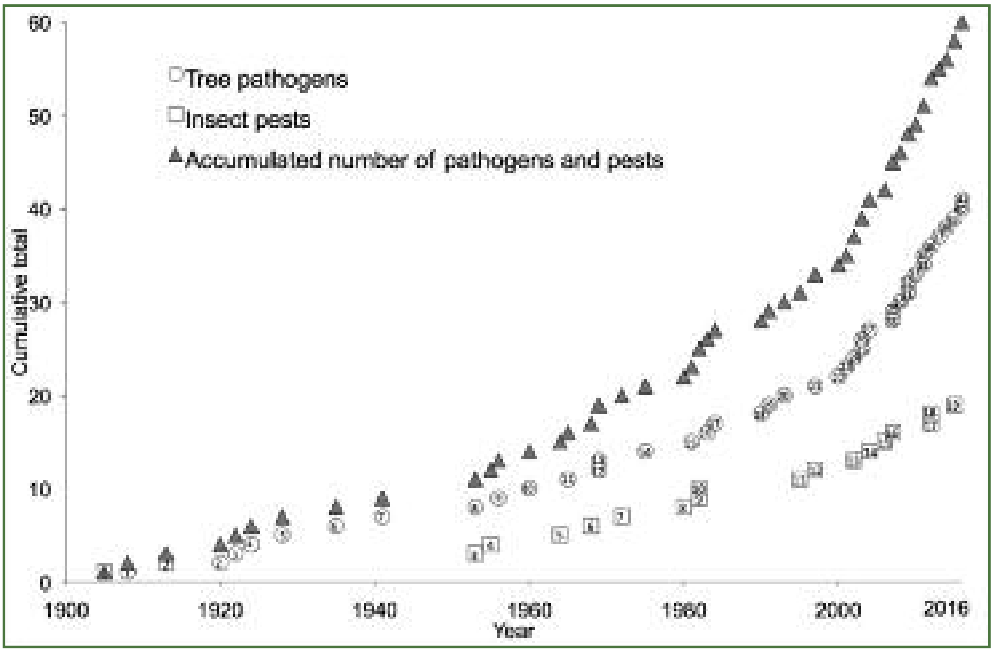
Forest Resilience in British Forests, Woods & Plantations - the ecological components

Jonathan Spencer begins a new four part series on how we can increase resilience, starting with a look at woodland ecology.

Across the UK trees are facing serious challenges from the increasing impact of tree pests and diseases (see Figure 1). The IPCC Fourth Assessment Report (IPCC, 2007) asserts that the global surface temperature is likely to increase by 2.4-6.4° by the end of the 21st century, and in spite of initiatives set in train to limit average global temperature increase a rise of at least 2° seems inevitable. In combination, these expose our native and forest trees to increasing environmental stresses.

These projected global average temperatures have not been experienced since before the onset of the quaternary ice ages. These changes will occur within the economic lifespan of trees established over the next decade and well within their biological lifetimes. This article is the first in a short series of four that explores the important need to establish forest resilience in British woods and forests in the face of environmental change. Later articles will explore the establishment of resilience in recently planted forests dominated by stands of non-native spruce and other conifers outlining the implications for forest planning and management; why tree species diversity, especially those valued for timber production, is so limited in north western Europe and the implications of this in the development of more resilient forests in the future. The final article will explore the implications of forest resilience for policy and practice, and an outline proposal for a forest policy framework for addressing woodland conservation and forest management will be presented, with suggested approaches for ancient woodland, existing forests and to new afforestation.

The four articles are intended to provide an outline rationale that will allow forest managers to increase forest resilience in ways best suited to their location and the character of the woods in their charge.



The cumulative numbers of new tree pathogens and insect pests identified in the UK shown over time since 1900. The total accumulated number of pathogens and pests are also shown. Reproduced with kind permission of Dr Joan Webber, Forest Research, Alice Holt Research Station. (Freer-Smith & Webber, 2015)

The ecological components of forest resilience

Forests have many unique properties, related to their high rates of primary productivity and their high levels of associated biodiversity. Complex interactions between plants and fungi, between trees, shrubs and other plants for light and water, the interdependent development of forest soils, forest composition and forest history, and the extremely efficient mechanisms within forests for securing and circulating nutrients from forest soils, all drive these high levels of productivity and biodiversity. In addition, the processes within forest soils driven by fungi and other micro-organisms, in a rather bewildering array of species and processes, support tree disease resistance and forest resilience (Kimmins, 2004; Moore et al., 2011).

