressure.

Ericoid dwarf shrubs are often prominent components of the vegetation, with the field layer generally dominated by ling heather *Calluna vulgaris* in open pinewoods and blaeberry *Vaccinium myrtillus* and cowberry *V. vitis-idaea* in denser pinewoods. Crowberry *Empetrum nigrum*, bell heather *Erica cinerea* and cross-leaved heath *E. tetralix* are minor components, and cranberry *Vaccinium oxycoccos/microcarpum* is found locally in bog pinewood and bearberry *Arctostaphylos uva-ursi* in rocky pinewoods on scree. Crowberry does however appear more abundantly in higher altitude pinewood fragments, and bog blaeberry *Vaccinium uliginosum* may have been associated with high-altitude Caledonian Pinewood in the past (it can be abundant in Norwegian pinewoods). Aside from dwarf shrubs, purple moor grass *Molinia caerulea* and bracken *Pteridium aquilinum* are the main field layer components, with the former more prominent in the west. Over time, heavy browsing pressure can remove dwarf shrubs and allow purple moor grass and bracken to become dominant.

A subset of pinewood herbs and one fern are Caledonian Pinewood or boreal woodland specialists, including creeping lady's tresses *Goodyera repens*, serrated wintergreen *Orthilia secunda*, one-flowered wintergreen *Moneses uniflora*, twinflower *Linnaea borealis*, and pinewood bracken *Pteridium pinetorum*. These are generally rare but occur most frequently in eastern pinewoods. Other species occur in a wider range of habitats, but lesser twayblade *Neottia cordata*, intermediate wintergreen *Pyrola media*, common wintergreen *Pyrola minor*, chickweed wintergreen *Trientalis europaea*, and common cow-wheat *Melampyrum pratense* can be more frequent in Caledonian Pinewood. Cloudberry *Rubus chamaemorus* may have been associated with higher-altitude

Caledonian Pinewoods on deep peat/humus in the past, and still occurs in this habitat in parts of Glen Affric.

Bryophytes are often prominent in the ground layer, with pleurocarpous mosses dominant except in wetter areas where *Sphagnum capillifolium* hummocks can cover large areas. Ostrich plume feather moss *Ptilium crista-castrensis* is strongly associated with Caledonian Pinewood and other northern woodland types. Oceanic bryophytes and Wilson's filmy fern *Hymenophyllum wilsonii* are widespread in Caledonian Pinewood in the temperate rainforest zone, where they often grow on rocks or as epiphytes.

Different epiphytic bryophytes grow preferentially on tree species with specific bark properties. Higher altitude Caledonian Pinewood fragments in the temperate rainforest zone can also support Northern Hepatic Mat species, including purple spoonwort *Pleurozia purpurea*, lesser whipwort *Bazzania tricrenata*, juniper prongwort *Herbertus hutchinsiae*, and the endemic northern prongwort *H. borealis*. These grow on the ground or on exposed roots or lower trunks of trees, and northern prongwort has been recorded as an epiphyte. Some bryophytes are deadwood specialists and grow primarily on fallen trees at specific stages of decay. These include green shield-moss *Buxbaumia viridis*, which is a rare species associated with conifer and birch logs in the east of Scotland.

The canopy of Caledonian Pinewood is generally dominated by wild Scots pine *Pinus sylvestris* although birch (mostly *Betula pendula* in the east and *Betula pubescens* in the west) can be locally dominant, particularly in the west. Oak *Quercus sp.* and alder *Alnus glutinosa* may also be locally prominent. Rowan *Sorbus aucuparia*, eared willow *Salix aurita*, holly *Ilex aquifolium*, and juniper *Juniperus communis* can be locally prominent in the understory. Aspen *Populus tremula* may have been more important in the past, but is rare and often restricted to topographic refuges today. Some Caledonian Pinewood is expanding into areas with dwarf birch *Betula nana* in Glen Derry and Glen Cannich. Dwarf birch may have been an important shrub in high altitude and bog pinewoods in the past.

2.4. Invertebrates

Caledonian Pinewoods are key habitats for threatened invertebrates, with over 60 associated Red Data Book invertebrate species (Mason *et al*. 2004). Many of these depend upon continuity of standing and fallen deadwood, or the relatively open structure of old growth Caledonian Pinewood, and some feed directly on Scots pine needles, cones, or pollen.

Summers (2018) reports that the most abundant invertebrate groups in Caledonian Pinewood at Abernethy were fungus gnats (Mycetophilidae) and gall midges (Cecidomyiidae) in the canopy, wood ants on the ground, and mites (Acari) in the soil. The abundance of moth caterpillars and wood ants was greatest in areas dominated by *Vaccinium* species (Blaeberry and Cowberry), while ground spiders and bugs were more abundant in areas dominated by heather. Beetles (Coleoptera), particularly predatory ground beetles (Carabidae) and rove beetles (Staphylinidae), were the most species-rich group recorded, and species richness was greatest in old growth Caledonian Pinewood.

