# Climatic disequilibrium threatens conservation priority forests

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**Abstract**

We test the hypothesis that climatic changes since 1800 have resulted in unrealised potential vegetation changes that represent a ‘climatic debt’ for many ecosystems. Caledonian pinewoods, an EU priority forest type, are used as a model system to explore potential impacts of two centuries of climatic change upon sites of conservation importance and surrounding landscapes. Using methods that estimate topographic microclimate, current and pre-industrial climates were estimated for 50 m grid cells and simulations made using a dynamic vegetation model. Core Caledonian pinewood areas are now less suitable for growth of pine and more favourable for oak than in 1800, whereas landscapes as a whole are on average more favourable for both. The most favourable areas for pine are now mainly outside areas designated to conserve historical pinewoods. A paradigm shift is needed in formulating conservation strategies to avoid catastrophic losses of this habitat, and of many others globally with trees or other long-lived perennials as keystone species.

## Introduction

Biodiversity conservation strategies often focus upon site-based conservation of habitats characterised by their vegetation composition (e.g. EU Habitats and Species Directive, Council of the European Union 1992). Implicit in many of these strategies is an assumption that a site's current vegetation reflects the current climate. Numerous studies have addressed species' potential responses to projected future climatic changes, and the implications of these responses for biodiversity conservation strategies (see e.g. Araújo et al. 2004; Bagchi et al. 2013; Hole et al. 2011). Historically rapid climatic change, however, began two centuries ago in some regions, driven by increases in greenhouse gas concentrations since 1750 (Hartmann et al. 2013). These climatic changes have elicited various species' responses, including geographical range shifts (Mason et al. 2015; Parmesan 2006). Even mobile species' responses, however, often lag behind climatic changes resulting in a 'climatic debt' (Devictor et al. 2012). To-date, potential vegetation responses to historical climatic changes have received little attention. Given the inertia of plant communities, most of which are dominated by long-lived species (Smith 1965), and the importance of relatively infrequent disturbance events in facilitating such communities' responses to climatic change (Bradshaw and Zackrisson 1990; Prentice et al. 1991), however, it is possible that much of Earth's vegetation has accumulated a climatic debt.

Our primary aim was to test the hypothesis that climatic changes since 1800 have resulted in potential vegetation changes across landscapes of conservation importance. We chose the Caledonian pinewoods (Figure S1, Supplementary Information) as a model system to investigate because they lie at the climatic margin of Eurasian boreal forests, representing their south-westernmost and most oceanic extremity. It is likely, therefore, that their geographical extent is climatically constrained, and we thus hypothesised that they might be particularly sensitive to climatic warming. Our results show clear evidence of substantial climatic debt, with areas currently most climatically suitable for *Pinus sylvestris* (Scots Pine), the keystone species of this priority forest type, not coinciding with historical pinewoods identified as conservation targets. This has far-reaching implications for biodiversity conservation strategies because many forest types, as well as other vegetation types dominated by long-lived perennials, likely have accumulated similar climatic debts.

## Materials and Methods

### *Forest type*

Scotland's Caledonian pinewoods (Figure S1, Supplementary Information), dominated by *Pinus sylvestris*, are identified as a priority forest type by the EU Habitats and Species Directive (Council of the European Union 1992). As the only priority forest type restricted to Scotland they are of particular regional conservation importance. They support an assemblage of boreal species, many close to or at their south-westernmost and/or most oceanic range margin. They are also the habitat of *Loxia scotica* (Scottish Crossbill), the United Kingdom's only endemic bird. The present Caledonian pinewoods are scattered remnants of forests that expanded across the Scottish Highlands *ca*. 8800–5800 years ago (Birks 1989), thereafter dominating large areas (McVean and Ratcliffe 1962) until decimated in recent centuries by extensive felling, particularly during the two world wars (Darling 1947). Ten Special Areas of Conservation (SACs) have been designated for their protection, together representing > 85% of their remaining area (JNCC).

### *Study landscapes*

We examined three landscapes spanning the latitudinal extent of remnant Caledonian pinewoods, namely Glen Affric, Glen Achall and Rannoch (Figure S1, Supplementary Information). The latter two include the Rhidorroch and Black Wood of Rannoch Caledonian pinewood SACs. All three are of high relief, dominated by west–east trending valleys, and have remnant Caledonian pinewoods mainly on north-facing slopes (Figure 1, Figures S2 and S3, Supplementary Information). 'Core areas' of native Caledonian pinewood in each landscape were mapped following the Caledonian Pinewoods Inventory (Forestry Commission 1999) that recorded the extents of native pinewoods identified by Steven and Carlisle (1959). Only 'core areas' were considered because these had trees ≤50 m apart and other attributes identifying them as historical native woodlands. The landscapes also support upland birch woodlands, generally at higher elevations and dominated by *Betula pubescens* (Downy Birch). Rannoch and Glen Affric have small areas of upland oak woodland, mainly at lower elevations and/or on south-facing slopes, mostly dominated by *Quercus petraea* (Sessile Oak), and often with *Corylus avellana* (Hazel) present. Upland ash woodland, dominated by *Fraxinus excelsior* (Ash) with *C. avellana* and *Ulmus glabra* (Wych Elm), occupies low elevation areas underlain by Durness Limestone at the west end of Glen Achall. Higher elevation areas of all three landscapes support mosaics of dwarf-shrub heathlands, blanket peatlands, grasslands and montane communities. All three include extensive areas modified by human land use, with areas of plantation forestry at Rannoch and Glen Affric, and predominance of non-woodland vegetation below the potential treeline reflecting current and historical grazing and burning (Burnett 1964).

