Forestry Commission

Research Note

Encouraging biodiversity at multiple scales in support of resilient woodlands

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Woodland ecosystems are integral to our health, well-being, security and economy, but they face a number of pressures including climate change, land-use intensification, and emerging pests and diseases. This Research Note explores the links between biodiversity, measured at different levels of organisation (genes, species and communities), and the ability of woodland ecosystems to withstand and adapt to changing conditions and disturbance. Using examples drawn from the literature, the Note identifies and discusses a range of biophysical attributes that can positively influence these different elements of woodland biodiversity and therefore enhance ecosystem resilience. These characteristics are considered at a range of spatial scales, from the fine-scale attributes of individual trees and stands, through to features characterising entire woodlands and the environmental condition, composition and configuration of the landscape contexts that they fall within. In acknowledgement of the intrinsic value of biodiverse woodlands, and of the multiple ecosystem services they provide, the Note emphasises the importance of taking action to safeguard biodiversity and to improve woodland resilience at these multiple scales. Some of the implications for forestry management are discussed; actions that can be taken to enhance biodiversity are highlighted according to the spatial scale of implementation and the organisational level of biodiversity affected. The information in this Note has been compiled for use by woodland managers, other practitioners and policy makers, with a focus on British woodlands in all their forms, from production forests to native woodlands.

Introduction

Woodland ecosystems – prized but under threat

Trees and woodlands are valuable, treasured parts of the landscape. They provide essential habitats for a wide range of species, and this biodiversity underpins an array of ecosystem services integral to our health, well-being, security and economy. In addition to storing carbon, supplying timber and regulating the environment, they also offer opportunities for people to interact with nature and to benefit from many non-timber products and services (Quine *et al*., 2011; Sing, Ray and Watts, 2015). However, woodland ecosystems face many pressures including climate change, land-use intensification, urbanisation, emerging tree pests and diseases (e.g. ash dieback), invasive species (e.g. rhododendron and grey squirrel), and browsing damage from expanding deer populations (Fuller and Gill, 2001) (Figure 1).

Many of the current anthropogenic pressures on woodland ecosystems have an historical context; the existing wooded landscape is a legacy of policies and land management practices that have been implemented over time. In the last 120 years there has been a dramatic shift in the cover, composition, spatial configuration and structure of woodlands across the UK, and this has driven changes in woodland communities and affected woodland specialists in particular. Following large-scale clearfelling during periods of war (1914–18 and 1939–45), woodlands were largely planted and managed for their timber potential; there was a focus on non-native conifer plantations, which often comprised single species and age classes, managed on a clearfell and replant rotation (Mason, 2007). Furthermore, many small, privately owned broadleaf woodlands are now largely unmanaged, following a sharp decline in the use of traditional woodland management techniques such as coppicing and wood pasture (Hopkins and Kirby, 2007). This neglect, alongside a narrower set of management regimes and high grazing pressure from expanding deer populations, has resulted in lowland broadleaf woodlands becoming increasingly shady and dense with fairly uniform stand structures, poor understorey cover and reduced areas of open space (Amar *et al*., 2010; Broome *et al*., 2017). In combination with high ecological isolation, this change in woodland structure has contributed to a decline in many woodland bird and specialist ground flora species (Fuller and Gill, 2001; Fuller *et al*., 2007; Hopkins and Kirby, 2007; Quine *et al*., 2007).