Many invertebrate species in Caledonian Pinewood are monophagous, which means they have specialised to feed on a single plant species, and high proportion of phytophagous (plant-feeding) species feed on tree foliage. Consequently, species richness is expected to scale with increased plant and specifically tree species richness. The rare chequered skipper butterfly *Carterocephalus palaemon* feeds on the foliage of purple moor grass tussocks that grow on the edge of woodland or in glades, particularly on south facing slopes (Forestry Commission Scotland, 2009). It is found in Caledonian Pinewoods in Lochaber and north Argyll.

Rich invertebrate assemblages are associated with decaying wood, and different species are specialised to different phases of decay (Stokland *et al*. 2012). Species adapted to live in hollow trees appear to be more dispersal limited than those associated with snags and logs (Stokland *et al*. 2012). Scottish wood ants *Formica aquilonia* and northern wood ants *Formica lugubris* build prominent domed nests in Caledonian Pinewood. In turn, these can support specialised assemblages of myrmecophiles (species that live within ant nests), including springtails, mites, beetles, and the rare Shining guest ant *Formicoxenus nitidulus*. In Finland, the species richness of myrmecophilous beetles was greatest where Scottish wood ant nests were larger, more abundant, and closer together (Päivinen *et al*. 2004).

2.5. Birds

45 bird species are associated with mature pinewood habitat in the Highlands (Mason *et al*. 2004). These include conifer specialists like capercaillie, crested tit and Scottish, common, and parrot crossbills. The Scottish crossbill is endemic to conifer forests in Scotland. Some species are associated with old growth pinewood, including capercaillie, redstart and crossbills (Summers 2018).

Great spotted woodpeckers are a keystone species in Caledonian Pinewood. They excavate holes in standing deadwood – a key resource for bird diversity – which can go on to support hole-nesting and roosting birds, bats, and honey bees (Summers 2018). Hole-nesting birds include redstarts, wrynecks, swifts, crested tits, great tits, and starling. The crowns of old Scots pines are favoured nest-building sites for osprey, golden eagle, and sea eagle.

Some species nest in Caledonian Pinewood but feed elsewhere (eg. osprey). For species that do feed in Caledonian Pinewood, key resources include pine needles (eg. capercaillie) and cones (eg. crossbills), blaeberry shoots and berries (eg. capercaillie), heather seeds (eg. bullfinch), rowan berries (eg. migratory fieldfare and redwing), and invertebrates (eg. tree pipit and redstart).

2.6. Mammals

Significant components of the Caledonian Pinewood mammal fauna were driven to extinction, including all large carnivores (lynx, wolf, and brown bear), some large herbivores (elk and possibly aurochs), and other species like wild boar and beaver. Wild boar and beaver have since been reintroduced and are spreading. Wild cat is also considered functionally extinct, but relict populations or hybrid populations (with feral cats) remain at some sites. Red squirrel, pine marten, red deer, and roe deer were reduced to small populations in the past but have since largely recovered. However, deer populations have increased to densities sufficiently high to prevent successful tree regeneration at landscape scale, and their behaviours are no longer actively influenced by large carnivores. This is the main ecological barrier to Caledonian Pinewood recovery. The full effects of elevated levels of herbivory are explored in Section 9 of Appendix 3.

Other mammals supported by Caledonian Pinewood include foxes *Vulpes vulpes*, badgers *Meles meles*, bank voles *Myodes glareolus*, wood mice *Apodemus sylvaticus*, and bats, with common pipistrelle *Pipistrellus pipistrellus*, Soprano pipistrelle *Pipistrellus pygmaeus*, Daubenton's bat *Myotis daubentonii*, and brown long-eared bat *Plecotus auritus* recorded at Abernethy (Summers 2018). Livestock and feral goats are also present at some sites. Key resources for mammals include tree and shrub cover for shelter and nesting, and abundant vegetation (beavers, deer, extinct large herbivores), fruits and seeds (wood mice, bank voles, foxes, badgers, pine marten, red squirrels), invertebrates (bats, wood mice, foxes, badgers, wild cat), vertebrate prey (wild cat, pine marten, extinct large carnivores), eggs (foxes, badgers, pine marten, red squirrels) and carrion (foxes, badgers, pine marten) for feeding.