***Experimental design***

We tested our hypothesis by simulating each landscape's potential vegetation at 50 m grid resolution under recent (1981–2010) conditions and those prevailing two centuries ago (1786–1815). We performed these simulations using the process-based dynamic vegetation–ecosystem model LPJ-GUESS (see Supplementary Information for details). Recent climatic conditions were obtained from datasets compiled by the UK Meteorological Office (Perry and Hollis 2005; UKMO 2012). Historical climatic conditions were estimated from monthly temperature and precipitation time series as described below. Recent $[CO_2]_{atm}$ was specified as 350 ppmv, whereas for the historical simulation 280 ppmv was used following ice-core evidence (Etheridge et al. 1996). A 1:250,000 peat-depth map for Scotland (Bown et al. 1982) was sampled at points corresponding to the centres of the 50 m grid cells. These were classified as having organic or mineral soil, according to whether peat depth was ≥0·5 m or <0·5 m respectively. The influence of complex topography on microclimate was captured by downscaling regional climatic conditions to the 50 m grid as described below. Each grid cell's estimated climate was used to drive an LPJ-GUESS simulation for a single 0·1 ha patch in that cell. Impacts of changes in climate and $[CO_2]_{atm}$ over the past two centuries were explored by mapping simulated aNPP of individual PFTs and PFT combinations, and by computing relative differences between the two experiments in mean simulated aNPP of PFTs across the whole of each landscape and for Caledonian pinewood core areas within each.

***Historical climate estimates***

Monthly mean temperature and precipitation anomalies for 1786–1815 relative to 1981–2010 were estimated using long-term meteorological records available from the UK Meteorological Office (Alexander and Jones 2000; Parker et al. 1992; UK Met Office 2016). Unfortunately, neither the temperature nor precipitation dataset for Northern Scotland extends to the pre-industrial period, whereas the Hadley Centre Central England Temperature (HadCET – 1772–2015) (Parker et al. 1992) and England and Wales Precipitation (part of HadUKP – 1766–2015) (Alexander and Jones 2000) datasets both do so. In order to estimate monthly anomalies for the pre-industrial period for Scotland, we therefore regressed the available time series for Northern Scotland (temperature 1910–2012 (UK Met Office 2016); precipitation 1931–2010

(Alexander and Jones 2000)) onto the relevant years of the longer time series. The resulting regressions mostly showed highly significant relationships (see Tables S1 and S2, Supplementary Information) and were used to estimate monthly values for 1786–1815 for Northern Scotland from the longer time series. Thirty-year means of the monthly values were calculated and anomalies generated by subtracting the 1981–2010 from the 1786–1815 mean (temperature) or calculating the ratio of the 1786–1815 mean to that for 1981–2010 (precipitation).

***Microclimate estimates***

Within-landscape patterns in solar radiation, temperature and effective precipitation were estimated by downscaling data for the recent period using a digital terrain model (DTM), and extrapolated to the historical period using a change-factor approach.

Downscaling was carried out using a combination of: (i) gridded (5 x 5 km) data interpolated from the national network of meteorological stations and available at daily (temperature) or monthly (precipitation and sunshine hours) temporal resolution (Perry and Hollis 2005); (ii) hourly meteorological station data for 1981–2010 (UKMO 2012), obtained from the UK Meteorological Office; and (iii) a 10 m resolution DTM (Ordnance Survey 2012) resampled to the 50 m grid. Minimum temperatures were downscaled by modifying regional air temperatures (interpolated from the 5 km data using a linear regression against latitude, longitude and elevation) to incorporate the influence of cold-air drainage using an elevation difference approach (Bennie et al. 2010). Maximum temperatures were downscaled in a similar way, taking into account how slope, aspect and hill-shading influence solar radiation reaching the vegetation surface (Bennie et al. 2008), using this to scale each grid cell's diurnal temperature range. Monthly mean temperatures were calculated as the mean of the daily minimum and maximum temperature series. The amount of precipitation reaching a grid cell was modelled in relation to topographic position; this amount was then modified by re-distributing run-off using a TOPMODEL approach (Beven et al. 1984). Downscaling methods are further detailed in the Supplementary Information.