Sustainably managed, biodiverse woodlands are resilient woodlands

The biodiversity and resilience of ecosystems are typically interdependent across a range of scales and contexts; more

Figure 1 Examples of the pressure on woodlands resulting from disease, invasive species and herbivores: a) a tree suffering from ash dieback, b) rhododendron clearance, and c) a red deer stag.

biodiverse woodlands are generally better able to resist or adapt to future changes, thereby supporting their long-term ecosystem service provision and the safeguarding of this biodiversity (Thompson *et al*., 2009; Rasche, Fahse and Bugmann, 2013; Isbell *et al*., 2015; Guyot *et al*., 2016; Guerrero Ramírez *et al*., 2017). This synergistic relationship means that measures aimed at enhancing either biodiversity or resilience are generally compatible. Recent advances in environmental policy and forestry have been stimulated by a growing recognition of these links and an acknowledgement of the intrinsic value of biodiversity. For example, diversification is embedded within the UK Forestry Standard (UKFS) guidelines as a cornerstone of sustainable woodland management (Forestry Commission, 2017). However, wider implementation of these guidelines is required on the ground.

It cannot be assumed that the components and levels of biodiversity currently supporting woodland ecosystem functioning will continue to be appropriate and sufficient under future environmental conditions; more ambitious efforts to sustain and, in some circumstances, alter or enhance levels of diversity, may be needed to improve ecosystem resilience in a rapidly changing environment (Oliver *et al*., 2015; Defra, 2018). Efforts to improve the resilience of the UK's woodlands are particularly pertinent because the frequency and intensity of many pressures on woodland ecosystems are expected to continue rising and the interactions between these pressures can magnify their negative effects (Seidl *et al*., 2017; Hansen *et al*., 2018). A more nuanced understanding of the links between biodiversity and resilience is therefore required; identification of drivers operating at different scales should help to fine tune management recommendations and thus improve targeting of their application in order to achieve a more biodiverse, resilient wooded landscape.

Aims

This Research Note discusses the interlinkages between woodland biodiversity and resilience, where woodland biodiversity is understood to encompass the entire ecosystem, including the species that trees support. The discussion focuses on two questions:

- How does biodiversity influence woodland ecosystem resilience?
- What environmental and woodland features influence biodiversity and resilience at different spatial scales?

The first of these questions is addressed by exploring the links between woodland biodiversity and ecosystem resilience at three levels of biological organisation:

1. Genes (adaptive genetic diversity within a species)
2. Species (diversity between species within a community)
3. Communities (diversity between communities within a landscape).

To answer the second question, environmental and woodland characteristics that can influence woodland biodiversity and resilience (Figure 2) are identified at these different spatial scales:

1. Trees
2. Stands
3. Woodlands
4. Landscapes.

The implications for forestry management are briefly discussed and key actions for enhancing woodland biodiversity identified.

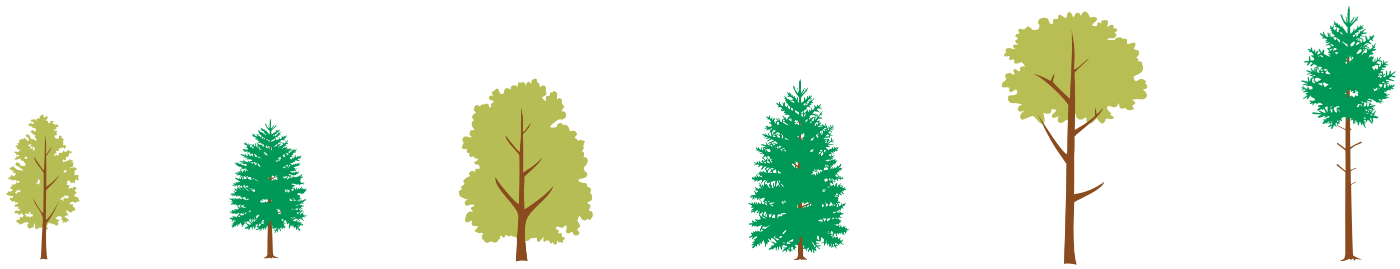
What is meant by biodiversity and resilience?