Definitions of resilience

Forest resilience is a term widely used in discussions on forest adaptation to climate change but it is not a widely understood term. Some useful definitions are presented below:

"*Resilience is the capacity of a forest to withstand or absorb external pressures and return, over time, to its pre disturbance state*." (Holling, 1973; Walker and Salt, 2006)

An alternative more dynamic perspective sees resilience as:

"*The capacity of the forest to continue to provide most, or all, of the ecosystem services, even if the composition and structure are permanently altered by disturbances.*"

(CBD Technical Series No.43, 2009)

And very technically:

"*Resilience is an emergent property of ecosystems that is conferred at multiple scales by genes, species, functional groups of species and processes within the system.*"

(Gunderson, 2000; Drever et al., 2006)

Each definition has some value and can be used in different situations. All, however, have an underlying message that resilience is dependent on biodiversity; in the genetic variation of forest trees, tree species diversity or the structural diversity of forest stands, underpinned by forest soil biodiversity below ground and forest biodiversity above ground. All the available scientific evidence strongly supports the conclusion that the capacity of forests to resist or accommodate change, or recover from disturbance, is dependent on biodiversity at multiple scales (CBD Technical Series No.43, 2009).

Some forest types are resilient without being resistant. Pine forests are not resistant to fire and readily burn, but are resilient in that they also readily return over time to their original structure and composition. Indeed, many species in such forests depend on such disturbance for germination and natural regeneration to occur; fire in pine forests is a classic example. These forests are adapted to severe disturbances. By contrast, other forests are resistant to change but lack resilience once significant disruptive change has been wrought. Some ancient woodland tree communities fall into this category.

Measures taken to enhance forest resilience (through enhancing species, age and structural diversity and supporting the development of forest soils) essentially move simplified stands towards conditions found in more natural forests. Measures that promote forest resilience are widely regarded as promoting nature conservation and biodiversity aims alongside a wider array of other ecosystem service benefits (Gamfeldt et al., 2013).

Forest resilience then is the capacity of a forest to absorb or withstand impacts and disturbances, both physical (in the form of weather events, droughts, frosts and floods etc.), and biotic (such as outbreaks of disease or insect outbreaks), and return over time to something like its pre-disturbance state. A 'resilient' forest ecosystem is able to maintain its 'identity' in terms of its taxonomic composition, structure, ecological functions and process rates (CBD Technical Series No.43, 2009).

From a utilitarian perspective forest resilience can also be considered as the capacity of a forest to continue to provide most or all of its current suite of ecosystem goods and services whilst absorbing external impacts and recovering to a condition something like its original pre-disturbance state, where it can continue to deliver the same or similar range and quantity of goods and services (the ecosystem services derived from the natural capital asset, the forest itself).

The components of forest resilience

The resilience of a forest ecosystem is fundamentally determined by its biological and ecological components. These are listed below:

- The diversity of tree species and of other species in the forest ecosystem (including and especially micro-organisms in the soil and forest litter).
- The genetic variation within species.
- The wider regional pool of species and ecosystems from which genetic material can flow.
- …and hence the extent, condition and character of the surrounding landscape.

For forest managers resilience in forests valued for the production of timber and other wood products should rely on:

- Intact functioning forest soils that drive nutrient and water cycling.
- Genetic variation within tree species.
- Tree species diversity within forests or stands.
- Structural diversity within and between stands.

Forest soils

As with vascular plants, fungal diversity develops through time and forests established on non-forest vegetation or newly disturbed soils take time to develop a mature complement of forest fungi and other micro-organisms. Different tree species influence soil formation and create varying conditions for the soil biota that perform key functions of nutrient extraction from underlying rocks. Mixed stands of

Bialowieza Forest, Poland. Mixed mature old growth stands of oak, lime, hornbeam and aspen; wetter hollows and sumps support stands of Norway spruce and alder. Mixed stands can provide for tall and well formed timber trees under a range of silvicultural interventions, including in this instance long established non intervention! (Photo: Jonathan Spencer)

conifers and broadleaves in temperate forests consistently support more diverse and efficient forest soils with regard to nutrient extraction and tree performance (Humphrey et al., 2003).

The role of arbuscular mycorrhizal fungi in resilience

The role of mycorrhizal fungi in the health and performance of trees has long been appreciated (Killham, 1994). Their role in supporting forest resilience is mediated through several important and interacting mechanisms.

Firstly, mycorrhizal fungi grow at higher water potentials than tree roots, potentially supporting plants at times of drought stress. This is coupled with extensive and pervasive hyphal networks giving access to deeper and less accessible ground water than might otherwise be available (Moore et al., 2011).