***LPJ-GUESS***

Simulations used 22 PFTs (Table 1 & Table S5, Supplementary Information) representing the principal tree, shrub, dwarf-shrub and herbaceous taxa found in the landscapes. Some PFTs corresponded to species (e.g. *Pinus sylvestris*) or species groups (e.g. *Quercus* spp.), whereas others represented species sharing functional traits but not necessarily within the same clade (e.g. boreal evergreen shrub). Parameterisation of PFTs followed Allen *et al*. (2010) with two minor exceptions. Firstly, for graminoid PFTs values of zero for the *phengdd5ramp* parameter were replaced by values of one (to overcome a divide-by-zero error that arose when transferring the program from a Windows platform to a Linux environment). Secondly, *P. sylvestris* establishment was restricted to soils whose water content fell to <0·8 of field capacity during at least June–August. Without this restriction it established and grew on very wet soils where field observations showed seedlings generally failed to establish, those that did so failing to thrive, probably because a suitable mycorrhizal associate was absent. Other parameters followed Allen *et al*. (2010), except only one patch was simulated in each grid cell. Two simulations were made for each landscape, one using recent and one historical climatic conditions and $[CO_2]_{atm}$. Simulations ran for 1500 years starting from bare landscapes, the first 500 years being a spin-up period; aNPP of each PFT in each grid cell was averaged over years 501–1500 of the simulations.

## Results

Annual mean temperature in northern Scotland was estimated to have increased by 0.69°C since 1800, with greater warming in winter (September–February mean increase 0.85°C) (Table 2). Total annual precipitation hardly changed, although with a slight tendency for less summer and more winter precipitation (Table 2).

In all three landscapes, mean simulated aNPP of *Pinus sylvestris* in Caledonian pinewood core areas was significantly lower under present than pre-industrial conditions, whereas in the overall landscape it had increased (Table 1, Figure 2, Table S3, Supplementary Information). The greatest relative decrease was in the Rhidorroch pinewoods of the northernmost landscape, whereas the largest relative increase was for the Rannoch landscape, the most southerly site with the highest mean simulated *P. sylvestris* aNPP. Decreases in mean values for core areas reflected both generally reduced *P. sylvestris* aNPP and an increased number of 50 m grid cells within these areas with zero simulated *P. sylvestris* aNPP (Black Wood of Rannoch: pre-industrial 4.77%, present 13.01%; Glen Affric: pre-industrial 35.36%, present 39.83%; Rhidorroch: pre-industrial 87.74%, present 93.03%). At Black Wood of Rannoch mean aNPP of the 5% of 50 m grid cells with the highest *P. sylvestris* aNPP values was only marginally lower for present than pre-industrial conditions, indicating that small areas within the SAC remain favourable for *P. sylvestris*.

Rhidorroch also had only slightly reduced mean aNPP of the 5% of 50 m grid cells with the highest *P. sylvestris* aNPP values, whereas at Glen Affric there was a small increase.

In all three landscapes the relative decrease in *P. sylvestris* aNPP in Caledonian pinewood core areas was paralleled by relative decreases in those areas of aNPP of other tree PFTs of a boreal character (e.g. *Betula* (tree), *Populus tremula*) and of non-tree PFTs, whereas aNPP of tree PFTs characteristic of the nemoral zone (e.g. *Quercus*, *Alnus glutinosa*) showed relative increases in these areas (Figure 2, Table 1). Nemoral trees also increased in simulated aNPP in the overall landscapes, as did the boreal trees including *P. sylvestris*, and as in general did the dwarf shrub and forb PFTs. Graminoids, however, decreased in the overall landscapes. Although having the greatest relative increase only at Black Wood of Rannoch, absolute aNPP values for *Quercus* were much higher than those of other nemoral tree PFTs and it increased markedly in core Caledonian pinewood areas of all three landscapes (Table S4, Supplementary Information).

Our results showed three other features relevant to efforts to conserve Caledonian pinewoods, especially in the context of projected future climatic changes. Firstly, they emphasised that the present predominantly unwooded, treeless character of the three landscapes, and of Scottish Highland landscapes generally, is largely a consequence of historical and ongoing human activities (Burnett 1964). Simulated tree and shrub aNPP indicated potential present forest and woodland extents much greater than those of remnant native woodlands (Figures S4–6, Supplementary Information). Secondly, a particular consequence of these human activities is absence of *P. sylvestris* from large areas at intermediate elevations relatively favourable for its growth. It is excluded from these areas principally by high intensities of both Red Deer (*Cervus elaphus*) and Sheep (*Ovis aries*) grazing, as well as often by deliberate relatively frequent burning. Especially under the present climate, however, these areas are generally more favourable for *P. sylvestris* growth than are core areas of remnant Caledonian pinewoods. This pattern is likely to be even more marked under future projected climatic conditions. Thirdly, climatic changes of the past two centuries have rendered large parts of all three landscapes, especially at lower elevations, more favourable for growth of *Quercus* and other nemoral trees. In particular, in all three landscapes core areas of Caledonian pinewoods are, under present climatic conditions, much more favourable for growth of *Quercus* than of *P. sylvestris* (Figure 1, Figures S2 and S3, Supplementary Information).