Biodiversity represents 'all heritability-based variation at all levels of organisation, from the genes within a single local population, to the species composing all or part of a local community, and finally to the communities themselves that compose the living parts of the multifarious ecosystems of the world' (Wilson, 1997, p.1). The biodiversity of a woodland ecosystem is related to properties of the trees and stands they contain and, at a larger spatial scale, the composition and spatial configuration of the surrounding patchwork of woodlands and ecosystems. These are shaped by numerous interlinking drivers operating over a range of temporal scales, including current and historical environmental conditions (e.g. the climate, soils and geology) and land management practices. The implications for forestry management are briefly discussed and key actions for enhancing woodland biodiversity are identified in relation to the spatial scale of implementation and the level of biological organisation targeted.

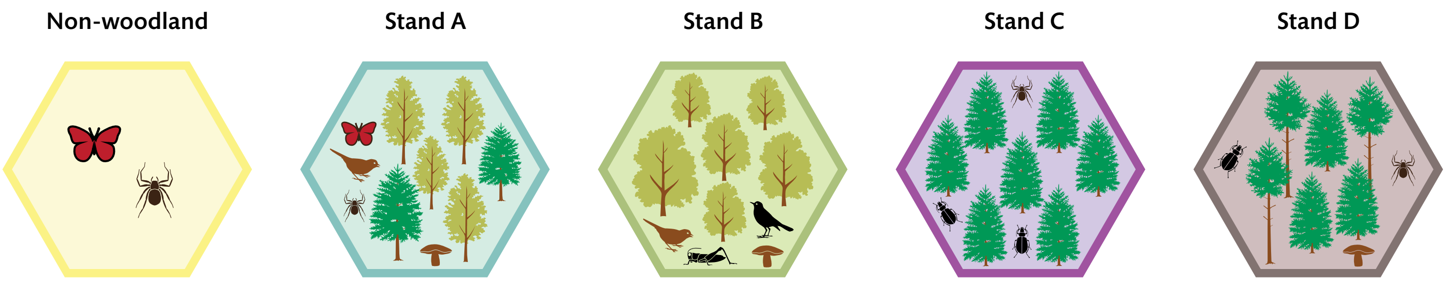
The term resilience has become prevalent in the scientific literature and UK environmental policy in recent years, but the definitions provided are sometimes ambiguous and can vary between authors and scientific disciplines (Fuller and Quine, 2016; Newton, 2016). In this Research Note the ecological resilience of woodland ecosystems refers specifically to their ability to absorb disturbance while maintaining the major habitat-forming species that define their structure, functions and the ecosystem services they underpin (Newton, 2011; O'Leary *et al*., 2017). Resilience incorporates both the woodland ecosystem's ability to resist changes in response to disturbance or, failing this, its capacity to recover functioning via adaptation.

Figure 2 Woodland biodiversity can be managed at multiple spatial scales from the tree to the landscape. The associations of woodland species with trees can be influenced by characteristics at the tree scale, such as tree species, phenotype, genotype, or growth stage. Different combinations of these trees make up woodland stands (symbolised with hexagons). Together these stands form woodlands, each with their own distinct physical characteristics (e.g. shape, size and topography) and associated biodiversity. At the landscape scale, woodlands vary according to the spatial configuration of neighbouring woodlands, along with the composition of the intervening landscape matrix; this landscape context also influences woodland biodiversity. As a general rule, larger, more genetically, structurally and compositionally complex woodlands that are well-connected with other woodlands will have higher levels of biodiversity (e.g. Woodland 1).