Secondly, mycorrhizal fungi have several strategies to combat pathogen attack (Moore et al., 2011) by:

- Excreting of anti-fungal and anti-bacterial substances. (80% of *Tricholoma* species produce antibiotics, and *Boletus* and *Clitocybe* are known to produce anti-fungal substances.)
- Stimulating the growth of other soil micro-organisms, which themselves inhibit or limit pathogen growth.
- Stimulating the plant itself to produce antibiotics under the control of the mycorrhizal fungus.
- Providing structural protection of the root and rootlets by their thick fungal sheaths. This mechanical barrier gives effective protection because plant pathogens need access to plant tissue to infect it; they cannot usually infect other fungal tissue.

Arbuscular mycorrhizae have been of proven effectiveness in reducing the effects of pathogenic pests such as root nematodes (Moore et al., 2011, p.407). In part, this may be mediated through the plant's own response to mycorrhizal infections, with a thickening of cell walls or the production of phytoalexins, which may lead to an improvement in resistance to pathogens and soil pests.

Mycorrhizal fungi supply the tree with access to key minerals (phosphates, magnesium, calcium, potassium and other important trace elements), along with nitrogen in the form of nitrates. In exchange, the tree supplies the fungus with products of photosynthesis. When soil nutrients are in plentiful supply the trees reduce investment in their association with fungi, which may lead to issues of pathogen vulnerability when artificial fertilisers are used in forest stands to promote growth.

Ash regeneration, West Woods, near Winchester, Hampshire. Adoption of natural regeneration allows for the extensive reassembly of genetic variation from existing parent genetic material and, provided deer and other herbivores are controlled, overcomes erratic but important events such as insect outbreaks or incidents of drought. (Photo: Jonathan Spencer)

Effects of climate change on forests and forest soils

The effects of climate change on forest soils are unprecedented and unpredictable. Such evidence as there is points to major disruption of established energy and material flows and to a long period of readjustment. Tree species composition, forest productivity, litter decomposition, water availability and nutrient cycling will act together to determine the response of forest soils to climate change (Lukac and Godbold, 2011). Increases in soil temperature will raise the rate of organic matter decomposition and nutrient release through enhanced microbial and chemical activity. Higher rates of water loss can also be expected. Cold climate forests, which typically have large root systems and faster metabolisms to utilise the much shorter period of summer activity, can rapidly increase their activity as a short term reaction to soil warming. Root mortality may increase with an increase in soil temperature. Water stressed roots are also likely to have shorter life spans and higher mortality. Severe hot spells, likely to be accompanied by drought, will impose significant mortality on fine roots and the impact may be felt for much of the subsequent growing period. The adoption of forest management practices that maintain forest shade and avoid exposure of forest soils to sun and drying winds are likely to be effective mitigation measures.

In broadleaved forests the presence of hornbeam, lime, ash and birch litter promotes earthworm activity (Rackham, 1980; Stewart, 2004). In upland forests birch, rowan and aspen similarly enhance earthworm activity and abundance. The activity of earthworms promotes drainage in soils otherwise prone to waterlogging. They also improve tree performance by encouraging deeper rooting and enhanced mycorrhizal activity (which are greatly inhibited by waterlogged anaerobic soils). This may be particularly important in monocultural stands (of beech or oak for example) that have a strong tendency to create mor soils with little or no earthworm activity leading to gleyed poorly aerated soils on heavy clays.

The presence of broadleaved litter also promotes the breakdown of the superficial conifer litter horizon (the needle litter makes for a cold and unaerated layer inhibiting breakdown and incorporation into the soil), improving drainage and reversing gleying. A key role of native broadleaves within such forests will be to restore and maintain forest soils and to re-establish deeper more extensive networks of fungal hyphae connecting forest trees to subsoil and underlying rock. Of note here may be the observation that in native North American forests, the finer root masses of spruces and other conifers are confined to a depth of about 30cm below the surface, while those of broadleaved associates such as aspen can be found up to a metre depth (Startsev et al., 2007).

Corsican pine plantation, Thetford Forest, Norfolk. The reliance on one timber crop species, planted in monocultural stands of even age and spacing, led eventually to their comprehensive demise in the face of Dothistroma needle blight. The forest is now being replaced with varied planted species and associated natural regeneration, established within the forest conditions of the retained heavily thinned Dothistroma stricken stands. (Photo: Jonathan Spencer)

