
Understanding the implications of climate change for woodland biodiversity and community functioning

Synthesis of the key findings

Pam Berry, Environmental Change Institute, University of Oxford

Yuko Onishi, Environmental Change Institute, University of Oxford

James Paterson, Centre for Environmental Management, University of Nottingham

Report commissioned by the Forestry Commission (UK) - January 2012

Introduction

Forests and woodlands are important parts of the landscape of the UK covering three million hectares (an area slightly larger than Wales), which equates to 13% of our total land area. The tree species composition of the UK is a result of a gradual migration in response to the climatic change since the last glaciers retreated over 10,000 years ago. Woodland community assemblages have developed in relation to climate, but also soils, human interference and biotic interactions. The concern now, for many ecologists, is to attempt to understand how *future* climate change will affect our native species and if this will alter woodland community structure and function.

There is much evidence of recent climate change impacting upon species in Europe and the UK, although there is much less direct evidence for habitats. The impacts on species may be of interest if the species is of key importance to the habitat's composition - for example tree species for woodlands - and may help in understanding the implications of climate change for woodland biodiversity and community functioning. There are many approaches to identifying and projecting the impacts of environmental pressures, including climate change, on biodiversity and the sensitivity of habitats to future climate change can be established by a number of approaches. These include extrapolation of observed and experimental data and niche and dynamic vegetation modelling.

This synthesis report summarises the work done in an earlier report commissioned by the Forestry Commission *Understanding the implications of Climate Change for woodland biodiversity and community functioning*¹, which reviewed the known effects of climate change on woodland biodiversity and functioning. It provides a more readable document free from the bulk of the methodology, tables and references; should you need to explore the issues in this document in more depth, please refer to the main technical report.

1 Berry, Onishi & Paterson. 2011.

Review of the effects of climate change on biodiversity

Peer-reviewed and grey literature investigating the implications of climate change for woodland biodiversity were reviewed in order to establish how climate change has already begun to affect plant and animal ecology of species found in woodland habitats, including their physiology, distribution, phenology and evolutionary pathway.

Physiological responses

All species respond directly to climatic factors and for many species climate is largely the defining element governing their growth and reproduction. It is important to note however, that whilst it is comparatively easy to study the response of species to climatic factors or even combinations of factors (which better reflects reality), scaling up to community and ecosystem response is much harder. Three main response factors of future climate change are temperature, water availability and CO₂, others though (not discussed here) include extreme events, such as drought, storms, floods and fire. Evidence of the effects of these factors on growth is accumulating, although it is not always easy to disentangle their relative contributions.

Plant responses to temperature, water availability and CO₂ have been well-studied and a number of generalisations regarding responses can be made. Plant responses to temperature are well-recorded and it is clearly one of the major determinants of species' growth and distribution. Dendroecological studies in the UK and the rest of Europe have highlighted variations in growth for species along climatic (temperature and precipitation) gradients over centuries. Other responses to changes in temperature include effects on the abundance of plants with winter seed chilling requirements and effects on reproductive systems. Temperature can also have direct impacts on plant physiology on a day-to-day basis: for example extreme heat can reduce photosynthesis and increase respiration in many temperate tree species. However, the most important response to increased temperatures is likely to be the extension of the growing season for most species in northern Europe and a reduction in growth in southern Europe. However, in the UK, warmer winters may reduce natural regeneration for species that require winter chilling to induce seed germination.

Water is a significant limiting factor for plant growth and will play an important role in community composition in the future. Not only will annual precipitation in the UK decline, but extreme events, such as drought and flood, are very likely to increase. Reduced water availability limits growth through a reduction in water uptake in the roots which reduces the water potential (along a root to leaf gradient); however, different species demonstrate a range of ecological responses to water availability. These different effects are likely to change the competitive balance in communities and may result in changes in community dominance. These effects may be further enhanced by delayed responses to drought in some species due to an inability to recover from a breakdown of photosynthetic ability.

For most temperate woodland plants, increased levels of CO₂ stimulate growth, generally through a net increase in photosynthesis. Although there is often a long-term adjustment of photosynthesis to increased CO₂, and this response frequently interacts with temperature and water availability, the overall pattern, certainly at a forest stand level, is for increased growth for many woodlands in Europe. Work done by the Forestry Commission suggests that UK forests will experience increases in productivity, although there will be strong regional differences due factors like drought. Increased growth is not the only response though: for example, the ratio of carbon to nitrogen in the leaf is also affected by CO₂, which has consequences for decomposition, herbivory and frost resistance. Reproduction and germination are also affected by CO₂, but responses vary across species.

Range and altitudinal shifts

The role of climate in determining a species' distribution has long been known and evidence of species' range shifts during previous cooling and warming events is well documented through extensive palaeoecological studies. However, whereas these studies have demonstrated the migration of species often tracked a relatively slow changing climate after glacial periods (except the Younger Dryas period), more recent climatic change has occurred at a faster rate. This poses problems for many species that are not able to migrate quickly enough (e.g., tree species), but already we have recorded distribution changes from a range of taxa. Two main responses have been documented in species: range shifts, where the distribution of a species has moved (usually polewards) as the climate has warmed (in southern England, some continental mobile species are beginning to appear regularly); and, altitudinal or elevational shifts where montane and sub-montane species have shifted their zone of occurrence to higher altitudes. Many of these effects have been seen in more mobile taxa (e.g., butterflies, birds), although we are already witnessing the decline of some plant species at the rear edge of their distribution, as well as shifts in elevation for a number of shrub and tree species in Scandinavia. Long-lived perennial plants present a more difficult group to study as they can often have significant lags in response.

These changes are not only determined by temperature, long-term changes in precipitation can also affect species' distributions. In the southern or rear edge of species' distributions, precipitation is known to be limiting factor for survival and recent changes in precipitation patterns have started to affect some species in southern Europe (e.g., beech in northern Spain).

Phenological change

Perhaps the largest collection of observations recording climatic change responses is in the study of phenology (animal and plant life cycle events) and this aspect of species' biology has been the focus of a number of reviews and studies on a range of taxa. Some studies observing phenological response date back many decades or even centuries and often records have been maintained by non-academic observers. For plant phenology, the range of responses recorded has been large, but

the most common are for dates of first flowering, bud burst and leafing; while, autumn events are less well recorded.

The main patterns observed thus far are earlier response of spring events, like bud burst or first flowering dates and slightly delayed leaf fall, but responses can vary across species. For example, some studies have reported a greater response in northern latitudes, although this pattern reflects differences in regional climate changes.

Reports focussing solely on the responses of woodland plants are not common, but similar results have been reported so far; for example, in Slovakia, six woodland herbs species have shown earlier onset of flowering in response to climate over the last decade. Similarly, in other studies of - or including - European forest tree species, a general pattern of advancing leaf or flowering dates over the last few decades due to warming spring temperatures has been reported. In the UK, the Woodland Trust's *Nature's Calendar* survey, which uses the public to record a range of phenological events for animals and plants in spring and autumn, has a wealth of data demonstrating that climate change is having a dramatic effect on woodland species (e.g., common oak is now leafing 10 days earlier on average than in the 1980s).

Adaptation

Although there are widespread records of species' populations responding to climate change by migrating or becoming locally extinct, many species also have an ability to adapt *in situ* to new climatic pressures. This may occur with species that have a large phenotypic plasticity (the ability of individuals to modify their behaviour, morphology or physiology in response to altered environmental conditions), but other factors like fecundity and biotic interactions, may play a part. Adaptation is also likely to vary within species throughout their distribution; for example, the genetic diversity of species' populations at range margins is sometimes more impoverished due to the fragmented nature, low fecundity or effects of introduced species on the population resulting in lower adaptation. Species with large distributions and large populations with high genotypic variation are more likely to adapt to climate change, despite a possible generational response lag.

Foresters have made use of inter-specific genetic variation in tree species for years and have drawn on different provenances to meet suitable local climatic conditions. This artificial mixing of genetic diversity may well actually benefit some species: many woodlands in the UK are composed of native species, but often their provenance is foreign; therefore, woodlands that have genetic provenances of species (e.g., common oak) from lower latitude European countries, may well be better adapted to future climate change.

Phenotypic plasticity is not the only feasible adaptation response, as some species are capable of rapid evolution. However, for many species there will be constraints on evolutionary response including the lag between climatic change and response (e.g., for most perennial plants); lack of genetic variation (e.g., in small populations); and erosion of genetic variation. This means that

plants that are likely to evolve to adapt to climate change will be small, have short life cycles and have large population sizes.

There is some evidence that plants can adapt to rapid climate change through evolution, for example, one study has shown that the annual field mustard (*Brassica rapa*) was able to respond to drought conditions by selecting for earlier flowering in the population under study. However, the evidence suggests for many woodland species, once phenotypic plasticity is stretched to its limit, the options in the face of climate change are either migration or local extirpation.

Exploring the potential impacts of climate change on woodland Priority Habitat species

In order to explore how woodlands may be affected by climate change, we used a bioclimatic envelope model (see Box 1) to examine the potential distribution changes of 178 woodland species in the British Isles. 31 of these were tree species, 18 shrub species, 86 ground flora species, 11 mammals, 1 moss, 5 lichens, 4 butterflies, 14 birds, 1 beetle, 1 bee, 4 ants and 2 amphibians. The overwhelming pattern was for species bioclimatic space *gains* and mean figures for all species and all scenarios to vary from 12% to 100% gain. These responses are primarily described in terms of the change in climate space (i.e., the possible future distribution of a species governed solely by climate) in the British Isles, but significant differences between the countries are noted, as some species have the potential to gain climate space one country (e.g. in Scotland) and lose it in another (e.g. England) and thus while the net change may be small these gains and losses are important. Their significance for woodland composition, structure and function are assessed using knowledge of their ecology and other research on the species concerned.

Box 1: Modelling methodology

The backbone of this study was based on results from bioclimatic envelope modelling (BEM). Most of the species modelling used in this study was based on an artificial neural network (ANN), but a number of species with 'presence-only' data were processed using Ecological Niche Factorization Analysis (ENFA). ANNs are proving increasingly popular because of their wide applicability and their ability to cope with complicated scenarios; these traits have commended them to ecologists who often favour them because of the complexity of many ecological problems. The raw data required for modelling are reliable current plant species distributions; these were sourced from various published distribution studies including the Atlas Florae Europaeae. The BEM models works on the basis of a correlation between species distribution and environmental factors. The inputs used (absolute minimum temperature expected over a 20 year period, annual maximum temperature, growing degree-days above 5°C, accumulated annual soil moisture deficit and accumulated annual soil moisture surplus) all have a direct physiological limiting function for plant growth and were fed into the neural network along with an interpolated presence/absence data set for each species. For birds different environmental data were used based on knowledge of factors affecting their distribution in the UK. To cover as much of the possible variation in anticipated climate change two main climate change scenarios (SRES A2 and B1) were used which cover much of the range of possible driving forces of future GHG emissions. These two scenarios were then used at three different time-periods (2011–2020, 2041–2050 and 2071–2080) and were derived from two global climate models (HadCM3 and PCM). Model performance was tested using two widely used techniques, Cohen's kappa statistic (a test of the proportion of species' presences or absences that are predicted correctly after taking into account chance agreement) and the area under the receiver operating characteristic (ROC) curve (AUC).