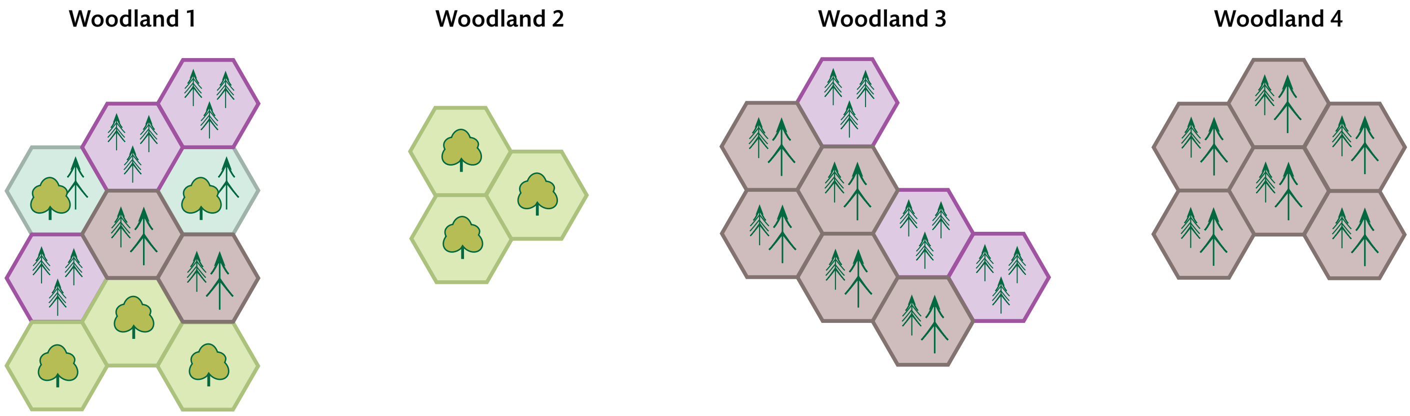
Tree scale Illustration of individual conifer and broadleaf trees. These trees can differ in terms of species, phenotype, genotypes/clone and growth stage.



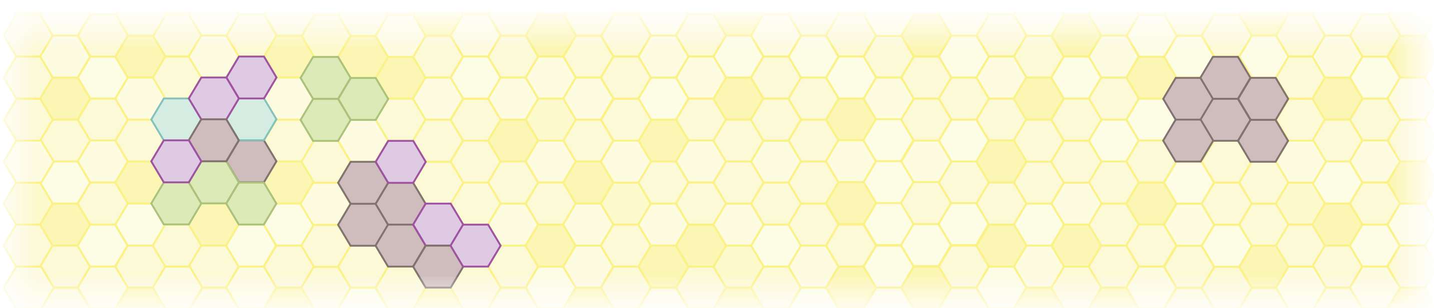
Stand scale Stands composed of different trees and their associated biodiversity.



Woodland scale Multiple stands making up four woodlands.



Landscape scale A mosaic of woodlands in an unforested landscape matrix, showing the arrangement of woodlands 1–4.



How does biodiversity influence woodland ecosystem resilience?

Biodiversity tends to be assessed in terms of the number of species present, as this is often the easiest unit to measure. However, it is important to consider variation at multiple levels of biological organisation, from genes to communities. Here, the links between woodland biodiversity and resilience across these levels are explored.

Adaptive genetic diversity

At the genetic level, biodiversity provides the building blocks for local adaptation. Species with high levels of adaptive genetic diversity have a greater likelihood of containing individuals within their populations with the appropriate genetic make-up to survive and reproduce under altered conditions. This diversity arises from the slow accumulation of mutations, that is, random changes in the sequences of DNA distributed across the entire genome. Genetic diversity in some woodland species can be traced back to times when glaciers and ice sheets covered a large part of the Earth's surface, which restricted their ranges to refugia. During these long glacial periods, species accumulated random mutations and populations from isolated refugia became differentiated.