3. Disturbance

Resilient Caledonian Pinewoods can recover after disturbance. We consider disturbances to be events that cause or contribute to the death of established (maturing, mature or old) trees. These can be linked to weather or other abiotic factors, or biotic factors like competition and overbrowsing. Recovering health after disturbance often requires regeneration to be able to take place. Disturbances identified in Caledonian Pinewood include:

3.1. Windthrow

Established trees can be blown over by strong winds. This usually happens because the wind-force on the crown levers the root plate from the soil on one side, causing the tree to become destabilised and fall to the forest floor, or be suspended by debris. Trees growing on shallow or waterlogged soils, exposed ridges, or on the woodland edge may be particularly susceptible to windthrow. Provided damage is not too great and sufficient root contact with the soil maintained, some trees can survive windthrow and regrow as ‘phoenix trees’. Broadleaved trees phoenix more readily as they can resprout from fallen trunks, while Scots pine relies upon regrowth from surviving parts of the crown and branches. Phoenixing can be prevented or impaired if regrowth is overbrowsed by large herbivores. Where windthrow results in tree mortality, recovery can only take place through regeneration. Based on preliminary observations, we considered windthrow to be a significant cause of disturbance at some sites.

The root plates of windthrown trees can act as elevated ‘safe sites’ for regeneration in Caledonian Pinewoods, where young seedlings can establish out of the reach of livestock and deer. This is particularly the case in the western Highlands, possibly due to the wetter climate which mitigates against drought (root plates typically contain only pockets of soil which, due their elevated position, are likely vulnerable to desiccation). Trees that have regenerated on root plates or stumps typically have unusual lower trunks, which with some practice can be discerned in the field even after the root plate or stump has largely rotted away.

Larger Caledonian Pinewoods are more likely to be able to absorb disturbance caused by windthrow. This is because wind speeds are heterogenous at landscape scale, due to variation in landform and topology, and because trees themselves reduce wind speed downwind of themselves. Consequently, there is less chance that a high proportion of trees will be disturbed by windthrow at the same time. Recovery following windthrow disturbance depends on phoenix trees being allowed to regrow and natural regeneration taking place. This can be impaired or prevented by overbrowsing. Natural regeneration outwith current woodland boundaries could help with adaptation to windthrow, as pinewood could ‘find’ safe sites in the landscape where exposure to windthrow is reduced.

3.2. Lightning strike

Established trees or other vegetation can be struck by lightning. This exposes the tree to a temporary burst of extreme energy and heat, damaging or killing the crown and splintering bark along the trunk to create a lightning scar. The tree and surrounding vegetation can catch fire, which may spread depending on conditions. Based on preliminary observations, we considered lightning strike not to be a significant cause of disturbance in Caledonian Pinewood: direct effects are very localised, and human ignition sources are a much more common cause of fire.

Larger Caledonian Pinewoods are more likely to be able to absorb disturbance caused by lightning strike, as there is less change that a high proportion of trees will be impacted at the same time.

Recovery following lightning strike disturbance depends on natural regeneration being able to take place, which can be impaired or prevented by overbrowsing.

3.3. Snow-loading

Established trees can have their crown damaged or drop branches when heavily loaded with snow. Based on preliminary observations, we considered snow-loading not to be a significant cause of disturbance in Caledonian Pinewood as direct effects are relatively small.

Larger Caledonian Pinewoods are more likely to be able to absorb disturbance caused by snow-loading, as there is less change that a high proportion of trees will be impacted at the same time. Recovery following snow-loading disturbance depends on natural regeneration being able to take place, which can be impaired or prevented by overbrowsing.

3.4. Drought

Established trees and other vegetation can become stressed or die when exposed to drought conditions, particularly if drought is prolonged. Trees exposed to other stressors may be more susceptible to death during droughts, and trees stressed by drought may be more susceptible to disease. The risk of fire and severe fire is higher during droughts as ground vegetation is more flammable. Different tree species have different tolerances to drought. We were unsure whether drought is a significant cause of disturbance in Caledonian Pinewood. It is possible that some unexplained synchronous tree mortality has been caused by drought, or drought may have been a contributing factor.

Larger Caledonian Pinewoods are more likely to be able to absorb disturbance caused by drought. This is because drought impacts are heterogenous at landscape scale, due to variation in hydrology and the shading effects that trees themselves have on reducing evaporation from the soil during intense heatwaves. Those those that support more tree species are also more likely to be able to absorb drought disturbances and recover, as different species have different tolerances to drought. Recovery following drought disturbance depends on natural regeneration being able to take place, which can be impaired or prevented by overbrowsing. Natural regeneration outwith current woodland boundaries could help with adaptation to drought conditions, as pinewood could ‘find’ safe sites in the landscape where exposure to drought is reduced. Adaptation could also be assisted where there is good genetic diversity within tree species, and abundant natural regeneration on which selection pressures can act to produce more drought tolerant individuals.