Here, we highlight some of the more interesting model results for selected species - for a more complete breakdown of the model data and a more detailed discussion of the implications for different woodland habitats please refer to the technical report.

Tree and shrub species response

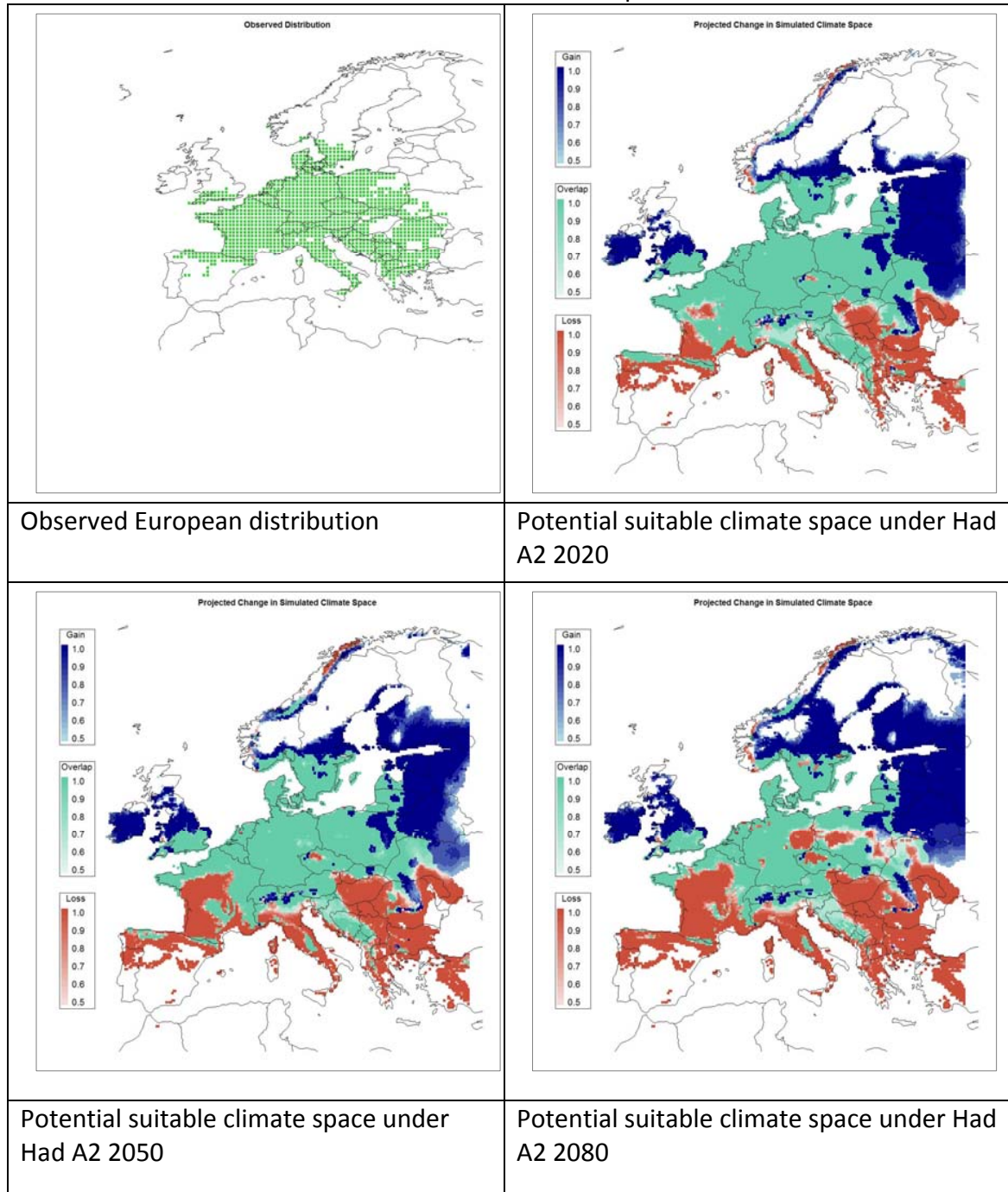
The dominant canopy tree species in the UK - common oak, sycamore, beech (Figure 1), ash, silver birch - demonstrated an overall slight loss of climate space. Surprisingly, beech only loses climate space in the two 2080 scenarios (and even then only by 2% for the whole of the British Isles). Common oak gains space in all but one time slice (Had A2 2080), and then only loses 14%. The contrast between these two species is slightly surprising considering common oak's better tolerance of drought. A breakdown of the regional responses shows that common oak could lose most space in England and gains the most in Scotland. Beech follows this pattern, except it also has quite large losses in Wales.

Ash has a similar response to common oak in that it might only lose climate space in the three 2080 scenarios; not surprisingly it only maintains or gains space in Scotland, conversely it is projected to lose the most space in England.

On the whole, the main woodland shrub species do quite well and 13 of the 18 species should maintain or gain climate space. Of these, gorse, heather, Midland hawthorn, privet, dogwood,

buckthorn and spindle all respond better. The worst performers are cowberry, bramble, gooseberry and raspberry, but even hazel could lose a small amount of bioclimatic space. These losses are greatest in England and minimal in Scotland; dogwood, spindle and buckthorn *could* all gain large amounts of bioclimatic space in Scotland.

Figure 1: Changes in projected suitable climate space for *Fagus sylvatica*, beech. Green = overlap between current and future climate space; red = future loss of current climate space; blue = new future climate space



Woodland ground flora

The number of ground flora potential winners and losers is more complex; there are a number of species, that might lose bioclimatic space in England and Scotland (twinflower is a good example), but there are also some species that appear to do badly in Wales, but nowhere else: ryegrass, wood sorrel, Yorkshire fog, hedge woundwort, common cottongrass, tall oatgrass, tufted hairgrass, wood sedge, honeysuckle, Lords and Ladies, hare's tail cottongrass, globeflower and hogweed.

Animal species response

Of the mobile species there are a number of possible major winners including pool frog, Bechstein's bat, lesser horseshoe bat, Barbastelle bat, red squirrel, roe deer, dormouse and the tree sparrow. The species that lose most bioclimatic space are four ant species (Scottish wood ant, narrow head ant, southern wood ant, hairy wood ant), seven bird species (pied flycatcher, Scottish crossbill, spotted flycatcher, song thrush, bullfinch, black grouse, capercaillie); two mammals (yellow-necked mouse, brown hare); the great crested newt; and the pearl-bordered fritillary.

In Scotland, nearly all mammals could gain new climate space (except brown hare, which loses 9%) and for the other mobile taxa the only species that might lose space are pearl-bordered fritillary, pied flycatcher, Scottish crossbill, fieldfare, mining bee, Scottish wood ant, narrow head ant and hairy wood ant. In England, a number of species run a risk of becoming extinct by 2080 including pied flycatcher, black grouse, bullfinch, narrow head ant and hairy wood ant.

Other notable species

The native bluebell has to contend with the spread of alien bluebells '(Spanish') and further hybridisation is a possible future threat; however, a study in south-central Scotland showed that currently increasing rainfall was associated with increasing native and decreasing alien densities and that the presence of aliens was more related to human factors.

Capercaillie is projected to lose all suitable climate space under some scenarios by 2050s or 2080s, although the above studies suggest that warmer, drier summers should favour the species. The key species with which it is associated - Scots pine and bilberry - do not show significant losses and thus if its habitat can be maintained and the other pressures affecting its survival can be addressed, climate change could have a less severe impact on this species.

Dormouse, which is primarily found only in England is threatened mainly from changes in woodland management practice, particularly the cessation of hazel coppicing and stock incursion into woodland, as well as woodland fragmentation, since short distances, possibly as little as 100m, form absolute barriers to dispersal, unless arboreal routes are available. However, dormouse shows a mixed climate change response, with a possible decline under both the HadCM3 scenarios, but an increase under the PCM scenarios, thus suggesting the climate space of this species is quite sensitive to climate.

The projected increase in suitable climate space for the stag beetle across much of Britain and Ireland under the high scenarios represents much of its former range. It requires dead wood, possibly with a preference for oak. This could mean a reduction in suitable future habitat in southern England, although it does lose suitable climate space in some of this area under a 2080s high scenario. This is a thermophilous species, with the mean average temperature in Belgium being largely found within the 16.5°C mean July isotherm, although some authors suggest that its distribution is limited by the amount of rainfall.

Potential new species?

If native tree species decline under future climate change scenarios British woodland managers may have to consider non-natives species to maintain woodland tree canopy cover (even if this suggestion is likely to be very controversial). Some continental European tree species have similar ecological niches to native tree species potentially threatened by climate change in Britain; for example downy oak (a species that gains a lot of space in Britain in the model) for common oak; and some have similar decay processes too e.g. sweet chestnut and common oak.

Looking further afield, the eastern oriental beech is known to be more drought tolerant than common beech. Other potential replacement species include narrow-leaf ash, which also gains a lot of climate space in England and Wales, for common ash; and by 2080 Manna ash may even be a suitable replacement. However, much more comparative work needs to be done to establish which species will provide similar niche opportunities for specialists and which, if any, tree would offer a suitable replacement for drought affected beech (or oak or ash), before consideration of replacement tree species becomes a realistic option. There are also issues relating to plant hygiene and, in addition, a fundamental shift in thought would be needed to allow the introduction of exotic species onto sites of conservation importance where the current management strategy is to maintain the current native species composition. Guidance on dealing with the changing distribution of tree species in England addresses controversial 'possible' native species, such as sycamore, and puts in context the value of species like sweet chestnut and pines, but the clear presumption is that more 'exotic' species are not recommended. However, for new woodland plantings, a more diverse mix, with species drawn from continental Europe, may increase the resilience of the UK woodland stock in the future.

Habitat responses - impacts on Priority Habitat woodlands

Wood-Pasture & Parkland

This Priority Habitat has areas that have been managed by grazing and characteristically has at least some veteran trees or shrubs. Ninety-eight of the species modelled were known to be associated with woodland pasture and parkland. Of those, 17 were tree species, 8 shrubs and 51 ground flora species. The overall mean change in species climate space for all scenarios was a slight gain of 9% for the British Isles. The most successful tree species were (in descending order) field maple, small-leaved lime, wild apple, yew, beech, common oak and cherry which all could extend

their climate space. The trees that might lose climate space were hornbeam, ash, sessile oak, aspen, silver birch, downy birch, sycamore and wych elm.

The two key wood-pasture tree species, beech and common oak, generally have a good outlook, although both lose space in England by 2080 (oak by 47%). However, beech's greater intolerance of drought is further complicated due to the lack of data on determining if woodland or parkland trees are more sensitive than forest trees in these conditions. Long term studies at Denny Wood, New Forest, an ancient wood-pasture, indicate that over a 40 year period beech trees were the most severely affected by drought, although some oak were killed too and drought susceptibility increased with tree age. Similar effects of drought have also been noted on beech in other (closed) woods, such as Lady Park Wood in the Wye Valley. Furthermore, trees have been shown to have greater transpiration rates, (and hence water use) at woodland edges than deeper in woodlands, due to the edge trees having greater exposure to wind currents. Trees in more open wood pasture similarly may be more exposed, but this could be counterbalanced by less competition for ground water from grassy vegetation than from other trees in dense woodland.