Natural selection acts to differentiate populations via genetic adaptation by allowing survival of those individuals that are best adapted to the conditions at a particular site. Individuals of a given species also have some capacity to alter their structure or physiology to compensate for changes in their environment. This is termed 'phenotypic plasticity'. If environmental change exceeds the limit of an individual's phenotypic plasticity then that individual will either fail to thrive or die prematurely thus contributing little or nothing to the next generation. Environmental change may not have an equal effect on all species because they differ in their capacity for phenotypic plasticity and/or genetic adaptation. When interacting species do not track changes in climate at a similar rate this can lead to phenological decoupling (Johansson *et al*., 2015). For example, increasing spring temperatures have been shown to increase the peak emergence of caterpillars, but not the timing of egg hatching of the great tit (*Parus major*), whose young feed on the caterpillars (Visser *et al*., 2006). This loss of synchrony, or decoupling between prey and predator, may have severe consequences for the predator's survival.

Genetic diversity can decline in small isolated populations of woodland species through the process of genetic drift, whereby the variations of some genes are lost by random chance. However, this loss may be counteracted by gene flow from populations within neighbouring woodlands. Although most gene flow occurs at a relatively local scale, long distance gene flow events do occasionally occur. These act to homogenise the within-species diversity of individuals in woodlands across large geographic scales. The amount of gene flow between populations depends on several factors including a species' reproductive strategy, the dispersal abilities of its pollen and offspring, and the arrangement of woodlands in the landscape. From the study of certain tree species (e.g. birch and Scots pine), it can be inferred that native species tend to contain high levels of adaptive diversity and are generally efficient in producing large quantities of pollen and seed, which can be distributed across the landscape. For instance, even in a small isolated stand of Scots pine in Spain, where the nearest population of this species was 30 km away, over 4% of the pollen that fertilised the seed came from outside the stand (Robledo-Arnuncio and Gil, 2005). This availability of seed pollinated by distant pollen may increase a population's ability to adapt to threats such as climate change and novel pests and diseases via natural selection and gene flow. These processes will only work if there are regular cycles of flowering, seed production and regeneration that are encouraged by management actions including gap creation, prevention of overgrazing, and control of deer and squirrels.

Species diversity

The UK has at least 50 native tree and shrub species and numerous long-standing non-native species (e.g. sweet chestnut and sycamore). These species differ in many respects including lifecycle, number of associated species, response and vulnerability to environmental stresses (e.g. droughts and pests), ecosystem functions and environmental requirements (e.g. soil and water) (Figure 3). The diversity of characteristics among tree and shrub species can make woodland ecosystems more resilient to environmental change. For instance, higher tree species diversity in mixed stands has been linked to the reduced efficiency of insect herbivore pests locating their preferred host tree(s) (Guyot *et al*., 2016; Jactel *et al*., 2017). The greater availability of feeding resources and microhabitats available for their natural enemies also reduces pest prevalence compared with monocultures (Jäkel and Roth, 2004; Jactel and Brockerhoff, 2007). A similarly significant tree species dilution effect has been found in relation to the spread of important plant pathogens such as *Phytophthora ramorum* (Haas *et al*., 2011), *Armillaria* (Gerlach *et al*., 1997) and *Heterobasidion* (Piri, Korhonen and Sairanen, 1990; Jactel *et al*., 2017).

In many cases it has been shown that it is the diversity in the characteristics of tree and other woodland species that tends to be a better predictor of woodland resilience, rather than simply the number of species (Vehviläinen, Koricheva and Ruohomäki, 2007; Nadrowski, Wirth and Scherer-Lorenzen, 2010; Cadotte,

Figure 3 A stem crack in a Noble fir, illustrating the damage drought can cause to trees. Diverse, mixed-species woodlands are generally better able to maintain ecosystem functioning under extreme conditions because they are more likely to contain trees with traits enabling them to survive.