3.5. Waterlogging

Permanent waterlogging can occur in basins or depressions where drainage is naturally impaired, or can develop more widely in oceanic areas following deforestation. Temporary or seasonal waterlogging can occur following heavy rainfall. Waterlogging can confine rooting to surface soil layers, making trees more susceptible to windthrow. Waterlogging can also cause stress and contribute to tree death if it becomes more permanent. However, some tree species are adapted to waterlogged conditions. Based on preliminary observations, we considered waterlogging not to be a significant cause of disturbance in Caledonian Pinewood, although its long-term effects on soil may impact woodland expansion into deforested parts of the western Highlands.

Larger Caledonian Pinewoods are more likely to be able to absorb disturbance caused by waterlogging. This is because waterlogging impacts are heterogenous at landscape scale due of variation in hydrology. Additionally, prolonged waterlogging may be mitigated by the evapotranspiration by trees. Pinewoods that support more tree species are also more likely to be able to absorb waterlogging disturbances and recover, as different species have different tolerances to waterlogging. Recovery following waterlogging depends on natural regeneration being able to take place, which can be impaired or prevented by overbrowsing. Natural regeneration outwith current woodland boundaries could help with adaptation to waterlogging, as pinewood could 'find' safe sites in the landscape where exposure to waterlogging is reduced. Adaptation could also be assisted where there is good genetic diversity within tree species, and abundant natural regeneration on which selection pressures can act to produce more drought tolerant individuals.

3.6. Erosion

Erosion occurs primarily on riverbanks, ravine-sides, cliffs, and steep slopes, and can dislodge trees and other vegetation. It can occur due to heavy loading on unstable substrates or be linked to river processes, and may interact with other factors such as windthrow, snow-loading, and flooding. Dislodged trees are unlikely to survive. Based on preliminary observations, we considered erosion to be a significant cause of disturbance at some sites. This is because some fragments of Caledonian Pinewood are confined to erosion-vulnerable topographic refuges (ravines, cliffs) and hold small populations of Scots pine, so even localised erosion can have significant impacts on the population.

Larger Caledonian Pinewoods are more likely to be able to absorb disturbance caused by erosion. This is because erosion impacts are often localised. Recovery following erosion depends on natural regeneration being able to take place, which can be impaired or prevented by overbrowsing. Natural regeneration outwith current woodland boundaries could help with adaptation to erosion, as pinewood could 'find' safe sites in the landscape where exposure to erosion is reduced.

3.7. Fire

Fires occur following ignition in areas with flammable vegetation. Ignition sources can be natural (lightning) or artificial (burning by people), most frequently the latter. Repeated burning is a feature of muirburn management which is carried out in some Caledonian Pinewoods and in parts of the surrounding landscape. Fire spread is influenced by topography, wind speed and direction, fuel loads, and vegetation flammability:

- Fires usually spread upslope more rapidly than downslope.
- Fires usually spread more rapidly when wind carries fragments of burning material ahead of the main fire to seed additional fires. They also spread more rapidly in the direction of the wind.
- Fires spread widely where fuel loads are contiguous, and are most intense where fuel loads are high.
- Fires can only spread if vegetation is flammable. The composition and structure of vegetation influences flammability, with dry woody or dead thatched material often most flammable (eg. tall ling heather, thatched bracken or purple moor grass). Flammability is highest during periods of drought.

Fire impacts depend on the extent, intensity, and frequency of fire, and whether it jumps into the canopy. Most fires consume ground vegetation and can damage regeneration, but do not kill established trees. The lower trunks of Scots pine are fire adapted, with thick plates of bark that help protect the living tissues from fire impacts. However, some intense fires can jump into the tree canopy and become extremely destructive, burning and killing the crowns of trees. Broadleaved tree species often resprout from the base following fire. Based on preliminary observations, we considered fire to be a significant cause of disturbance at some sites.

Larger Caledonian Pinewoods are more likely to be able to absorb disturbance caused by fire. This is because fire impacts are heterogenous at landscape scale due of variation in topology and hydrology. Pinewoods that support more tree species are also more likely to be able to absorb fire disturbances and recover, as different species have different levels of vulnerability to fire, flammability, and ability to resprout afterwards. Recovery following fire depends on natural regeneration and regrowth being able to take place, which can be impaired or prevented by overbrowsing. Natural regeneration outwith current woodland boundaries could help with adaptation to fire, as pinewood could 'find' safe sites in the landscape where exposure to fire is reduced.

3.8. Felling

Felling involves cutting establish trees down at the base of the trunk and often removing the timber. Caledonian Pinewoods were widely impacted by felling in the past. Recent felling is concentrated within a few sites part-managed for commercial forestry in the east, where Scots pine is targeted, and Plantation on Ancient Woodland Sites, where non-native conifers are targeted as part of restoration work. The responses of trees to felling differs by species, with broadleaves capable of resprouting from stumps while conifers cannot (unless some live foliage remains below the cut). Based on preliminary observations, we considered felling to be a significant cause of disturbance at some sites.