Upland Oakwood

There are believed to be between about 70,000 and 100,000 ha of Upland Oak woods in the UK and it is found mostly throughout the north and west of the UK. The Priority Habitat classification is mainly based on the prevalence of oak and birch in upland sites, rather than edaphic association.

Many of the main species associated with Upland Oak woods were modelled here (including all the canopy trees and much of the shrub and ground flora). Notable omissions from the species list include some of the main bird species often associated with the woodland type (e.g., redstart, wood warbler) and some mosses. Otherwise, the 86 Upland Oakwood species modelled give a fairly good representation of the community type. The modelling results suggest that these woods are perhaps one of the least vulnerable habitats to climate change with a possible mean change in bioclimatic space for trees of +18% (perhaps not surprising given that most of these woods are to be found in Scotland and north-west England). The dominant tree - sessile oak - also does well and could gain 25% new space in Scotland.

Hornbeam could dramatically increase its range into Scotland and may become a competitor to the dominant sessile oak in the future along with beech and sycamore (both of which gain space). However, sessile oak has been shown to be highly tolerant of drought which could lead to a change in competitive balance between it and other species (notably common oak, beech and ash) in the future. Silver birch also loses significant bioclimate space in Scotland (particularly along the coastal areas where this habitat is found).

Other notable changes in this habitat could include a possible decline in cowberry (27% of space lost in Scotland), but expansions of blackthorn and privet. Of the main ground flora species in this

habitat, the biggest losers of bioclimatic space are wood sorrel, common male fern and common dog violet.

Lowland Beech and Yew Woodland

121 species were modelled for this habitat, including 24 tree species, 12 shrub species and 85 ground flora species. Beech is the dominant tree species and in southern England it is at the northern edge of its (native) range; the same species is found much further south in Europe.

The results suggest that beech will mostly thrive in the projected climate scenarios, but since its distribution extends into lower latitudes in continental Europe this is not surprising. There are other aspects of climate change, however, that may reduce its capacity to respond. Water stress from prolonged droughts is known to reduce growth and canopy and may result in increased mortality. Periods of drought may become more frequent in the future and this may have significant impacts on its survival. In north-east Spain, at the southern limit of beech, high spring and summer temperatures have decreased growth and tree establishment of beech at lower altitudes. Drought has also strongly limited the growth of populations in this area and changes to its distribution are already occurring. By 2050, Forestry Commission studies predict that the same will happen to beech in south east England.

In addition, even if beech does not lose climate space it may lose the competitive edge over other tree species. Beech is dependent on available soil water to maintain growth and although the model results suggest that it will fare better than both oak species, it is highly likely, given a succession of drought years, that oak will cope better than beech. The response of beech to drought also depends on soil type and the underlying hydrology; beech on chalk may be able to access additional moisture via capillary action, but those on acid gravels and weakly gleyed soils may be at a greater risk of drought. Also, older trees seem more likely to move into a period of decline and mortality following drought episodes, whereas young trees may be able to respond well if shade and competition from mature trees is reduced.

The other major tree species in this habitat is yew. Although pure yew woodlands are rare in the UK (Kingley Vale in Sussex stands out as the best example), yew can often form small stands in other woods. Yew is considered to be quite tolerant of heat and drought and this is seen in the results for England (small gain of 2%); in Scotland, where it is commonly only found in churchyards, it could gain 19% in bioclimate space. Although yew is a slow coloniser and depends upon the right scrub conditions to develop, it is possible that it will increase its range in calcareous woods in Scotland in the future.

Upland Mixed Ashwoods

This is a particularly important habitat in the North-west of the British Isles, but also can be found infrequently in England and is fairly widespread on the continent on steeper slopes. Upland

ashwoods predominate on steeper gorge sites, the canopy is usually dominated by ash, but often accompanied by sessile and common oak, sycamore and birch whilst hazel and hawthorn are the commoner shrubs; towards the north and west field maple becomes less abundant and rowan, alder and wych elm become more prevalent. The ground layer normally consists of dog's mercury, enchanter's nightshade, ground ivy, ivy and stinging nettle, as well as the following species which may all lose bioclimatic space: common male fern, nettle, wood avens, wood sorrel and common dog violet.

The species composition of this habitat is very well covered with 95 species modelled (including all the main canopy and shrub species), although important missing species include dark red helleborine, Jacob's ladder, autumn crocus and whorled solomon's seal and a number of beetle, flies and other invertebrates.

Like the oak woods, upland ash woods seem quite resilient to climate change in the north west of the British Isles (in Scotland the mean change in bioclimate space for the trees is +15%) with only five species possibly losing more than 50% of their bioclimate space (Lady's slipper orchid, Herb Paris, common cow wheat, bird cherry, wood vetch). Furthermore, species that are just beginning to migrate into the north-west may do much better in future (e.g., small-leaf and large-leaf lime could increase by 33% and 54% respectively). However, silver birch could lose 19% of its space (although this may be countered somewhat by local topography, as these woodlands are usually colder and wetter than the surrounding open countryside). Alder may also increase if wetter conditions in winter allow. In the understory, common hawthorn may continue to expand its range, although it may have to compete more with blackthorn (+31%).

Wet Woodland

The species composition of this habitat is reasonably well covered with 67 species. The majority of species modelled in wet woodlands cope quite well with the various climate change scenarios (mean 34% gain for the British Isles). These woodlands are dominated by alder, silver birch, goat willow and grey willow, but also ash and occasionally common oak and sycamore. Wet woodlands are found on poorly drained and seasonally wet soils on a range of soil types, including nutrient-rich mineral and acid, nutrient-poor organic ones. Often wet woods occur within wet flushes in other woodland types (e.g. with upland mixed ash or oakwoods).

Of the main tree species, both willow species, birch and sycamore could decline by more than 10%, but all the tree species show a decline in England and one of the important shrub species, buckthorn, increases by 21%. The implications of these changes could be quite profound as all many of the dominant canopy species could struggle in southern Britain; the picture is somewhat better for Scotland as alder and grey willow could both increase their range. However, this pattern may be overridden if local site conditions stay wet enough to ensure the continued growth of these species.

Native Pine Woodlands

This habitat has only 34 species represented, although all the main tree species, including Scots pine have been modelled. Native pine woodlands are dominated by Scots pine, although birch, rowan, alder are also found and sessile oak occurs infrequently.

In Scotland, Scots pine is projected to lose suitable climate space significantly under the high emission scenarios (A2) and moderately under the low emissions scenario (B2) by 2080. Silver birch is also projected to decrease its suitable climate space in Scotland, although most of its climate space within pine woodlands remains until 2080. On the other hand, alder and sessile oak are projected to increase their suitable climate space. There is little change projected for downy birch and rowan.

For understory small trees and shrubs, the suitable climate space is projected to decline for common juniper, while that of aspen, holly, hazel, bell heather and crowberry shows little change. Some ground flora species are projected to lose their climate space, including lesser twayblade and twinflower.

A study in Sweden found that the climate-related mortality in Scots pine occurred mainly in the early stages (first 20 years) of a tree's life cycle. Scots pine is thought to live for about 300 years and the trees in the later stages are mostly not immediately affected by changes in climatic conditions. Thus, it seems unlikely that its range will be markedly reduced in the next 100 years or so, despite the projected losses of their climate space. However, Scots pine has been shown to be vulnerable to extreme water deficits in drought conditions which may impact lowland populations more.

Indirect impacts of climate change on Scots pine include increased risks from pests and diseases due to warming. Already, a fungal disease, red needle blight, which infects a wide range of pine species, has increased in the UK since the late 1990s, with the first outbreaks occurring in Scotland in 2002. In addition, increases in winter temperatures have led to the northward spread of the pine processionary moth in Italy.

At present, sessile oak do not occur frequently in pine woodland. However, as the climate becomes less favoured for Scots pine and more favoured for sessile oaks, the frequency of sessile oak stands may increase. With sessile oak increasing, the associated species including fungi, mycorrhizae, mosses, lichens and invertebrates may also increase. Alder and rowan may increase too as their climate space remains in the future. An increase in the dominance of broadleaved trees at the expense of Scots pine will affect some of the characteristic species in pine woodlands, such as Scottish crossbills and wood ants, as these species are strongly associated with Scots pine.

Colonisation of Scots pine communities would depend also on various factors other than climate, including soil types, land cover, and grazing practices. For example, if land-use and grazing pressure

allow, scrub species may shift above the current treeline and broaden the upper edge of pinewoods. Juniper and montane willows may also shift to higher elevations where soil conditions allow.

While the projected changes in temperatures and rainfall are likely to bring a negative impact on Scots pine, enhanced CO₂ concentrations are likely to have a positive effect on the height, diameter growth, and needle biomass. The increase in leaf and needle production will increase shading on the forest floor, which will then affect the species intolerant of shading. For example, heather may disappear from areas within the pinewood where light intensity falls below 40% of that under open conditions, although its suitable climate space is projected to remain. Growth of wavy hair grass may also be limited by shade. Thus, species composition may change through losses of the shrubs and grasses together with their herbivores and this will in turn lead to changes in ecosystem functioning.

Disturbance events are likely to become more frequent under climate change. While fires can kill much of the vegetation, they can often aid in the regeneration of Scots pine. Silver birch may also regenerate well following a burn, as the open competition-free conditions produced are ideal for seedling establishment and growth. Thus, depending on the regeneration rates, species composition may be affected.

Grazing, particularly by deer, has been identified as the major factor limiting the regeneration of the native pine woodlands. Deer populations are adversely affected by cold, wet weather, and thus the population densities and ranges are likely to increase due to climate change. Therefore, unless appropriate management actions are taken, climate change is likely to increase grazing pressures.

Lowland Mixed Deciduous Woodland

138 modelled species are associated with this habitat, not surprising given its ubiquitous 'catch-all' status and distribution throughout the British Isles. Clearly then, this habitat is found on a range of soil conditions and throughout the lowland areas of the British Isles. This woodland tends to be of great value for conservation because many of the remaining examples of it are considered *ancient semi-natural woodlands*.

All the main tree species are represented and many typical shrub and herb layer species are included too. The results of the modelling could have some interesting implications for the future of lowland woods in the British Isles. In particular, the potential massive increase of large-leaved lime (and to a lesser extent small-leaved lime) could change the make-up of the canopy in woods where these species are found (which are not many, but could feasibly increase with the aid of human intervention). This could result in woods that begin to resemble the wildwoods of lowland Britain before human intervention. Other notable possible increases include true service tree and wild service tree, both very rare. Field maple, which is at its northern limit in northern England, could also increase, as could wild pear.

The most notable potential loser in this habitat is wych elm (which is already becoming rarer due to Dutch elm disease). In England, hornbeam, sycamore, birch, ash, aspen and common oak *could* all lose space; again, this highlights the possibility of a major switch in the dominant canopy species from oak, ash and sycamore to (and occasionally hornbeam) to the lime species.