## Discussion

These findings have important implications not just for conservation of Caledonian pinewoods, but for formulating and implementing conservation strategies globally. They show that there is an urgent need for conservation strategies to look beyond the current paradigm of designating sites for conservation on the basis of their present vegetation. Whilst many bodies concerned with biodiversity conservation have recognised the need for strategies that take a dynamic view with respect to individual species' spatial responses to climatic change (see e.g. Hopkins et al. 2007; RSPB 2008), the need also to recognise the importance of landscape-scale ecosystem dynamics is less widely acknowledged. The need for strategies to look beyond protected areas, recognising that species must move across the wider landscape in order to adapt to climatic change, is widely acknowledged (see e.g. Dickinson et al. 2015; European Union 2013; Hopkins et al. 2007; Huntley 2007; Lawton et al. 2010). The possibility that priority habitats may already be unsustainable within areas designated for their protection must also be taken into account. That many species already have accumulated a climatic debt, having failed fully to adapt to historical climatic change, also is now widely accepted (see e.g. Devictor et al. 2008; Devictor et al. 2012). That ecosystems too may have accumulated substantial climatic debts, however, is not generally recognised. Finally, there is a need to take a longer-term view than those that typify most, if not all, current biodiversity strategies, because longevity of the 'keystone' plant species means terrestrial ecosystem dynamics in many cases have inherent timescales of centuries. Strategies that consider only decades are unlikely to succeed in the longer term. Furthermore, we already have committed the Earth to at least several centuries of climatic change and elevated $[CO_2]_{atm}$, because the Earth system includes relatively slow components that will take centuries to regain 'equilibrium', notably polar ice sheets and land-surface properties that are determined largely by the nature of the vegetation.

In the particular case of the Caledonian pinewoods, unless an appropriate approach is adopted that recognises their existing climatic debt, the need to accommodate their spatial dynamics at landscape scales, and the time scales over which these dynamics take place, then substantial losses seem inevitable. Areas most favourable for *Pinus sylvestris* growth now and in the future, but from which it is currently absent, urgently need to be identified and protected. Our results provide guidance about the locations of such areas in the landscapes examined, where they are generally at higher altitudes than the remnant pinewoods. In most cases active management of these areas will be needed to encourage colonisation by

*P. sylvestris*, including sowing of seed harvested from remnant native pinewoods (RSPB 2014) because these are often sufficiently distant from areas now suitable for colonisation that natural seed dispersal may be inadequate. Such measures are not alternatives to established efforts to sustain remnant pinewoods (Scottish Natural Heritage 2015), but a necessary complement to those efforts. These remnant woodlands are not only a vital seed source for colonisation of new areas, but in the short term will continue to provide the habitat necessary for species requiring mature areas of this forest type (e.g. *Loxia scotica*). It is thus necessary to strive to maintain them, so far as this is possible, until newly colonised areas mature sufficiently to provide habitat for such associated species. Continuing climatic change, however, will render this increasingly difficult, especially if it favours pests and pathogens that could potentially cause widespread and rapid mortality of *P. sylvestris*, such as the fungal pathogen causing *Dothistroma* needle blight (Scottish Natural Heritage 2015).

All ecosystems dominated by long-lived perennial plants will show similar inertia and are likely therefore to have accumulated similar climatic debts. There is thus a pressing need for a paradigm shift in the formulation of global biodiversity conservation strategies. These strategies must recognise the extent to which present vegetation, especially forests, has likely accumulated a climatic debt, rendering efforts to maintain it in its present state and/or present location ineffective in the longer term. Instead, sites with current and future potential to support valued vegetation types must be identified, designated and actively managed to accelerate the vegetation dynamic processes that will transform the vegetation (e.g. RSPB 2014). Such a strategy will be particularly valuable and successful in high-relief landscapes, where required species' displacements are over relatively short distances. Civil society engagement in strategies to conserve ecosystems will also be easier when those ecosystems are familiar to and valued by the local population (e.g. RSPB 2014).

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**References**


Alexander L.V., Jones P.D. (2000) Updated precipitation series for the U.K. and discussion of recent extremes. *Atmospheric Science Letters* **1**, 142-150.

Allen J.R.M., Hickler T., Singarayer J.S., Sykes M.T., Valdes P.J., Huntley B. (2010) Last glacial vegetation of northern Eurasia. *Quat Sci Rev* **29**, 2604-2618.

Araújo M.B., Cabeza M., Thuiller W., Hannah L., Williams P.H. (2004) Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. *Global Change Biol* **10**, 1618-1626.

Bagchi R., Crosby M., Huntley B. *et al.* (2013) Evaluating the effectiveness of conservation site networks under climate change: Accounting for uncertainty. *Global Change Biol* **19**, 1236-1248.

Bennie J., Huntley B., Wiltshire A., Hill M.O., Baxter R. (2008) Slope, aspect and climate: Spatially explicit and implicit models of topographic microclimate in chalk grassland. *Ecol Model* **216**, 47-59.

Bennie J.J., Wiltshire A.J., Joyce A.N. *et al.* (2010) Characterising inter-annual variation in spatial pattern of thermal microclimate in a UK upland using a combined empirical–physical model. *Agric For Meteorol* **150**, 12-19.