Disturbance caused by chronic felling can be eliminated by avoiding felling in Caledonian Pinewoods. Larger Caledonian Pinewoods are more likely to be able to absorb disturbance caused by felling. Recovery following felling depends on natural regeneration and regrowth being able to take place, which can be impaired or prevented by overbrowsing.

3.9. Competition

Established trees can be gradually weakened over time by competition with other trees. Competition can be over space, light, nutrients, and other resources, and have long lead in times before resulting in tree death. When not suppressed by climatic/climate-soil effects, temperate-associated tree species are generally more competitive than boreal-associated tree species. This is relevant to impacts from climate change, which are described in Section 4.2. Introduced plants can be more competitive than native plants, and this is considered in Section 4.3.

3.10. Senescence

Trees become senescent and die when they reach the end of their natural lifespan. Based on preliminary observations, we considered senescence to be a significant cause of disturbance at many sites.

Larger Caledonian Pinewoods are more likely to be able to absorb disturbance caused by senescence. This is because there is a lower chance of a high proportion of trees dying from senescence at once. Additionally, pinewoods that support a diverse age structure of different tree species are more able to absorb senescence disturbance and impacts will be heterogenous over time. Recovery following senescence depends on natural regeneration and regrowth being able to take place, which can be impaired or prevented by overbrowsing.

3.11. Disease

Tree diseases can weaken or kill trees over time. Most tree diseases are host specific, and so impact certain tree species and not others. Some can infect healthy trees, while others only cause disturbance following weakening of the tree by other stressors. Vectors for diseases also vary, but include wind, water, soil (often transported by machinery), or animals. Resilience to tree diseases is considered in Section 4.4.

3.12. Insect defoliation

Outbreaks of phytophagous (leaf-feeding) insects can defoliate trees, but this is rare in Caledonian Pinewood and primarily effects regeneration. Most defoliated trees recover, though repeated defoliation may result in death. Based on preliminary observations, we considered insect defoliation not to be a significant cause of disturbance in Caledonian Pinewood.

Larger Caledonian Pinewoods are more likely to be able to absorb disturbance caused by insect defoliation, as there is less chance that a high proportion of trees will be disturbed at the same time. Recovery following defoliation depends on natural regeneration and regrowth being able to take place, which can be impaired or prevented by overbrowsing.

3.13. Debarking

Deer, livestock and feral goats can damage trees though debarking. This can occur through fraying (rubbing antlers on trees) or feeding. The greatest impacts on established trees typically occur on species with thin bark or where trees are rare in the landscape and impacts concentrated. Debarking of old Scots pine was recorded in some areas where deer numbers were very high. This may make trees more susceptible to disease, and can result in tree death if debarking occurs around the whole trunk (ring barking). Based on preliminary observations, we considered debarking to be a significant cause of disturbance at a few sites where only a handful of Scots pine remain.

Disturbance caused by debarking can be reduced by lowering herbivore impacts to a Low or Medium level as defined by Armstrong *et al*. 2020. Larger Caledonian Pinewoods are more likely to be able to absorb disturbance caused by debarking, as there is less chance that a high proportion of trees will be disturbed at the same time. Those that support more tree species are also more likely to be able to absorb debarking disturbances, as different species have different susceptibility to debarking. Recovery following debarking depends on natural regeneration and regrowth being able to take place, which can be impaired or prevented by overbrowsing.

4. Change

Resilient Caledonian Pinewoods can sustain their health during change. As the climate crisis intensifies, shifting bioclimatic envelopes for different tree species are expected to lead to changes in biotic interactions, particularly increased competition between boreal associated and temperate associated trees. This is likely to lead to displacement of boreal associated species, including Scots pine. However, competition is currently heavily influenced by levels of herbivore impact, which are selectively favouring some regenerating species over others or suppressing regeneration completely. Biotic interactions may be further influenced by introduced pathogens and non-native plants. As well as altering biotic interactions, the climate crisis is expected to drive increases in the frequency and intensity of disturbance events. Expected changes are described in more detail below:

4.1. Ongoing change caused by chronic overbrowsing

Ongoing change caused by chronic overbrowsing. We define overbrowsing as browsing sufficient to arrest tree regeneration. Two types of overbrowsing are distinguished:

- Blanket overbrowsing, which occurs when all tree species are impacted by overbrowsing. Caledonian Pinewoods exposed to chronic blanket overbrowsing are unable to recover after disturbance as regeneration cannot take place. Over time, they become dominated by senescent trees as those that die are not replaced, and eventually the woodland is lost.
- Selective overbrowsing, which occurs when some but not all tree species are impacted by overbrowsing. Selective overbrowsing alters the competitive relationships between tree species, over time leading to impoverished tree diversity relative to the potential. When regeneration occurs in pulses, even a short period of selective overbrowsing coincident with a regeneration pulse can lead to diversity impoverishment over long time periods. This is because competitively favoured trees can pre-empt limiting resources such as space and light, helping cement their competitive advantage.