Upland Birchwoods

Upland birchwoods are exclusively found in Scotland and are, not surprisingly, dominated by both birch species, as well as less frequent numbers of willow, aspen and even juniper. Because of the fast-growing and pioneer nature of this woodland type it is quite dynamic in terms of its boundaries and location. The soil type is usually acidic, but it can occur on more base-rich soils.

79 species in this habitat are covered by the modelling, including all the major tree species, but also many of the important and commoner shrub and ground flora species. Both birch species could lose bioclimatic space (silver -19% and downy -9%), as could other important tree species (rowan - 4%; grey willow -4% and in the 2080 scenarios wych elm too). However, both oak species could increase in bioclimatic space and although neither are pioneer species like birch, this habitat may well lose out to Upland Oak woods.

Analysis of the results in relation to the National Vegetation Classification (NVC)

The National Vegetation Classification (for Woodlands and Scrub) is a phytosociological description of twenty-five woodland and scrub communities found in Britain. Using the NVC for analysing climate change effects on woodland communities offers some advantages over the Priority Habitats. Because NVC habitats are classified using distinct phytosociological relationships, gradual change in species composition may result in changes to the overall community classification. This is less likely than the Priority Habitats perhaps (as they are so broad) and poses some interesting questions for ecologists as well as conservationists. The NVC, as a (fairly) easy classification to use, would provide woodland managers an opportunity to gauge community change over the coming years more easily. This, at least offers more scope for improving adaptation options. Here we briefly discuss two fairly common and species-rich NVC communities.

NVC W8 Fraxinus excelsior-Mercurialis perennis-Acer campestre woodland

This lowland ash-dominated woodland is fairly ubiquitous in Britain (in fact one of the sub-communities can be found on higher slopes too), although it is more of a rarity on the continent (possibly as foresters prefer to encourage oak for timber). A comparison with the results from the *Lowland Mixed Deciduous Woodland* Priority Habitat allows us to pick out the W8 species from the W10 (although in reality W8 and W10 share many species, but differ in the dominance of the main canopy species, not surprisingly ash and oak). Although W8 is probably the 'climax' woodland on the very base-rich soils where rainfall is less than 1000mm (out-competing even oak), it requires a certain amount of soil moisture to grow comfortably. In situations under future drier (in southern

England) and warmer conditions the dominance of ash may begin to be threatened by common oak which has a greater tolerance of drought. It may even see a return to the prehistoric patterns of small-leaf and large-leaf lime dominance on these soil types where they are still present (e.g., Wye valley and the White Peak); if warmer and drier summers become more prevalent then an increase in lime is a distinct possibility, especially if a more planned recovery/re-introduction programme is adopted. Certainly the modelling results suggest that the lime species are capable of doing very well under future climate change and whilst other species also do well (the service trees, wild pear and field maple), the limes are the only two, other than oak, that are major canopy species.

However, it is perhaps more likely that oak will be a more common successor to ash-dominated woodlands (except in the really base-rich soils) if only because oak is very common and the limes, although widespread, are not very abundant (heavy browsing from deer would also reduce the chances of limes spreading). On the more northerly facing and damper sites though ash is likely to hold on and maintain the W8 community composition for longer.

NVC W10 *Quercus robur*-*Pteridium aquilinum*-*Rubus fruticosus* woodland

The NVC W10 oak woodlands are found on slightly more acidic soils than the W8 community, although they share many species. Their edaphic preferences lie in between the base-rich soils and the truly acidic podzols that W16 and W17 prefer, in this regard it is not surprising that they can be very species-rich. The relative climate change tolerance of both oak species suggests that many W10 woods should remain fairly intact in terms of their dominant canopy species; however, like W8, the lime species may prove to be more successful colonisers in the future if already present in southern British woods. Similarly, on the more acidic sites with W10, sweet chestnut could compete more with oak and start to replace it. In the north, where oak still outcompetes beech (and hornbeam), there may be a gradual shift in dominance to beech (although this is already happening and many managers of W10 ancient semi-natural woods in the north actively control beech). In the wetter parts of Scotland, W10 may also succeed W11 as the climate becomes drier.

Discussion

Application of bioclimate models

Bioclimate envelope models have a number of theoretical and practical difficulties, not least of which is the actual extent to which (current) climate governs species' distributions. Each species' current distribution represents the realised niche of that species, but future bioclimatic space under climate change scenarios provide a fundamental niche (i.e., it does not take into account biotic and other factors). At smaller scales other determinants affect species' distribution, including biotic factors like competition, facilitation and mutualism; but also intra-population factors like phenotypic plasticity; geographic factors like soil type, land-use, human management, fire and fragmentation. However, whether these factors exert any control over macro-scales is still disputed.

So, given that these models have a number of caveats limiting their utility, do they have any use in modern predictive ecology? They do at least offer a quick and (relatively easy) assessment of potential climate change impacts for large numbers of species, particularly if there are few data on a species' physiology and ecology. There is, though, plenty of room for improvement - general calls for improving data quality, processing and evaluation abound; in fact the limitations of bioclimatic models are well known and development addressing any of these issues is a step forward (and indeed many research groups are doing just this). Perhaps some issues stand out more than others though, and given the complexity of community dynamics, some are perhaps more attainable. Suggestions for incorporating species' migration, as well as a better understanding of species' trailing edge dynamics are imperatives. One other possible improvement would be to incorporate more realistic community assembly processes, an approach that would perhaps be best achieved by adopting species' traits.

Comparison with Ecological Site Classification results

The Forestry Commission Ecological Site Classification (ESC) system is designed to provide foresters with an easy tool to select ecologically suited species to any given site in the UK. While both ESC and SPECIES models project the potential changes of suitable conditions for tree species under future climate scenarios, comparison of the results are complicated, partly because the suitability changes projected by ESC models are different from the climate space changes projected by SPECIES. The changes in the suitability classes in ESC represent the changes in timber productivity. It follows that the effects of reduced suitability under the future climate are likely to be seen in the form of reductions in productivity, rather than complete loss of the species from the site. In addition, ESC does not take account of the species distributions and does not indicate if the species is planted at the 'suitable' site.

For example, looking at beech, the ESC projections under Low and High scenarios in 2050 and 2080 showed that, under all but the 2080 High emissions scenario, the suitability in east and west Wales, northern England, and eastern and western Scotland are projected to increase. In contrast, the suitability in eastern England declines to the extent that under the 2080s High emissions scenario, there is virtually no area deemed 'suitable' for beech in the region. In fact, by 2080, the ESC models show that the southern limit for beech will be in northern France. The model thus projects the likelihood of a significant regional shift in the occurrence of beech as a productive forest species.

The SPECIES projections also suggest possible distribution shifts, indicated by climate space expanding northwards in Scotland and decreasing in parts of southern England, although much of eastern England, where the suitability projected by the ESC models is reduced, are projected to remain as suitable climate space even if there is a concomitant reduction in productivity. As beech is sensitive to droughts, stronger summer drought projections by the UKCIP02 High emissions

scenarios relative to the HadCM3 A2 scenarios may have resulted in a significant reduction of suitable areas by the ESC models.

Potential impacts on woodland structure

Understanding individual species' response to climate change is very useful, but scaling those responses up to community responses is a difficult task. The complexity of most natural communities means that it is extraordinarily difficult to predict outcomes - for example, biotic interactions (competition, facilitation, herbivory, mutualisms) between species at different trophic levels are all likely to be affected by physiological, phenological and migratory responses. However, evidence of community change is occurring at some well-studied locations. One study in the US has shown a shift in vegetation types since the 1950s due mainly to a higher occurrence of severe droughts; and evidence from Spain where many European plant species are at the limits of their southern distribution is also burgeoning. At the other extreme there is also evidence that Arctic and alpine communities are changing too.

In this area of study it is also worth noting the results of experimental work on community response to climate change. Clearly, this field has practical limitations because of the difficulties of replicating climatic effects on natural systems - one approach has been to use small chambers but these are rarely used on patches containing more than a few co-existing species. Another limitation is that it is very difficult (and expensive) to study anything other than small forb or grass ecosystems: examples are most common for alpine and tundra ecosystems but also calcareous grasslands.

There have, however, been a few studies on woodland ecosystems looking at the competitive balance between species, but these have been limited to the tree seedling cohort due to the obvious difficulties in working with mature trees. Similar work has also been undertaken in shrubland ecosystems, but also looking at seedling recruitment. One pattern that is emerging from these studies is the relative importance of species interactions (mainly competition and facilitation) under climatic change in determining community assembly, although other factors may play a part too (herbivory, mutualisms). Current thinking emphasises the growing importance of facilitation (species interactions that benefit at least one of the participants and neither suffer any loss of performance) under higher abiotic stress conditions (e.g., the rear edge of a distribution).

The modelling results suggest that for many of the woodland Priority Habitats the different responses of their component species will result in changes to woodland structure, if only due to changes in the dominance of some canopy species. The dominant tree species that will be more tolerant of climate change are likely to increase their competitive edge over those with lower tolerance to drought and heat. This could lead to increases in both oak species, both lime species (where they are locally abundant), beech (in northern Britain, but declining in southern England) and possibly some non-native species, such as sweet chestnut and downy oak. However, perhaps not all these species changes will lead to massive structural changes to communities; some species

may be very suitable functional matches for the species they replace (e.g., sweet chestnut and oak). However, palaeoecological data highlights the fact that woodland composition and structure has changed considerably over long time-scales and whilst current climate change is occurring at a far greater rate than in recent prehistory, some change to woodland structure may not necessarily be a bad thing.

Perhaps the greatest changes to structure will occur in the south-east, where the most extreme temperature and drought conditions are likely. In these conditions, woodlands on free-draining soils - including *Lowland Mixed Deciduous* and *Lowland Beech and Yew Woodland* - are most at risk. If planned adaptation is not a considered and proactive strategy these woodlands may even struggle to maintain a dominant canopy cover, particularly if conditions are too dry even for oak. Over a series of warmer and drier years, woodlands may eventually start to die back and more tolerant shrub species (hawthorn for example) and smaller tree species (whitebeam) may become dominant in the canopy.

Potential impacts on woodland function

The deeper consequences of community change are beginning to be understood now and the implications for changes in ecosystem function due to climate change are concerning. For example, changes to climate affecting the phenology of species may disrupt long-standing synchronous ecological relationships. This has particular importance for woodlands with such a diversity of taxa and huge trophic webs present in most woodlands.

Changes to forest ecosystems resulting from climatic change may have serious repercussions for a range of ecosystem functions including forest productivity, carbon sequestration, soil protection which can lead to flood control and resilience, climate regulation, timber production, pest regulation and leisure and recreation. The results presented here clearly highlight that woodland function will change in the future; what remains difficult to assess is what the change will be and how fast it will occur. Competitive interactions between dominant tree species are often controlled by small differences in soil type, moisture and climate, so changes in climate over the next few decades are likely to bring about gradual switches in dominance in canopy species. Whether these changes will have deleterious impacts on ecosystem function is difficult to say. Research focussing on the importance of the proportional abundance of a species in a community to ecosystem function suggests that removing a functional group (e.g., canopy trees) from an ecosystem is more important than its relative dominance. Although most of this research has been based in grassland communities, if this pattern proves to be reinforced in woodlands, it suggests that replacing one dominant tree species in a woodland with another will not have major consequences for ecosystem function.