Beven K.J., Kirkby M.J., Schofield N., Tagg A.F. (1984) Testing a physically-based flood forecasting model (TOPMODEL) for 3 UK catchments. *J Hydrol* **69**, 119-143.

Birks H.J.B. (1989) Holocene isochrone maps and patterns of tree-spreading in the British Isles. *J Biogeogr* **16**, 503-540.

Bown C.J., Shipley B.M., Bibby J.S. (1982) *Soil and Land Capability for Agriculture: South-west Scotland. Handbook to accompany the 1:250 000 scale Soil and Land Capability for Agriculture maps, Sheet 6*. The Macaulay Institute for Soil Research, Aberdeen.

Bradshaw R.H.W., Zackrisson O. (1990) A two thousand year record of a northern Swedish boreal forest stand. *J Veg Sci* **1**, 519-528.

Burnett J.H., editor. (1964) *The Vegetation of Scotland.* Oliver and Boyd, Edinburgh and London.

Council of the European Union. (1992) Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. European Commission, Brussels.

Darling F.F. (1947) *Natural History of the Highlands & Islands*. Collins, London.

Devictor V., Julliard R., Couvet D., Jiguet F. (2008) Birds are tracking climate warming, but not fast enough. *Proc R Soc Lond, Ser B: Biol Sci* **275**, 2743-2748.

Devictor V., van Swaay C., Brereton T. *et al.* (2012) Differences in the climatic debts of birds and butterflies at a continental scale. *Nat Clim Chang* **2**, 121-124.

Dickinson M., Prentice I.C., Mace G.M. (2015) Climate change and challenges for conservation. Grantham Institute Briefing Paper. Imperial College London. London.

Etheridge D.M., Steele L.P., Langenfelds R.L., Francey R.J., Barnola J.M., Morgan V.I. (1996) Natural and anthropogenic changes in atmospheric $CO_2$ over the last 1000 years from air in Antarctic ice and firn. *J Geophys Res-Atmos* **101**, 4115-4128.

European Union. (2013) *Guidelines on Climate Change and Natura 2000*.

Forestry Commission. (2016) Caledonian Pinewood Inventory. (https://data.gov.uk/dataset/caledonian-pinewoods)

Hartmann D.L., Klein Tank A.M.G., Rusticucci M. *et al.* (2013) Observations: Atmosphere and Surface. pp. 159-254 in T.F. Stocker, D. Qin *et al.* editors. *Climate Change 2013: The Physical Science Basis Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Hole D.G., Huntley B., Arinaitwe J. *et al.* (2011) Towards a management framework for key biodiversity networks in the face of climatic change. *Conserv Biol* **25**, 305-315.

Hopkins J.J., Allison H.M., Walmsley C.A., Gaywood M., Thurgate G. (2007) Conserving biodiversity in a changing climate: Guidance on building capacity to adapt. Department for Environment, Food and Rural Affairs. London.

Huntley B. (2007) Climatic change and the conservation of European biodiversity: Towards the development of adaptation strategies. T-PVS/Inf(2007)3. Council of Europe, Convention of the Conservation of European wildlife and natural habitats. Strasbourg.

JNCC. (2016) Habitat account - Forests: 91C0 Caledonian forest. (http://jncc.defra.gov.uk/ProtectedSites/SACselection/habitat.asp?FeatureIntCode=H91C0)

Lawton J.H., Brotherton P.N.M., Brown V.K. *et al.* (2010) Making Space for Nature: a review of England's wildlife sites and ecological network. Defra. London.

Mason S.C., Palmer G., Fox R. *et al.* (2015) Geographical range margins of many taxonomic groups continue to shift polewards. *Biol J Linnean Soc* **115**, 586-597.

McVean D.N., Ratcliffe D.A. (1962) *Plant communities of the Scottish Highlands*. Her Majesty's Stationery Office, London.

Ordnance Survey. (2012) Land-Form PROFILE user guide v5.4 – 8/2012. Ordnance Survey. Southampton.

Parker D.E., Legg T.P., Folland C.K. (1992) A new daily central England temperature series, 1772–1991. *International Journal of Climatology* **12**, 317-342.

Parmesan C. (2006) Ecological and evolutionary responses to recent climate change. *Annu Rev Ecol Evol Syst* **37**, 637-669.

Perry M., Hollis D. (2005) The generation of monthly gridded datasets for a range of climatic variables over the UK. *International Journal of Climatology* **25**, 1041-1054.

Prentice I.C., Sykes M.T., Cramer W. (1991) The possible dynamic response of northern forests to greenhouse warming. *Global Ecol & Biogeogr Letters* **1**, 129-135.

RSPB. (2008) Birds on the move: Introducing A Climatic Atlas of European Breeding Birds. Royal Society for the Protection of Birds. Sandy, Bedfordshire.

RSPB. (2014) Futurescapes: Cairngorms Caledonian Forest. Royal Society for the Protection of Birds. Sandy, Bedfordshire.

Scottish Natural Heritage. (2015) Planning for change: managing Scotland's pinewoods in a changing climate. Climate change adaptation case study. Scottish Natural Heritage. Edinburgh.