Change caused by chronic overbrowsing can be reduced and, over time, reversed by lowering herbivore impacts to a Low or Medium level as defined by Armstrong *et al*. 2020.

4.2. Ongoing and intensifying change associated with the climate crisis

Many older trees in Caledonian Pinewoods grew up during the ‘Little Ice Age’, a period between c. AD 1570-1900 when summer temperatures were significantly lower than the 20th century average. The current climate crisis, caused by anthropogenic greenhouse gas emissions, has increased temperatures by 0.7^{o}C and rainfall by 9% across Scotland over the 1961-1990 average. In coming decades, Scotland’s climate is predicted to warm further and become wetter in winter and drier in summer. Under a low global emissions scenario for 2080, average temperatures are expected to increase by 1^{o}C, and winters to become 5% wetter and summers 11% drier. Under a high global emissions scenario for 2080, average temperatures are expected to increase by 2.7^{o}C, and winters to become 19% wetter and summers 18% drier (Adaptation Scotland, 2021). This is likely to translate into:

- Changing microclimate within present-day Caledonian Pinewood, and shifting bioclimatic envelopes for different tree species. This may release temperate-associated tree species from climatic suppression, allowing them to outcompete stress tolerant but less competitive species like Scots pine.
- More frequent and intense disturbance events, including summer drought and increased fire risk, particularly in the east, and increased waterlogging and erosion in winter, which could

in turn lead to increased windthrow. Conversely, disturbance from snow-loading is likely to decrease. There is uncertainty around how the climate crisis will influence future storminess in Scotland.

Larger Caledonian Pinewoods are more likely to be able to absorb changes in microclimate. This is because microclimate varies across heterogenous landscapes, and so more safe sites are likely to be present in large than small Caledonian Pinewoods. Adaptation to changing microclimate requires natural regeneration to be able to take place outwith current pinewood boundaries, as this could facilitate colonisation of safe sites in the landscape where microclimatic change is reduced or favourable. Additionally, high genetic diversity in wild tree populations may allow future-competitive genotypes to emerge in regenerating tree populations.

4.3. Ongoing and unforeseen change associated with introduced plants

Ongoing and unforeseen changes associated with introduced plants. Introduced plants can become invasive and alter biotic interactions within ecosystems. In Caledonian Pinewood, a subset of introduced conifers including Sitka spruce, Lodgepole pine and Western hemlock are becoming invasive, along with the introduced shrub Rhododendron ponticum. Sitka spruce, Western hemlock and Rhododendron are heavily shade casting, and Western hemlock and Rhododendron shade tolerant. Competition for space, light and below-ground resources can negatively impact native plants, reducing the vigour and causing the death of native trees and shading out native ground vegetation. Resource pre-emption then prevents recovery. Invasion is facilitated by selective browsing of native trees and shrubs as described in Section x of Appendix 3. Non-native plants can be hosts for introduced pathogens, including *Dothistroma* on Lodgepole pine and *Phytophora ramorum* on Rhododendron. Some of these pathogens pose risks to native species.

Change caused by introduced plants can be reduced and, over time, reversed by removing them from Caledonian Pinewood and surrounding areas they could seed from. Additionally, colonisation and establishment could be reduced by reducing selective overbrowsing impacts, as these confer additional competitive advantage over native trees. Colonisation of woodland by invasive rhododendron is also facilitated by overgrazing of the field layer, which increases the number of regeneration niches available for the species (Cross, 1981).

Larger Caledonian Pinewoods are more likely to be able to absorb disturbance caused by introduced plants. This is because impacts are heterogenous at landscape scale due of variation in establishment and growth rates of introduced species. Natural regeneration outwith current woodland boundaries could help with adaptation, as pinewood could 'find' safe sites in the landscape where exposure to introduced plants is reduced.

4.4. Ongoing and unforeseen change associated with introduced pests and pathogens

Ongoing and unforeseen changes associated with introduced pests and pathogens. Introduced pests and pathogens can threaten native tree populations across whole regions and beyond, radically altering biotic interactions within forest ecosystems. Globally, some tree species are now critically endangered by introduced pathogens. In Scotland, introduced diseases have severely impacted wild populations of elm, and impacts on ash are intensifying and expected to be similarly severe. Risks to Scots pine from an introduced *Dothistroma* strain associated with Lodgepole pine has led to the removal of Lodgepole pine plantations around some Caledonian Pinewoods. An introduced *Phytophora* is impacting Juniper populations in Caledonian Pinewood. Introduced pests and diseases often have species specific impacts.