However, perhaps the biggest concern should be the lack of dominant canopy tree species diversity in the British Isles. If climate change opens up new niches for species, it is possible that our native flora does not contain a suitable species to fill a new niche. Compared to the continent,

which has considerably higher diversity of tree species, Britain is reliant on relatively few which may result in exotic or introduced species becoming more competitive (e.g., downy oak, larches, sweet chestnut). However, although exotic species may not necessarily fulfil biodiversity conservation aims, they could possibly maintain some important ecosystem functioning roles (e.g., productivity, shade).

Other factors

The impact of a changing climate is not confined to mature trees, but is likely to influence regeneration as well. Masting of beech and oak, for example, is quite likely to change in frequency and production. This has already been seen in other countries in periods of climatic change (e.g., Sweden), but numerous other factors also affect masting, such as atmospheric nitrogenous pollution, pollination success and seed predation. Resource masting theory suggests that extreme events, like drought, will reduce masting, but fruiting is not fully understood and the impacts of future climate are unknown.

Drought is also likely to affect seedling establishment in the absence of competition. Higher CO₂ levels will encourage tree sapling growth, but the effects of increasing temperature are likely to have a deleterious effect.

Biological adaptation to climate change

Autonomous adaptation responses are those which are undertaken by natural systems, without human intervention and include *in situ* genetic adaptation, phenological and physiological adjustments and dispersal (polewards or upwards). A number of factors can hinder this adaptation and contribute to vulnerability, including:

- Lack of opportunity for poleward migration
- Lack of opportunity for altitudinal migration
- Lack of opportunity for inland migration
- Limited dispersal capacity
- Barriers to dispersal e.g. oceans, urban areas
- Rarity/small population numbers
- Low genetic diversity
- Over-grazing by deer reducing tree regeneration
- Under-management of woodland leading to dense limiting regeneration capacity.

However, there are other factors which may affect the success of adaptation including:

- Little or no overlap between present and potential future distributions
- Endemism
- Restricted range – current and/or projected future range
- Loss of critical associated species – those with monospecific relationships are most likely to be affected

- Disruption of the synchrony in the timing of life cycle events (phenology) or of species' interactions e.g. great tits and caterpillars.
- Increase competition from invading species (both natives and exotics)

In many instances it is likely that human intervention will be required to increase the adaptive capacity of our woodlands. Human intervention, either reactively or proactively, constitutes planned adaptation strategies which are outlined below.

Adaptation strategies for biodiversity conservation

A number of planned adaptation options have been suggested for natural ecosystems and protected areas that range in scope and feasibility. Here, we briefly outline the basis for the main options possible for British woodlands.

Reduce and manage stresses from other sources and activities

One of the most common adaptation options discussed in the conservation literature is perhaps the most obvious too. Simply, if other threats and stresses are reduced (such as air pollution, over-harvesting, habitat conversion and species' invasions), species and habitats are likely to have greater resilience to climate change. A good example of this can be seen with trees under water stress: many species are quite capable of tolerating drought, however, if they are attacked by insect pests or pathogens also their resistance is reduced, which may lead to increased mortality within a population. In many woodlands, particularly near urban populations, this may be the key strategy and successful implementation could be the difference between maintaining ecosystem structure and function or a breakdown of a key element. Some woodland nature reserves in the UK are already encouraging neighbouring landowners to adopt agri-environment schemes to reduce the effects of fertiliser and herbicide drift on woodland ground flora.

Habitat restoration

Habitat restoration would increase the area of potential habitat for many species as well as buffer existing reserves and hence increase resilience. This aim links with reducing and managing stresses, as well as increasing landscape connectivity. Restored habitats in the landscape may allow migrating species a suitable habitat to move through. This is already a major aim of national conservation bodies (e.g., Natural England, the Wildlife Trusts), but further development of regional (and national) partnerships should be encouraged. The potential for this strategy in the UK is large because of a high number of privately owned degraded woodlands, and there are also grants available to woodland owners to bring woodlands back into biodiversity friendly management.

Increase landscape connectivity

As the British landscape is highly fragmented it is likely to be too much of a barrier for successful species tracking of climate change. The implementation of corridors and/or stepping stones to link

areas of habitat or reserves is a popular objective. In Britain, the Wildlife Trust is trying to implement a similar scheme by encouraging landowners and reserve managers of similar habitat type to increase their linkages to neighbouring reserves, and in Scotland the Glasgow and Clyde Valley Integrated Habitat Networks scheme is attempting a similar aim. Clearly, this would be a more useful strategy for mobile species, but even for many plant species, and in particular the wind-dispersed species, it will prove to be an important strategy (although a lot of woodland species are slow colonisers). Furthermore, by increasing colonising ability it is likely that ecosystem functioning will be maintained or enhanced by ensuring a greater genetic diversity in species populations. However, natural or assisted migration is considered a natural response to climate change for species although the risks of undesirable species migrating as well as 'native' species should be considered.

Increase landscape permeability

'Softening' the landscape through reduction in unfavourable management practices and increasing the area for biodiversity, e.g. through agri-environment schemes (e.g., Living Landscape scheme run by Wildlife Trusts) is seen as a potential means for improving species dispersal. Although not quite as desirable as creating habitat corridors, in a multi-use landscape, it is more likely to be an adopted strategy. Questions remain over its effectiveness however, and much work needs to be done to have a greater confidence in its ability to improve species dispersal under a changing climate.

Increase size and/or number of reserves

Long-standing biogeographical relationships between species richness and reserve size and number show that larger and more reserves offer greater biodiversity and hence maintenance or improvement of ecosystem functioning. This would also have implications for reserve connectivity, which may help species dispersal and migration. Additionally, like the first two strategies above, it will also help increase ecosystem resilience towards climate change. This strategy is perhaps more likely to be a successful strategy in the UK due to the ever-increasing resurgence in woodland planting (e.g., the Caledonian pine project in Glen Affric); however, it is also an opportunity to re-address conventional wisdom on plant species provenance as increasing genetic diversity in new woodlands is likely to improve climate change resilience.

Increase habitat heterogeneity

Increasing habitat heterogeneity within reserves increases the available niche space for a wider range of species to migrate, grow and reproduce under changing climatic conditions. Furthermore, it may also have an effect on reducing threats like pathogen transmission. Landscape heterogeneity should improve migration due to shorter dispersal distances and community reassembly as heterogeneous landscapes usually have greater genetic diversity (which increases adaptive variation) and species diversity (a richer range of taxa to better enable assembly into new communities). For the future of British woodlands this option is perhaps not as difficult as it first

sounds; foresters and conservation managers have been adjusting and creating new habitat structures for centuries (for example, coppice coupe rotations, shelterwood systems, ride and glade creation) and as a conservation strategy it is already commonly practised amongst many woods in the UK anyway. It should also help maintain and improve ecosystem functioning by creating new habitats, and hence, species diversity.

Focus on conservation efforts on north-facing slopes

Very few studies have examined the effects of topography and aspect on community structure but those that have confirm anecdotal evidence that aspect can have considerable effects on species composition. Some studies have reported differences of 2.5 to 3.0⁰C in annual mean temperature in adjacent chalk grassland slopes of different aspect - it would certainly seem then that focussing conservation efforts for high priority species and habitats on north-facing slopes would be a worthwhile strategy, as similar differences can be seen in woodlands. Modelling the utility of topography has rarely been done either, but this would help identify suitable target areas for conservation.

Translocations and re-introduction of species

Translocations have been practised on a range of species groups and are considered to be one of the main adaptation strategies. It may be especially beneficial for those species providing key services, such as pollination, or for replacing a key structural (i.e., tree or shrub) species. However, despite the fact that foresters have been successfully introducing species for centuries, there are a number of concerns about this approach (e.g., unintentional consequences of evolutionary change, new biotic interactions or invasive species risk). A number of questions arise when considering the process: how do you select the species to translocate? What are the legal, ethical and policy implications of translocation? Who decides to translocate a species? Should translocation just be used for climate change reasons or others like ecosystem function? Who is responsible for the success of the project?

Introduction of wider range of genotypes

For years conservation has worked on the assumption that for re-establishing habitats sourcing species from local provenance was crucial due to numerous generations' worth of adaptation to the local environment. Clearly, as climate change forces local conditions to change, this will require a new approach to the conservation of genetic resources. Foresters have been introducing different genetic stock of species for centuries; this approach may prove to be beneficial for conservation if species have southern European populations that will already be adapted to future British climates; e.g., beech seed from the drier zones in Northern Spain, Italy or southern France. Species with wide European distributions are likely to do better if genotypes from lower latitude sources are used in Britain; those species with small or narrow distributions may not fare so well.

One example of this already occurring is the Forestry Commission managed Jeskyns Community Wood in Kent. They have already started to plan for a future climate and have introduced a number of species from continental provenances, both native and non-native, which should cope better with climate change in 2050 and beyond. The species planted, all of which currently grow well in France, include small-leaved lime, hornbeam as well as walnut and oriental spruce. The Forestry Commission will maintain a monitoring programme to help advise on future plantings in other woods in the UK. If this strategy could be applied to a range of key species (not just trees and shrubs) within woodlands it may go a long way to help maintain ecosystem functioning.

Maintaining native community ecosystem structure and function

Maintaining structure in its simplest sense (i.e., a typical woodland with canopy, shrub and herb layers, etc), if deemed a priority (for example, to maintain ecosystem services like recreation, shade provision or productivity), would not be a difficult challenge, as there are numerous suitable species from warmer climates that could be used. However, maintaining structure *and* biodiversity value would be an altogether more complex task. Many of the above options would certainly enhance ecosystem resistance and resilience in the face of climate change, but ultimately some species may start to suffer and possibly create gaps or changes to the previous structure. The links between ecosystem *structure* and *function* are complex and indeed ecosystem function science is still a young discipline which is revealing contradictory relationships. We still do not know, for example, how many species in British woodlands are important components of ecosystem function and how many have 'functional redundancy'. Inherent to this will be individual species tolerance of future climate change and many woodland tree species will appear tolerant due to their long-lived nature; however, studies also suggest that *increasing* mortality in forest tree species may increase the evolutionary adaptation response to climate change by allowing faster population turnover (older, maladapted trees dying make way for new, better adapted seedlings).

Introduce new species to maintain habitat structure

Semi-natural habitats provide a range of ecosystem services that are important for society; these services may conflict with biodiversity conservation, but often they are mutually beneficial. The

establishment of 'neo-native' habitats is controversial, but may be an only option if maintaining certain ecosystem services is desired. For many non-native species that have ranges in central Europe, the question of whether they become neo-native may be academic, as without assisted migration many of them won't be able to migrate to the UK. In fact, we have created woodlands of non-native species in the past, e.g., sweet chestnut coppiced woods in the south-east which were introduced by the Romans. However, perhaps it is worthy of further discussion if there are suitable species that may be able to maintain habitat structure (and possible hence ecosystem function). There are a few continental European tree species, for example, that have similar ecological niches to some potentially threatened tree species in England (e.g., downy oak for common oak; narrow-leaf ash for common ash).