Smith A.G. (1965) Problems of inertia and threshold related to post-Glacial habitat changes. *Proc Roy Soc London, Ser B* **61**, 331-342.

Steven H.M., Carlisle A. (1959) *The native pinewoods of Scotland*. Oliver and Boyd, Edinburgh.

UK Met Office. (2016) Scotland Mean Temperature (Degrees C): Areal series, starting from 1910. (http://www.metoffice.gov.uk/pub/data/weather/uk/climate/datasets/Tmean/date/Scotland.txt)

UKMO. (2012) Met Office Integrated Data Archive System (MIDAS) Land and Marine Surface Stations Data (1853-current). NCAS British Atmospheric Data Centre. Harwell.

**Table 1: Changes in mean annual net primary productivity pre-industrial to present**

| | **Change in aNPP pre-industrial to present relative to pre-industrial aNPP** (%) | | | | | |
|---|---|---|---|---|---|---|
| **Plant functional type** | **Rannoch landscape** | **Black Wood of Rannoch** | **Glen Affric landscape** | **Pinewoods of Glen Affric** & neighbouring areas | **Glen Acall landscape** | **Rhidorroch pinewoods** |
| Boreal trees: | | | | | | |
| *Betula* (tree)* | 16.8 | -37.7 | 18.5 | -1.8 | 20.8 | -29.2 |
| *Pinus sylvestris* | 49.9 | -29.7 | 35.2 | -5.9 | 29.0 | -47.7 |
| *Populus tremula* | 6.4 | -43.0 | 14.1 | -13.9 | 10.3 | -43.4 |
| Nemoral trees/shrubs: | | | | | | |
| Nemoral broadleaved trees† | 335.5 | 166.8 | 195.9 | 293.6 | 210.2 | 520.1 |
| *Quercus* spp. | 295.7 | 724.8 | 64.5 | 92.4 | 64.5 | 40.6 |
| *Alnus glutinosa* | 182.3 | 209.8 | 84.2 | 84.2 | 78.1 | 50.3 |
| *Salix* (shrub/tree) | 24.3 | -32.4 | 19.1 | 2.5 | 27.1 | -30.2 |
| Non-trees: | | | | | | |
| Dwarf shrubs‡ | -4.6 | -23.9 | 5.5 | -5.8 | 0.8 | -8.9 |
| Forbs§ | 3.0 | -35.5 | 7.8 | -12.6 | 1.1 | -41.0 |
| Graminoids¶ | -31.6 | -58.7 | -23.4 | -41.7 | -29.1 | -84.8 |
| Total | 11.3 | 5.1 | 14.1 | 11.6 | 12.8 | 10.1 |

Aggregated PFTs are comprised as follows:

* *Betula pubescens*, *B. pendula*.

† *Corylus avellana*, *Fraxinus excelsior*, *Tilia cordata*, *Acer* spp., *Ulmus* spp.

‡ Boreal evergreen shrub, *Betula nana*, *Juniperus communis*, *Salix* (dwarf shrub), Ericaceae (dwarf shrub).

§ *Artemisia* spp., Chenopodiaceae.

¶ Gramineae (C3), Gramineae (cold C3), Cyperaceae.

**Table 2: Monthly mean temperature and precipitation anomalies**

| **Month** | **Temperature anomaly*** (°C) | **Precipitation anomaly†** |
|---|---|---|
| January | -1.20 | 0.99 |
| February | -0.09 | 0.99 |
| March | -1.37 | 0.98 |
| April | -0.48 | 1.01 |
| May | -0.13 | 1.04 |
| June | -0.17 | 0.99 |
| July | -0.55 | 1.09 |
| August | -0.51 | 0.94 |
| September | -0.68 | 1.03 |
| October | -0.85 | 0.97 |
| November | -1.35 | 1.02 |
| December | -0.92 | 0.96 |

* Calculated by subtracting the monthly mean value for 1981–2010 from that for 1786–1815.

† Calculated as the ratio of the monthly mean value for 1786–1815 to that for 1981–2010.

**Table 3: Annual net primary productivity of *Pinus sylvestris* in core areas of Caledonian pinewoods**

| | **Black Wood of Rannoch** | | **Glen Affric** & neighbouring areas | | **Rhidorroch** | |
|---|---|---|---|---|---|---|
| | Pre-industrial | Present | Pre-industrial | Present | Pre-industrial | Present |
| aNPP of *P. sylvestris* (g C $m^{-2}$ $yr^{-1}$) | | | | | | |
| Mean | 6.516 | 4.581 | 3.469 | 3.265 | 0.207 | 0.108 |
| Variance | $2.521 \times 10^{-2}$ | $2.441 \times 10^{-2}$ | $2.983 \times 10^{-2}$ | $3.361 \times 10^{-2}$ | $4.536 \times 10^{-4}$ | $2.461 \times 10^{-4}$ |
| *t* statistic* | 19.358 | | 3.477 | | 2.933 | |
| degrees of freedom | 4025 | | 7210 | | 415 | |
| *p* | $6.766 \times 10^{-80}$ | | $5.095 \times 10^{-4}$ | | $3.545 \times 10^{-3}$ | |

* *t* statistic calculated for a paired *t*-test; probabilities are for a two-tailed test.