Caledonian Pinewoods with higher diversity of tree species will be better able to absorb impacts associated with introduced pests and pathogens. This is because these impacts are typically selective on specific tree species. Large wild tree populations with high genetic diversity and successful natural regeneration are more likely to be able to adapt to and recover from changes associated with introduced pests and pathogens. This is because resistant genotypes are more likely to emerge.

5. Health and resilience characteristics

Based on Sections 2, 3 and 4, we identified and grouped components and traits likely to confer health and resilience to Caledonian Pinewood into four health and resilience characteristics. These are diversity, continuity, mobility, and connectivity. These characteristics informed our field survey design and helped frame our data analysis.

5.1. Diversity

Diversity is the range and quality of Caledonian Pinewood habitat components, and the genetic variability within tree species. Diverse Caledonian Pinewoods are healthier as they can support more wildlife, and more resilient to threats from disease and climate change as they can better resist and adapt to change. Key habitat components in Caledonian Pinewood identified are:

- **Living native trees and shrubs.** Many invertebrate species in the orders Coleoptera, Diptera, Hemiptera, Hymenoptera, and Lepidoptera, along with some mammals and birds, have specialised to feed on living tissues, flowers and fruits of specific native tree and shrub species or species combinations. Some species have also specialised to feed on living native trees and shrubs at early or late growth stages. Additionally, mycorrhizal fungi often have species specific or group specific levels of specialisation that can include specific growth stages. The richness of living native trees and shrubs at different growth stages is therefore an important component of Caledonian Pinewood health; Caledonian Pinewoods that support a range of living native trees and shrubs at different growth stages have a greater capacity to support associated species. The richness of living native trees and shrubs at different growth stages also contributes to Caledonian Pinewood resilience through a 'portfolio effect'. Portfolio effects describe the tendency for high diversity systems to be less volatile than low diversity systems. For example, the risk of severe negative impacts from an introduced pathogen, which often targets a specific tree species, would be relatively lower in a Caledonian Pinewood with high tree richness than one where tree richness is low. The high richness woodland would also be better able to recover its health after this kind of disturbance, as more unimpacted tree species are available to contribute regeneration. The presence and abundance/cover of different tree species was recorded during the field survey (see Appendix 2) and analysed (see Appendix 3).
- **Vegetation cover and layers.** Different species and species groups have different preferences for structural diversity within Caledonian Pinewood. Some prefer denser woodland or woodland with well-developed canopy and shrub layers, while others prefer more open conditions. The presence and cover of different vegetation layers is therefore an important component of Caledonian Pinewood health. The presence, cover, and species composition of canopy and understory layers was recorded during the field survey (see Appendix 2) and analysed (see Appendix 3).
- **Old growth features.** Old growth features are woodland habitat components that typically take a long time to develop, including trees that are old or dead, and those living with decay. Old growth features support a wide range of saprotrophic fungi and decay-feeding invertebrates, and some of the rarest Caledonian Pinewood species require specific old growth features to complete their lifecycles. For example, larval stages of the Pine hoverfly *Blera fallax* develop in rotting Scots pine stumps, while the lichen *Carbonicola anthracophila* grows on fire-charred dead pines. Old growth features can also provide nest sites for birds and mammals, and are important structural components of woodland. The presence and abundance of different old growth feature classes are therefore importance components of

Caledonian Pinewood health. The presence and abundance/cover of different classes were therefore by species during the field survey (see Appendix 2) and analysed (see Appendix 3).

- **Tree surfaces.** Caledonian Pinewoods can provide habitat for specialised plants and lichens that grow on tree bark (corticoles) or exposed wood (lignicoles). These species form communities that often grow together on particular kinds of tree surfaces according to bark chemistry, habitat longevity and continuity, light availability, exposure, competitive relationships, and other factors. Key communities in Caledonian Pinewood include:
  - The Lobarion, which is typically dominated by leafy lichens and develops on mature to old trees with neutral to basic bark.
  - The Parmelion, which includes lichens and bryophytes that typically grow on mature to old trees with acidic bark.
  - The Graphidion, which includes lichens and bryophytes that typically grow on twigs and branches with smooth bark.
  - Lignicolous lichens that typically grow on slowly decaying exposed wood.
  - Deadwood bryophytes that typically grow on moist fallen deadwood.