One problem (and a major ecological one) with introducing exotic species is that new species (or neophytes) may not provide suitable environmental conditions for a whole host of other species (e.g., invertebrates and fungi) and hence a breakdown in the food web may ensue. Replacement species should ideally have similar traits to the original species (e.g., same shade provision, habit, leaf decomposition rates). Would southern European oak species provide the same niche opportunities for fungi that common oak does? What species would offer suitable (if any) replacement niches for beech? Further research is required in this area. There is also an issue of plant hygiene to ensure that micro-organisms are not imported.

Improve inter agency and regional co-operation

This is perhaps one of the most crucial strategies as it has implications for translocation schemes, genetic stock harvesting, corridor and landscape permeability schemes, etc. Nationally, inter-agency cooperation is aided and abetted by Natural England and its other UK country equivalents, and as different conservation bodies are usually working for a common good, relationships are normally healthy. Attempts to include private landowners in conservation adaptation plans are mainly through incentive schemes for landowners, such as the HLS agri-environment scheme. However, these schemes, so far, pay less explicit attention to climate change adaptation and do not offer opportunities for participants to plan across regional landscapes.

Pan-European cooperation is traditionally well-founded in academic networks concerning biodiversity, climate change and conservation; however, in the practising conservation arena there are comparatively few cooperative bodies. Some exceptions are ENCA (a network of the heads of European Nature Conservation Agencies), which seeks to promote “management of our European landscapes to allow nature (as well as humans) to adapt to climate change... embedding ecological concepts of resilience and a healthy natural environment into the adaptation debate... aim[ing] for functioning ecosystems that are resilient to extreme events...”

At the European governance level, the EU is promoting cooperation through various activities including the NATURA 2000 policy directive which heavily invests in climate change adaptation research. Also, the Pan-European Biological and Landscape Diversity Strategy which seeks to

address climate change, but also aims to involve European NGOs. Finally, The EU's recent white paper on *Adapting to climate change: Towards a European framework for action* explicitly sets out a number of adaptation aims across sectors (including conservation) and aims to ensure that all member states have minimum level of 'adaptation competency'.

Ex situ conservation

The use of *ex situ* seed banks, captive breeding or zoos is seen by most as a last resort, however it may be the only realistic response for some rare species. The UK has a strong history in *ex situ* conservation and many of the oldest and largest botanical gardens, herbaria and arboreta have active conservation programmes. *Ex situ* conservation is, however, expensive and can create population health problems caused by a lack of genetic mixing.

Maintain and increase monitoring

This strategy is vitally important as it provides the only real method of understanding what change is occurring in the site and in what direction that change may be heading. Baseline data are necessary to understand change (and the direction of change) and also makes adaptive management easier (see below). Monitoring species' response to climate change is doubly important now and ideally should include measurements for growth (above- and below-ground), health (crown condition, pathogens), species' relative abundance, mortality, regeneration, soil water conditions and phenology. Unfortunately, monitoring is an expensive operation and very few programmes exist to track changes to species and habitats; however, although funding for monitoring is dwindling in some organisations, the UK does have an extensive Environmental Change Network with twelve monitored sites (including woodlands) throughout the UK.

Adopt adaptive management approach

Heavily dependent on monitoring, this approach is essentially an iterative process that adapts to and responds to ecological and environmental situations as they occur. It is seen as a crucial response in a range of sectors including conservation and forest management although it requires an ability to analyse data and have the facilities to respond to changes, so it is not a viable option for organisations with minimal resources. It also relies on an underlying faith in the further commitment to conservation in the face of climate change and thus can be sensitive to the vagaries of future environmental policy and funding. Ironically, many adaptive management practices can be learned from the forestry, which in recent decades has sought to manage forest in a more holistic and integrative manner. This process requires a good understanding of the ecological processes (e.g., regeneration, growth, competition, mortality), ecosystem processes (biogeochemical cycles, succession, disturbance, etc.) over various time-scales (it is also important to appreciate ecosystems are dynamic and not static).

Non-intervention

This approach stresses the importance of allowing ecological community processes to take their course (i.e., change), rather than allowing human intervention to preserve structural “habitat ideals” or particular species. This may result in a new suite of species and thus altered community composition. Although outcomes may be hard to predict, the approach may well be beneficial for ecosystem function if alternative management options are infeasible in terms of complexity, time, resources or space availability. It also provides opportunities for those species which are adapting autonomously to climate change, although their arrival could be facilitated by changing management regimes.

The conservation priority of a given species in decline will depend on a number of factors, including:

- 1) the perceived importance of the species,
- 2) the species’ remaining geographical extent,
- 3) the time-scale and severity of the decline, and
- 4) the significance of knock on effects on other species/habitats.

In practice, the first and second of these factors will be reflected in whether the species is recognised as of local, regional, national (e.g. BAP species) or international significance (listed in EU Birds or Habitats Directive). This list could be seen as indicating an increasing level of priority in order to meet conservation commitments and would make the laissez-faire approach less likely to be appropriate. Combining these priorities for the species with information on a species’ projected future distributions will further assist priority ranking, with rare species with little available future space warranting greater attention. In the context of climate change, a pervasive threat to most species, this can be assessed in terms of the degree of loss of suitable climate space. The final factor for consideration in determining the species’ priority is its role in relation to the wider ecosystem. This is often difficult to assess, but a single species may be critical to other dependant species or to particular ecosystem functions or services. For habitats, the equivalent question would be: Is the habitat critical to maintaining species of high conservation concern? For example, many tree species, such as beech and common oak, have saproxylic species associated with them, which would be adversely affected by their loss. Once the level of priority has been decided, then the feasibility of undertaking adaptation needs to be evaluated.

There are number of potential climate change adaptation options. In order to determine whether these management options are prioritised over the laissez faire approach the feasibility of each management option needs to be assessed. The flowchart in Figure 1 has been devised in order to facilitate this consideration. The level of priority, as detailed above, should be used first to decide

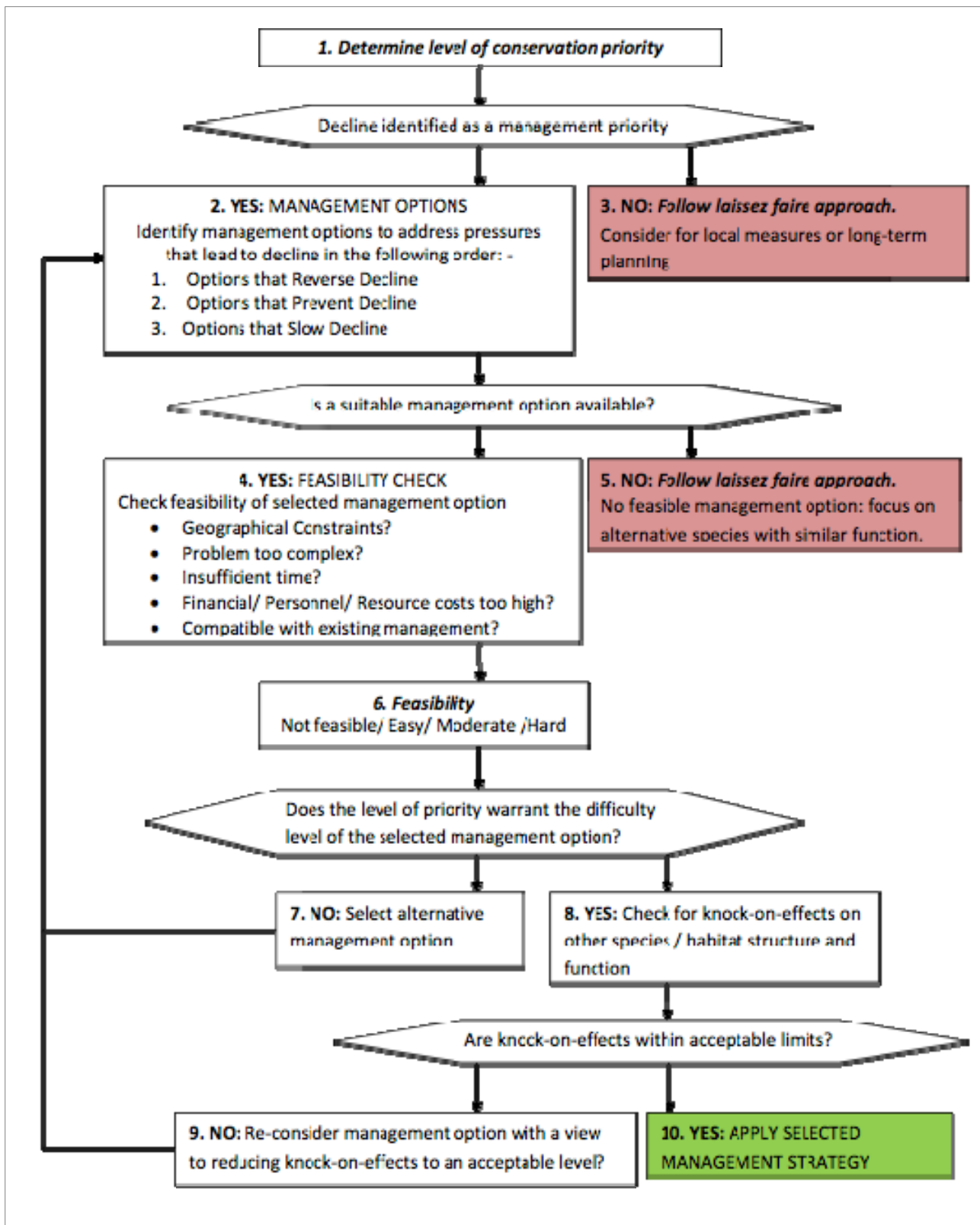


Figure 2: Flowchart for assessing the feasibility of adaptation to climate change.

whether a particular decline is a management priority (1). If it is (2), then the multiple management options available should be considered in turn, with priority given in order to those with the potential to reverse, prevent and slow the decline. These management options could include reducing pressures, such as grey squirrel damage, or climate change through managing water levels in beech woodlands. If decline is not a priority (3), then local measures might be taken

to counter adverse impacts and monitoring undertaken to see if the species' priority warrants upgrading.

Where a suitable management option is available (4), then its feasibility needs evaluating as there may be barriers to its implementation, which make it unlikely to be undertaken. Available geographical space is a key barrier. For example, in a climate change context, if there is little or no projected suitable climate space, then undertaking extensive measures might not be appropriate. Also, pressures related to land use and management may reduce the likely success of climate change adaptation measures, thus reducing the appropriateness of a management intervention beyond laissez faire. This could be especially relevant for certain Arctic Alpine species in Scotland if they are maintaining their range elsewhere e.g. in Scandinavia, even though the species, such as twinflower, may be of national importance. Similarly if a species losing future suitable climate space is also experiencing decline due to other pressures, and these pressures cannot be feasibly addressed and/or are projected to increase in the future then letting go might be more pragmatic. In some cases, habitat recreation could be an option, but when determining feasibility, time constraints need to be considered. Broadleaved woodland, for example may take 100+ years to get the necessary structure and function. Another measure, more applicable for species, is translocation, but this may have to be repeated to maintain new populations and will have financial and resource implications. It could be possible for lichens be transported northwards on suitable branches and then wait to see if they adapt to growing on a new tree species.