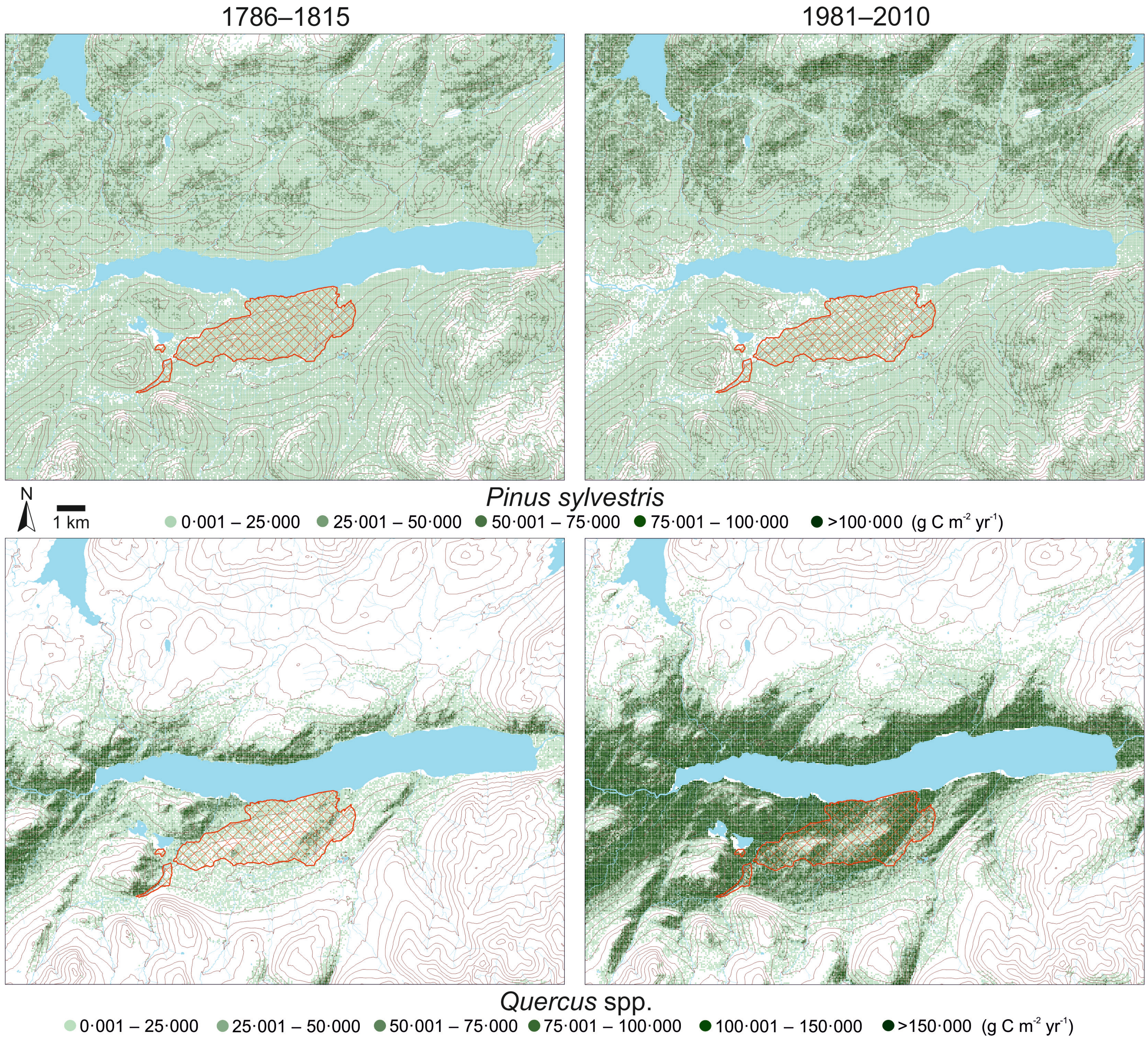
1786–1815
1981–2010
N
1 km
Pinus sylvestris
0·001 – 25·000
25·001 – 50·000
50·001 – 75·000
75·001 – 100·000
>100·000 (g C m⁻² yr⁻¹)
Quercus spp.
0·001 – 25·000
25·001 – 50·000
50·001 – 75·000
75·001 – 100·000
100·001 – 150·000
>150·000 (g C m⁻² yr⁻¹)

**Figure 1: Maps of the Rannoch landscape showing annual net primary productivity of *Pinus sylvestris* and *Quercus* spp.**

Contour maps illustrating the high relief typical of the study landscapes, the east-west orientation of the major valley, and in the red hatched areas the locations of core areas of Caledonian pinewoods, in this case the Black Wood of Rannoch (Forestry Commission 1999). Shading of the maps shows aNPP of *Pinus sylvestris* (top) and *Quercus* (bottom) simulated under pre-industrial (left) and present (right) climatic conditions. These PFTs represent the keystone taxa of the Caledonian pinewood and upland oak woodland habitats respectively, and can thus be viewed as 'proxies' for the habitats themselves. White areas have zero aNPP; darkest green shades indicate highest aNPP (colours scaled separately to the ranges of the two PFTs). Note how the proportion of grid cells with zero aNPP of *P. sylvestris* within the core area is greater under present climatic conditions, whereas areas at higher elevation in the north of the landscape have markedly increased aNPP of *P. sylvestris* under present conditions and are much more favourable for the growth of this tree than are the core areas currently designated for conservation of the Caledonian pinewoods habitat. Contours at 50 m intervals from the OS Terrain 50 data; water courses and water bodies from the OS VectorMap District data. Study landscape 19·6 km E–W by 15·4 km N–S.