The role of mycorrhizal fungi in carbon sequestration in forest soils

Trees contribute up to 20% of their photosynthate to their mycorrhizal fungi (Moore et al., 2011); a symbiotic trade-off supporting the extensive hyphal network deep into subsoil and bedrock, securing mineralised elements and making them biologically mobile and accessible to trees. These hyphal networks are constantly growing and retracting in their search for essential nutrients and the energy required is supplied by the tree in exchange. A great deal of the carbon supplied is used in creating the stiff glomalin hyphal sheaths of the mycorrhizal fungi (Treseder and Turner, 2007). The longevity of hyphae may be as short as two weeks and rarely extends beyond six months or so, and the glomalin is shed in large quantities as the hyphae extend and contract in search of materials. Designed to protect the fungus from the attacks of other fungal species, the glomalin is highly resistant to decay and as a result, when shed into the soil, remains for considerable periods of time, resisting utilisation by other elements of the soil biota. Its residency time, particularly in the deeper, colder soil horizons reached by broadleaved trees such as aspen, can be very prolonged. It is this long residency time coupled with the high rate of production and shedding of glomalin into the deeper, colder, less biologically active lower horizons that leads to the accumulation of soil carbon in maturing forest soils. The process is greatly enhanced by the presence in quantity of minor broadleaved trees amongst the conifer stands, such as birch, aspen, maples and others.

Tree and forest composition; functional diversity and forest productivity

In establishing tree diversity, and hence forest resilience, there is a need to ensure that within forest stands there are trees that can act in a complementary fashion that sustain function and performance.

For example, by having a small number of shade tolerant species capable of performing below the canopy of emergent timber trees (e.g. hornbeam or lime in temperate oak woods, or western hemlock and red cedar in northern spruce forests), a far higher percentage of the available light is captured throughout the life history of the stand, and nutrients in soils more efficiently captured from throughout the soil column. This can be complemented by a small number of faster growing early successional tree species (such as birch) that rapidly establish forest conditions and exploit the light and space created within well-lit conditions following harvest, windblow or heavy thinning operations. Aspen or alder perform a similar function on wetter soils. Most temperate forests consist of two or more tall emergents (usually timber producing species; a product of their evolved tall structure and competitive apical dominance), alongside a small number of shade tolerant understorey species and two or more early pioneers. This complementarity is reflected in primary production; biomass production in stands with five tree species can be up to 54% higher than stands with only one species (Gamfeldt et al., 2013). Sites monitored in the Forest of Bowland (Lancashire) support this view. Mixed stands of spruce and pine have clearly shown such interactions (Mason and Connolly, 2013) with the enhanced performance of both tree species attributed to mycorrhizal interactions and efficiency of exploiting available nutrients.

Early succession species have a key ecological role in rapidly re-establishing forest conditions following disturbance or forest operations, supporting soil mycorrhizae following felling, leaf fall restoring forest soils, and the provision of shade over exposed soils and drying out otherwise waterlogged prone soils. Rapid regrowth from roots, stumps and suckers of various tree species perform a similar function, rapidly restoring forests conditions, and creating cooler, better aerated soils favoured by mycorrhizal fungi (waterlogging and anaerobic soils following soil compaction or rising water tables seriously hinders soil fungal activity).

Identifying such groups of complementary species and understanding their comparative ecological roles within the forest (and their relevance to sustainable production) is the current challenge. In a project aimed at embedding forest resilience within forest management, Forest Research are pursuing the development of 'forest development types' as templates for natural and 'naturalistic' stands for use across the UK (Jens Haufe, Gary Kerr, Forest Research, pers. comm.).

Tree genetics and variation

Trees are amongst the most genetically diverse of all organisms (Hamrick and Godt, 1990). It is this genetic variation, both within and between natural populations of most tree species, alongside the diversity of micro-organisms in forest soils, that drives both forest productivity and is the foundation of forest resilience.

Because individual trees can live for such considerable lengths of time, and forest stands mature and change over decades to centuries, there is a general perception that trees are at a severe disadvantage in terms of responsiveness to environmental change. However, trees in forest communities are not simply dependent on their generational 'turnover'

Table 1. Forestry species in England. Five species of broadleaves make up 77% of total volume and six species of conifer make up 89% of total volume.
Measure: % representation in England; standing volume (m^3 over bark). (Forestry Commission, 2012)

Broadleaved species	% total standing crop	Conifer species	% total standing crop
Oak	32%	Scots pine	22%
Ash	14%	Sitka spruce	21%
Beech	14%	Larches	15%
Sycamore	11%	Corsican pine	12%
Birch	6%	Norway spruce	10%
Other (total)	23%	Douglas fir	9%
		Other conifers	11%

time to respond adaptively to events. Most trees mature and set seed at an early age (at about 20 years in most species, although in small amounts until later in the life of the tree) and the inherently high levels of genetic diversity that characterise most species, coupled with the ability of many to persist vegetatively for very long periods of time and to produce prodigious numbers of offspring when conditions allow, means that new associations of trees and new combinations of genes can arise over comparatively short periods of time. They are in effect, very responsive to change as populations of trees, and very resistant to change as individuals. They can certainly respond within the timescales of forest management operations and can rapidly recombine extensive existing genetic variation and express it in a very wide range of phenotypes in response to environmental change.