If there are no options (5), then this could be considered grounds for adopting the laissez faire approach and alternative species could be sought that would have similar functions within the ecosystem. This could include species from within the community that may be better adapted to the climate or new arrivals, as discussed earlier.

If action is feasible (4), then the level of feasibility of the action needs assessing (6). By balancing the conservation priority of a species with the feasibility of the management option a decision can then be made as to whether the species warrants the selected management option. If it is considered unreasonable (7) or if it is not feasible for any reason (6), then alternative management options of lower effectiveness (2) could be considered. If the action is deemed appropriate (8), then its impacts on other species, the community and habitat could be taken into consideration to ensure that unwanted consequences and trade-offs are not involved. An example of such a trade-off occurs in pine woodland, where if climate-related mortality in young Scot's pine could be reduced to assist its survival in Scotland, this would have the knock on effect of reducing sessile oak's potential to increase in abundance. If such knock-on effects are seen as undesirable then an alternative management option needs to be considered that either mitigates these effects or takes a different approach (2). If the impacts are considered acceptable, then adaptation management can be undertaken (10).

Thus the decision whether to “let go” of a species, by taking the laissez faire approach, should be driven by the conservation priority given to that species and the feasibility of undertaking the most appropriate management strategies. These decisions will necessitate subjective judgement and may depend on context of the ecological community and other demands on management resources. Decisions to let a species go should not be taken lightly, and would need to involve consultation of appropriate interested parties from both governmental and non-governmental organisations and academic spheres.

Data gaps

Only 178 woodland species were modelled in this study, but there are distribution data available for many more species associated with other woodland communities. Increasing the number of species modelled would therefore improve the power of the analysis. However, there is still a lack of distribution data for the vast majority of species at the European level, necessary for modelling. Similarly, pursuing functional trait approaches to understanding ecosystem response to climate change requires good quality data on plant (and animal) traits, not only for individual species, but also to cope with intra-species variation (particularly for studying community assembly patterns or evolutionary processes).

Further Study

Developing better modelling techniques

Another important area of research in improving projections of the possible consequences of climate change is the effects of species interactions. It is increasingly acknowledged that climate change affects species interactions and that these interactions affect species ranges and abundance, as well as ecosystem functioning. Models incorporating biotic interactions have been built, which indicate that the inclusion of these interactions improve the predictive performance. These models incorporate parameters indicating the effects of species' co-occurrence as biotic predictors, such as occurrence and basal area, in order to project the future changes reflecting the competitive and facilitative interactions. However, most of these models have been applied to a limited number of species within the same trophic level, whereas species actually interact in complex food webs encompassing different trophic levels. Thus, it remains a major challenge to include knowledge on multitrophic level interactions.

One of the useful approaches in exploring the consequences of climate change on population and community dynamics across trophic levels is ecological networks. Ecological networks describe the species present in a network, and their abundance, and also show the frequency of interactions between them. Ecological network research focuses on a guild of interacting species, e.g. food webs, mutualistic networks (e.g. plant-pollinator networks) and host-parasitoid networks. Some studies have shown that temperature-induced advanced flowering of plants reduces floral resource availability for many of their pollinators, and this mismatch is likely to result in curtailment of the field season for the pollinators and in some cases extinction of plant or pollinator species, and their

interactions. On the other hand, other studies have found that plants and their pollinators respond similarly. Although the application of a network approach in the context of climate change is increasing, studies for terrestrial species are still limited. More studies are available for marine organisms, for example, on the effects of temperature warming on host-parasite system and on the effects of induced range shifts of invasive species on trophic interactions.

Limitations of ecological networks in projecting biodiversity changes include their tendency to be biased towards species at the higher trophic levels, rather than at the base of the web and that well-defined networks are often from species-poor habitats. In addition, ecological network research often focuses on a subset of interactions and does not include different types of networks, e.g. food webs and host-parasitoid networks, and thus fails to describe complete networks in the ecosystem. Furthermore, ecological networks do not take account of behavioural flexibility, for example, pollinators' behavioural changes leading to foraging on and pollination of new plant species.

The network approach can be incorporated with bioclimatic envelope models using a conceptual framework. For example, in MONARCH 2, a hybrid approach was taken, whereby outputs from modelling were used to identify species which might be arriving in or leaving a habitat and then a conceptual framework was developed for each situation, based on species interaction matrices, particularly trophic interactions, and included the development of work on food web and niche space as mechanisms in community ecology. The outcome for the community depended on the position of the arriver/leaver within that community.

So-called 'hybrid' models are emerging, which are an alternative approach for including biotic interactions into the projection of future range changes. The hybrid models are developed from process-based models incorporating physiological responses and consist of various sub-models working at different spatial scales. These models can project dynamic range changes taking account of the effects of dispersal and competition. Complex interactions can also be expressed, including a novel interaction by a species encountering another at the leading edge of its range due to climate-induced range shift. Further development is promising, although these models are data hungry and require detailed knowledge of ecological processes that is usually unavailable for large numbers of species and regions.

Including species interactions is essential in improving projections of climate change impacts. Conceptual models integrating ecological networks into bioclimatic envelope models and the hybrid models can provide more realistic projections of climate change impacts than simple envelope models. However, both approaches are limited by data availability; defining a complete ecological network requires extensive search efforts and constructing a hybrid model requires detailed information on the physiology of organisms. Thus, more and better empirical data are necessary to parameterise and test these models, which would require further laboratory and field-based research and long-term monitoring.

Understanding community response: species or traits?

A number of strands in ecology have been trying to provide better generalisations and models of community dynamics by moving away from a traditional and individualistic taxonomic or species-based approach to one based on the response (or effect) of functional traits or groupings of traits. This approach is not new in ecology and although its development gained ground in the 1970s and 1980s, it wasn't until relatively recently that ecologists started to adopt it as a method to address a number of important issues in ecology and conservation. The trait approach in comparative ecology is not confined to plants alone and research into different taxa is ongoing.

Taxonomic approaches are often not able to produce generalised community responses to change, for example, congeneric species may have greater differences in response to environmental gradients than species totally unrelated, but with similar ecological niches. Community descriptions that are based on taxonomy can fail to recognise if two spatially separated communities with different species composition are structurally similar. Furthermore, species-based community analyses can sometimes suffer from redundancy and noise within the data which can reduce the power of the analysis. Ultimately, therefore, as long as trait variation is greater between species than within species, traits should provide an easier route to defining ecological generalities and hence definable rules in ecology. When species are grouped into functional types or guilds based on their shared or similar response to environmental factors these groupings are generally more useful for analysing responses to, for example, disturbance or to ecosystem functions like productivity. Hence, rules developed in one community may be applicable to another community in a different region or continent.

Trait-based approaches provide a more direct link between the environment and the community, as species presence is determined by so called 'environmental filters' for traits. This filtering acts hierarchically with traits that survive the overarching climatic filter then passing through further disturbance and/or interaction (with other organisms) filters and can provide a predictive link between vegetation and environmental conditions. Traits are also ubiquitous, whereas species vary immensely across geographic space (and time), this is particularly important in communities that lack detailed taxonomic description or the flora is understudied.

The utility of traits in prediction ecology has made them a popular base for studying community dynamics in response to a range of disturbances and environmental change. Trait composition in communities has been analysed across gradients of fertility and disturbance, or both. They have also proved useful for understanding invasive species ecology and community responses to fire.

An important aspect of trait-based research is in understanding trade-offs in plant design and functioning that appear consistent across biogeographic regions. Some of the most recognised patterns are: specific leaf area and leaf life span (leaves with higher leaf mass per leaf area tend to have a longer life span, but require greater strength to maintain them, however, short-lived leaves

are easier to produce); seed mass and fecundity (smaller seeds are produced in greater numbers, but their chances of survival under different conditions are far lower than large seeds); and, potential plant height and growth rate or shade tolerance (taller trees are often slower growers and shade tolerant when juvenile, smaller trees grow faster, but will eventually be overtaken by slower growing trees).

Gradients across varying climatic scales have provided ecologists with useful insights into plant responses to factors like temperature and precipitation. The growing interest in ecosystem function is also providing another avenue of research for trait-based projects. It is increasingly recognised that some traits not only respond to environmental factors, but can have an effect on ecosystem processes too; as they are measurable they can provide a quantifiable link to ecosystem function.

One of the main aims in trait-based ecology is to identify which functional traits are important for predicting population, community and ecosystem processes. However, as important as this aim is, it must also be couched in practicality for ecologists if they are to fulfil the aim of reducing complexity too. Hence, the need to provide relatively easy trait measurement, which is also inexpensive and can be standardised for ecologists anywhere, is paramount. These trait data are obtained from either field sampling, plants grown in a 'garden' environment with little environmental heterogeneity, or from laboratory screening (with even better control of the environment and also plant ontogeny). Plants for measuring should be healthy, well-grown and in well-lit environments (which may be difficult for woodland understory plants). Measurement data may be continuous (e.g., height, seed mass) or categorical (e.g., life form, dispersal mode); further consideration must also be given to phenological data due to its circular nature (i.e., to better identify the relative closeness of December and January values which may not be clear with numerical assignments such as '12' and '1').

Consensus on techniques for obtaining trait data from the field or laboratory is important; however, in recent years a range of trait databases have become available to European ecologists which have proved to be very popular in many comparative ecological studies.

Traits and community assembly

A major goal in ecology is to understand the processes behind community structure and assembly. Historical approaches to this goal have been quite varied and still continue to follow either a stochastic demographic route, or a more deterministic path, or both. Community assembly using plant traits is a relatively young aspect of trait-based ecology and is seen as one possible way of reconciling the approaches above. This has seen the creation of 'assembly rules' which are defined by abiotic factors first and then biotic controls that set the levels of dominance in a community. This approach is particularly useful because it defines relationships between traits - not species - and environmental conditions; in theory the concept thus fulfils the need for generalised principles, as these relationships can then be applied to regions with different species pools.

The ongoing development of the concept is building on the known relationships between traits and climate, disturbance and biotic interactions. For example, potential plant height is a long-standing trait associated with competitive ability, however, it is also known that trait/competition associations may vary across different environments: e.g., leaf and root traits are more important in dry and nutrient poor environments. In some environments, other biotic factors may be more important for community assembly; e.g., facilitation is known to be a key interaction in high stress environments. The study of the role of traits in different environments is slowly helping to identify the traits that respond to different environmental conditions. For example, identifying the traits that convey drought tolerance in communities may help to predict community outcomes under future climate change. But it is also worth noting that it is not just environmental parameters that need to be modified for climate change prediction, as other filters may be changed indirectly by climate too (e.g., new pest attacks, change in fire frequency, changes in species' competitive abilities).

New methods have been developed to model community assembly using traits from the local species pool. Under the assumption that abundant species are more important drivers of ecosystem processes in any given environmental state, community-weighted means of the traits selected can be calculated from species abundance data. This quantitative tool can then be applied to predicting the species' composition from different species pools using the most useful functional traits representing most of the total biomass. It also has the potential for predicting community structural change in response to different kinds of environmental (including climate) change.