  The presence of different tree surface classes are therefore importance components of Caledonian Pinewood health. Different growth stages of each tree species were recorded during the field survey, and tree surface classes assigned and analysed (see Appendix 3)
- **Ground vegetation.** As with living native trees and shrubs, many invertebrate species in the orders Coleoptera, Diptera, Hemiptera, Hymenoptera, and Lepidoptera, along with some mammals and birds, have specialised to feed on living tissues, flowers and fruits of specific herbs and dwarf shrubs. Some ground vegetation species are particularly important, including Blaeberry *Vaccinium myrtillus*, which supports the greatest richness and abundance of Lepidoptera caterpillars and produces insect pollinated flowers and seasonal fruits. The richness of ground vegetation, and the cover of key plants, are therefore important components of Caledonian Pinewood health. Presence and cover of certain ground vegetation species were therefore recorded during the field survey (see Appendix 2) and analysed (see Appendix 3).
- **Wood ant nests.** Wood ant nests support a range of myrmecophiles as described in Section 2.4. Additionally, wood ants are important predators of other invertebrates in Caledonian Pinewood. Their presence is there an important component of Caledonian Pinewood health, and so was recorded during the field survey (see Appendix 2) and analysed (see Appendix 3).
- **Soil.** Caledonian Pinewood soils support a wide range of fungi and micro-invertebrates, and are the substrate in which vegetation grows. However, we lacked specialist knowledge and understanding necessary to assess soil health during the field survey, and so this aspect of diversity was not assessed.

Genetic variability is another key component of diversity. Tree populations with high levels of genetic variability are more likely to be able to adapt to changing conditions, and wild tree populations typically support high levels of genetic diversity (Fady 2015, BiodivERsA 2014). This is true even for seemingly fragmented wild tree populations in the Scottish Highlands (eg. Provan, Bacles). Ensuring natural regeneration can take place freely is likely to be the most appropriate strategy to ensure maximum genetic diversity on which evolutionary processes can act (Fady 2015). We lacked the specialist knowledge, understanding, and resources to assess genetic diversity and so this aspect of diversity was not assessed directly. However, tree planting was recorded at some sites, and this could be used as a proxy for potentially poor genetic diversity.

5.2. Continuity

Continuity is the maintenance of diversity over time through regeneration of its component parts. In Caledonian Pinewoods, tree regeneration is a critical process in maintaining diversity, as most habitat components rely are ultimately dependent on living native trees and shrubs being replenished following disturbance. Regeneration of wild Scots pine is particularly important as this species characterises the habitat. However, Scots pine regeneration does not have to be always present in all areas, as the species is light demanding and does not regenerate well under its own canopy. Instead, Scots pine regeneration is expected in more open areas or, critically, following disturbance events (responsive regeneration) so that recovery can take place. Without regeneration or responsive regeneration, Caledonian Pinewoods lack resilience and will lose their health over time.

The presence and abundance/cover of different growth stages of different tree species in Caledonian Pinewood were recorded during the field survey, along with browsing rates on regeneration of each species (see Appendix 2). This allowed continuity to be analysed (see Appendix 3).

5.3. Mobility

Mobility is the ability of Caledonian Pinewood species, particularly wild tree populations, to move through the landscape. This allows trees to track changes in their bioclimatic envelopes caused by, and can counter historical fragmentation. Mobility requires Scots pine to colonise suitable areas beyond the current Caledonian Pinewood boundary, and ultimately for associated species to establish in the expanded woodland as it develops. Mobility is the key characteristic that allows Caledonian Pinewood to adapt appropriately to climate change.

The ability of trees to regeneration outwith current woodland boundaries depends on suitable regeneration niches being available for colonisation; seedlings being able to survive predation by deer, livestock, and other herbivores, as well as disturbances such as fire; and nutrient and light levels being suitable for growth.

Ahead of the field survey, plots were allocated across parts of the regeneration zone interpreted as being suitable for Scots pine establishment from the Native Woodland Model. During the field survey, the presence and abundance/cover of different growth stages of different tree species in these areas were recorded, along with browsing rates on regeneration of each species (see Appendix 2). This allowed mobility to be analysed (see Appendix 3).

5.4. Connectivity

Connectivity is the scale of Caledonian Pinewood and its components parts in the landscape, and how well joined up they are. Scale is important for diversity, as some species struggle to survive in small forest patches due to increased edge effects and large territory sizes. For example, modelled probability of Capercaillie occurrence is lower in Caledonian Pinewoods smaller than 700Ha (Summers, 2018). Additionally, larger Caledonian Pinewoods can better absorb disturbances and changes, as described in Sections 3 and 4. Well-connected Caledonian Pinewoods are also more resilient to large-scale disturbance, as species lost during the disturbance can recolonise from unimpacted areas more easily.

Notes on potential connectivity features were taken during the field survey, but most analysis was undertaken with reference to external data sets including the Caledonian Pinewood Inventory, Ancient Woodland Inventory, Native Woodland Survey Scotland, and Native Woodland Model (see Appendix 3).

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