Most gene flow in trees occurs over a few hundred metres, but often with a significant component from outside the wood or forest. Over time gene flow in trees can occur over large distances, particularly for wind pollinated or wind dispersed species. Consequently, gene flow in trees is more than sufficient to prevent loss of diversity through chance in widespread forest trees and there is little clear differentiation between British populations of common species. The majority of our tree species are outcrossing, which maintains high levels of genetic variation.

Most climate scenarios present change in terms of mean changes to parameters, such as temperature or rainfall (Broadmeadow and Ray, 2005), but it is likely to be extreme weather events such as droughts or floods, and the arrival of novel pests and pathogens that present the real challenges and have the biggest impact. The retention of forest level genetic variation will provide adaptiveness over the life cycle of individual trees, and the ability to address a number of eventualities. The adoption of natural regeneration or regrowth will be a key component in the management of resilient forests that allows for both the conservation and the expression of genetic variation in the face of changing circumstances.

Wider forest species diversity

Other species are also critical to forest function and resilience. Species that facilitate pollination (hoverflies, for example), seed dispersal (wild boar, small mammals, jays), nutrient cycling and soil aeration (notably earthworms and moles) all contribute significantly and in concert to the functioning of forest ecosystems and the health of the trees within them. Many insect species, notably wood ants in many northern forests, and parasitic wasps in all forest types, play critical roles in suppressing the impact of tree insect pests. Insect diversity, supported by tree species diversity and structural variation, introduces competitive and interactive pressures on insects regarded as forest pests.

A useful concept is that of ‘functional groups’; assemblages of species that perform similar functional roles within a forest (primary production in trees, pollination by range of insects, decomposition in soils etc.) and hence provide a level of resilience through redundancy. Redundancy describes the diversity of species involved in performing similar tasks, and that perform differently under varying environmental conditions (in soils these conditions might vary throughout the day, the season or between years). Species that appear on casual inspection to have limited roles may come to the fore under changing or extreme conditions, buffering the forest ecosystem from environmental change and disturbance. This 'redundancy' of species generates the ability of a forest to respond swiftly to changing conditions as they occur (Verhayen et al., 2016). This variable response has been termed 'functional response diversity' and is critical to ecosystem resilience (Elmqvist et al., 2003).

The need for forest resilience

Why are the components of resilience of such importance now? For the past century the Forestry Commission and many others have been steadily increasing the area of forest and woodland in England. Forest cover now constitutes some 10% of the country. However, much of this is of very recent origin, with most consisting of first or second generation near monocultural plantations on former open ground. The underlying soils are now fast becoming 'forest' soils, with a rapidly developing forest soil biota and with many of the early problems confronting foresters in establishing trees in challenging open conditions now replaced with problems associated with managing trees in forest conditions; deer and other herbivores, competition from forest vegetation and shade from competing trees.

Conversely, the soils, originally depleted of key nutrients or prone to waterlogging, and made available to forestry as of small value to agriculture, are now far more capable of accruing and retaining plant nutrients than they were at the time of establishment. Paradoxically though, their capacity to support future harvests of trees could be compromised by continuous extraction of forest products that threatens to significantly reduce forest productivity (Kimmins, 2004). Increased risks from novel pests and diseases, and site level stresses from a changing climate, are now adding to those resulting from past timber harvests, nutrient depletion or soil compaction from the use of heavy machinery. We remain dependent on a very small number of tree species for the majority of our forest production, which works against accelerating tree species diversity in UK woodlands (Table 1).

Alongside all these changes there has been a significant shift in the appreciation of what woodlands provide for society; functions beyond simple timber production, most notably in water quality, flood regulation and carbon sequestration, through to cultural meaning, enjoyment and recreation. These valuable goods and services are threatened by environmental change and novel biological threats. The climate that our woods and plantations will mature in will be very different from the more or less steady state conditions assumed by those drafting forest policy throughout the 20th century. Managing forest composition to address climate change is a challenge that will vary considerably from forest to forest and from location to location. However, the underlying biological realities remain much the same.

The adoption of resilience measures in British woods and forests requires a new framework for thinking about forest management; a rationale that accommodates present needs but addresses concerns for continued performance of our forests for the next and subsequent generations. This requires us to think differently about tree species assemblages, forest management practices and the supporting forest ecosystem. These will be examined further in the later articles in this short series.

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