Traits and ecosystem function

Plant traits have been shown to have responses to abiotic factors, but they also have implications for defining the relationship between community structure and ecosystem function. In a time when ecosystem services are recognised as being vital for human welfare, and concerns that climatic change and other global environmental drivers are having deleterious effects for society, the links between functional traits and ecosystem function are more important than ever.

Community-weighted means of traits is also key to understanding ecosystem function as important traits for resource acquisition and use are related to their overall contribution to the community which can also be 'scaled up' to the ecosystem level. The key aspect of this research is that it can be applied to different scenarios of land-use change or disturbance, so ecosystem function can be quantified across environments and it has important implications as a tool in valuing and protecting ecosystem services.

Trait-based approaches in ecology have also contributed to the relationship between biodiversity and ecosystem function. There is increasing confidence that it is not species diversity that is the

main component affecting ecosystem function, but rather functional diversity. Definitions of functional diversity vary, but essentially it can be described as the functional trait variation among species in a community. There are four main requirements for measuring functional diversity: the need for pertinent trait data for the species under study; traits weighted according to their functional importance; a statistical measure to cope with the form of measurement; and measurements that explain ecosystem processes.

Much work has gone into devising suitable methodologies for measuring functional diversity, but perhaps the two most common methods are assessing dissimilarity among species using their traits or assessing trait variance in a community. It has been suggested that stricter definitions and components of functional diversity should be ascribed by ecologists to break down functional diversity into functional richness, functional evenness and functional divergence (analogous to species diversity indices). However, already the concept functional diversity has been applied to predictions and measurements of various aspects of ecosystem function, such as ecosystem stability, nutrient cycling, decomposition and productivity.

The burgeoning use of traits in ecology reflects their versatility in explaining plant responses to environmental factors, as well as their utility in understanding ecosystem function, although the traits that confer these roles may not overlap. The growth of trait databases will be an important aspect of the further development of trait-based research, but so too will the refinement of our understanding of how different traits are important to the assembly of communities under changing climates.

Traits and British woodlands

In the context of this report a discussion of a trait-based approach is no good if it cannot be applied to the future of woodlands in the UK. Certainly the relatively easy methodology for using traits commends it working in many habitat types, and the burgeoning development of trait databases in the UK and Europe allows for easier analysis. In fact, most of the plant species studied in this report already have extensive autoecological data available, as do many of the non-plant species. In addition, new research has already adopted trait-based approaches in woodlands or wooded landscapes. A next step then could be to apply this model to understanding the effects of climate change on woodlands; a number of approaches are possible:

- Calibrate bioclimate models of species distributions further by analysing if species performance is affected by their traits;
- Predict species composition of woodlands based on traits;
- Analyse woodlands across climatic gradients using community-weighted trait composition to infer future changes in structure and function.
- Relate trait composition of woodlands to changes in ecosystem services.

Exploratory work in trait approaches to future woodland composition suggest that, because the pace of climate change is such, the migration of many plant species will not track climate sufficiently well, particularly given the fragmented landscape, and the future community assembly of woodlands in the UK may well draw from non-native plant sources (including our introduced garden flora). If community assembly filters can be predicted for future climates in Britain, further screening the plant traits of our common garden flora may provide an idea of the possible species likely to compete with native species. Alternatively, if species translocation from continental European countries becomes financially and politically expedient, knowledge of these trait characteristics will help identify candidate species from other lower latitude woodland habitats.

Conclusions

The evidence for the contribution of humans to climate change is now overwhelming and evidence of biotic responses is burgeoning too. Species respond to climate change in a number of ways including physiological, phenological, range shifts and evolutionary changes. While all these responses have been documented in European and UK flora and fauna in the last few decades, the evidence of changes to habitats in the UK is not yet conclusive.

Projecting biotic responses to climate change is problematic, but a number of tools are available. One of the most popular is a modelling technique that projects new bioclimatic space for a species' distribution under different climate scenarios. As this does not take into account factors, such as biotic interactions, caution is necessary when interpreting the results. A total of 178 woodland-related species for which modelling results were available demonstrated that many woodland species have quite different responses to climate change; some will be 'winners', but a considerable number will lose potential bioclimatic space in the UK in the forthcoming decades. Most species gained climate space, although there are some significant losers including pied flycatcher, twinflower and narrow-headed ant. Of the main winners, the two native lime species both stand out as potential future dominant canopy species, although beech and common oak also make very small gains. South-east England potentially will be hit hardest by species losses, with many species, including major canopy trees losing bioclimate space here from 2050. Many species that are dominant in the south today, however, will be more successful competitors in Scotland in the future. Although beech is already naturalised in Scotland, management of it in semi-natural woodlands may need to be re-evaluated. Most woodland shrub species do very well, although one of the main losers could be bramble, which has implications for ecosystem functioning in many woodlands. A number of mobile species gain bioclimate space, including some charismatic species, such as the red squirrel and dormouse, but other factors may prevent them from realising this. However, a number of species with strongholds in Scotland are likely to suffer including the Scottish crossbill, Scottish wood ant and capercaillie.

On the basis of the modelling of the impacts of climate change on a range of species associated with the woodland Priority Habitats, it is likely that Wood-Pasture and Parkland, Upland Oakwoods and Upland Mixed Ashwoods will see few changes. Lowland Beech and Yew woodland could

extend into northern Britain, but it may suffer losses, as although beech is projected to have suitable future climate space, in reality, its intolerance to drought may reduce its growth and competitiveness, especially in south-east England. This may result in shifts to more oak dominated woodlands. Yew woods, although comparatively rare, should remain fairly resistant to climate change. The species found in Wet woodlands have a mixed response in the modelling results, as both willow species suffer bioclimate space losses, although alder, a major component of many wet woodlands gains slightly. Lowland Mixed Deciduous Woodland, which is possibly the most ubiquitous woodland type in Britain should remain relatively stable. A number of important tree species could experience small losses which may affect the competitive balance in some woodlands (e.g., between ash and oak in ash woodlands), although there are some striking gains including three rare species (large-leaf lime and both service trees). This has implications for conservation, not least because lime used to be a dominant woodland canopy tree throughout much of Britain several thousand years ago. Upland Birchwoods and Scots Pine woodlands are possibly the major losers in this study. Both the iconic species in Upland Birchwoods (silver and downy birch) could lose bioclimate space, as well as the other major trees (rowan, grey willow and wych elm). The two winners are both oak species which suggests that even on the less stable soils and in canopy gaps, the birches may not be successful colonisers and oak may dominate. For Scots Pine woodlands, Scots pine is projected to lose significant amounts of climate space under the high emission scenario by 2080, although it is unlikely that this will lead to immediate range reduction due to the species' longevity. Pests and diseases of Scots pine are, however, likely to increase with warmer temperatures, but incidents of fire may increase, which often aid the regeneration of Scots pine and silver birch. Woodland structure, therefore, may change, with sessile oak stands possibly increasing, while Scots pine decreases, and subsequently, the species associated with Scots pine could also decrease, including Scottish crossbills and wood ants.

Of the 11 rare species projected to lose suitable climate space little is known about the potential effects on woodland functioning, although there is some evidence that it could be affected by the possible decline or loss of wood ants. Many of these rarer species, however, are currently more affected by land use and management practices, with climate change acting as an additional pressure. These potential losses need to be balanced against the possible expansion of some species associated with woodlands, such as some bats. In addition, there are continental species, such as downy and holm oak and manna ash, which could have future suitable climate space in the UK. These have similar ecological niches to some tree species potentially threatened by climate change in Britain, so while they may lead to a change in woodland composition there may be little change in some functions, but this needs further investigation.

In terms of functional groups, trees are projected to have a mean gain of 15%, while shrubs and ground flora species show a mean 1% loss/gain respectively. It should be noted, however, that these findings are based on a selection of British woodland species, although almost all major tree and shrub species are included. For the other taxa, where the number of species is smaller, mammals have potential gains in climate space, while birds and ants show losses. It is difficult to

predict whether new specialist species will replace those that are lost, as specialist species are often poor at dispersal; thus generalist species are more likely to be successful colonisers. If replacement does occur it is also hard to assess whether community structure and function will be maintained, as we have no (few) examples of this and is likely to be situation specific. The possibility of more competitive, possibly invasive, species becoming established could best be ascertained by checking successful species against their traits.

Predicting changes to woodland structure are difficult, partly because the model does not take into account biotic interactions, which are very important determinants of community structure at a small scale. Some inferences can be made by drawing on changes to woodland structure throughout recent and palaeoecological history, but even this is challenging. It is possible that non-analogue woodlands may arise consisting of species that hitherto have never been a major component of Britain's native woodlands (e.g., species from our garden flora or introductions from overseas for forestry). It is likely, however, that the major structural elements of our woodlands will, or can, be maintained.

Changes to ecosystem function are possibly even harder to predict, although it will be contingent on which functions are examined (e.g., a long and developed forestry science history allows us to predict biomass productivity very well). While many functions could be maintained, some on which specialist species rely, such as specific decomposition pathways, could be more challenging and require further research. If a non-intervention *laissez faire* approach is adopted then gradual community changes will be harder to predict.

Where climate change is identified as a potential threat to woodland composition, structure and functioning, then there are a range of adaptation measures, which could culminate in adaptive management to ensure that desired outcomes are achieved. It is also possible that the conservation of some vulnerable species may not be viable in the future and consideration should be given to non-intervention and seeking alternative species to maintain the habitat. The adoption of this approach can partly depend on whether interest is in a particular species or habitat composition or on ecosystem functioning. It is also worth noting that there are already numerous woodland planting initiatives underway in the UK (e.g., undertaken by the Woodland Trust, Forestry Commission, Local Wildlife Trusts) which will help to address many of the impacts that climate change presents to UK woods. These initiatives will increase species diversity, as well as help to maintain forest resilience in the future.

As this research has shown, there are still a number of research questions to be addressed, especially in relation to the impact of climate change on woodland structure and functioning. One promising approach for understanding ecosystem change and its consequences for functioning and ecosystem services is the use of traits. This offers an opportunity to understand how communities assemble, which is particularly useful for climate change studies when the future pool of suitable species may be novel or unknown. For more complex interactions between species at different

trophic levels, ecological networks can provide insights into the potential changes on food webs, plant-pollinator networks and host-parasitoid networks and they can be incorporated into bioclimatic envelope models using a conceptual framework. Alternatively, hybrid models which are built on species' physiological responses can also take account of species interactions. For all these approaches data limitations are a serious issue and further laboratory and field-based research and long-term monitoring is needed.

Based on bioclimate modelling outputs this report has highlighted those Priority Habitats which are considered most vulnerable to climate change, and has shown that while it is possible to give indicative outcomes, especially at the species level, there is still much to discover about the more complex habitat level. Also, using the literature, it has qualitatively explored the implications for woodland composition, structure and functioning. This is an area for much fruitful further work, both to increase our understanding of how ecosystems operate and how they affect the delivery of ecosystem services.