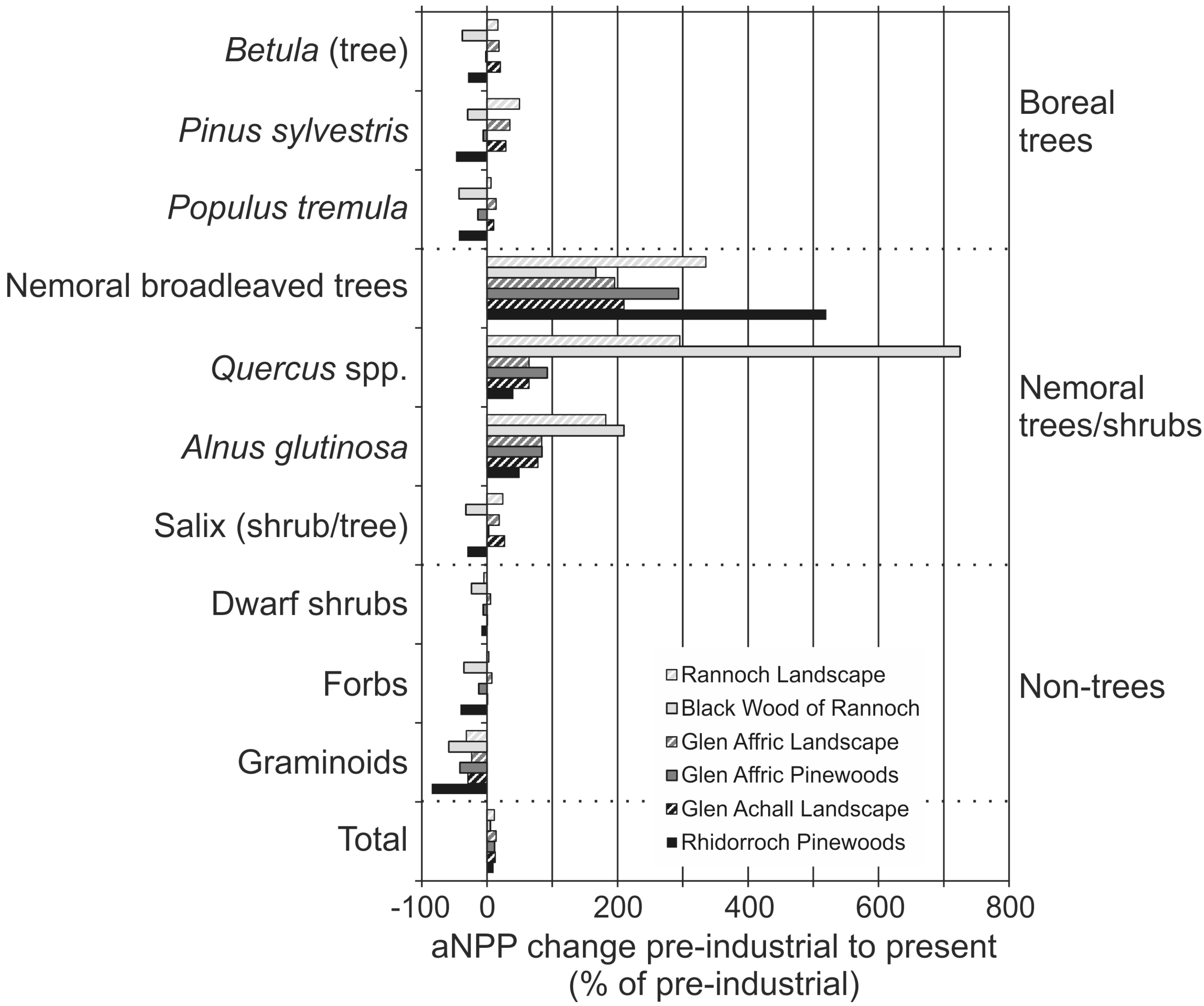


**Figure 2: Relative changes in mean annual net primary productivity**

Change in mean aNPP of six individual and four aggregated PFTs, and of the vegetation as a whole, in the three landscapes as a whole and in the areas of Caledonian pinewood in each. The difference in aNPP under present climatic conditions from that under pre-industrial conditions is shown expressed as a percentage of the mean aNPP under pre-industrial conditions. Negative values indicate PFTs for which conditions are now less favourable and *vice versa*.