Carscadden and Mirotchnick, 2011). This diversity may improve resilience by providing a broader spread of response and effect traits. Response traits relate to a species' response to external pressures on the woodland (e.g. drought or competition from invasive species), while effect traits are defined as the processes or services that the species provides (e.g. pollination or erosion control). In diverse woodlands composed of species with contrasting characteristics, response and effect traits are less likely to be the same among different species, potentially improving the resilience of the woodland as a whole. For example, in a diverse, mixed-species woodland, a drought may cause a decline in tree species with similar response traits to drought, with the result of the loss of erosion control services as an important effect trait provided by these species. However, there may be other tree species in the woodland with different, more resilient drought response traits that may survive to provide the same erosion control service. Similarly, it has been observed that orchards visited by both honey bees and wild bees are provided with a more consistent pollination service than those solely visited by the honey bees, which were inactive during periods of high wind (Brittain, Kremen and Klein, 2013). The existence of alternative species that can replace or complement a service or function provided by another species is termed functional redundancy (Laliberté *et al.*, 2010; Pillar *et al.*, 2013). Woodlands dominated by a keystone resource provider, a single species that exerts a significant influence on the composition and functioning of the woodland ecosystem, have limited functional redundancy; if the dominant species is removed then this is likely to trigger a cascade of loss of associated species and functions (Newton, 2011; Evans *et al.*, 2017).

Many, but not all, UK tree species can be categorised into taxonomic families of varying sizes, such as the oak, birch or lime families. Co-occurrence of tree species from the same family in a woodland is a good predictor of potential levels of functional redundancy. For species-rich families (e.g. willows and poplars of the Salicaceae family) there may be significant overlap among component species in terms of their response and effect traits. A high level of trait overlap provides a degree of resilience at the family level within a woodland community, where subtle but important differences in resource requirements between related species could ensure the survival of at least one or other species in a family subjected to environmental change (Karrenburg *et al.*, 2003).

Community diversity

Woodland species interact with each other in many different ways (e.g. pollination, predation and parasitism) and often evolve into distinct and complex woodland communities. These interactions can be based around particular tree species; for example, in the UK there are 955 species of organisms associated with ash trees, of which 11% are restricted or highly dependent on ash (Broome and Mitchell, 2017). Species interactions can also occur in association with particular communities such as wet woodlands, upland birch woodlands, or native pinewoods. The number and complexity of species interactions with particular tree species or woodland communities is expected to be highest among native tree species/woodlands as these relationships have had longer periods of time to evolve. Functional redundancy also plays a role at the community level; diverse woodland communities, with a complex network of interactions, are likely to be more resilient because multiple species may be providing the same service or function, for example, decomposition (Flynn *et al.*, 2009; Pillar *et al.*, 2013).

The UK contains several woodland community types that are of high conservation and cultural value in global terms such as the Atlantic hazelwoods, Atlantic oakwoods and Caledonian pinewoods. Where practicable, these rare and unique habitats should be protected, restored and reconnected using a targeted management approach in an effort to improve the survival of the many species that occupy and depend on them. There is a desire to conserve these iconic communities by attempting to strictly maintain their species assemblages into the future; this needs to be carefully weighed up against the potential gains in resilience to current or likely future environmental pressures from allowing or even facilitating some diversification. Additional approaches are being considered to influence the compositions of tree species with the objective of increasing resilience in other woodland communities. For some native tree species that are undergoing extreme decline, it may be possible to introduce an alternative non-native tree species to provide many of the same functional attributes (e.g. sycamore as a possible replacement for ash; see Mitchell *et al*., 2014). However, this will only be a partial solution because there will still inevitably be a loss of many species-specific associations and functions. Such introductions should be conducted with caution, particularly if based on a non-native tree species which could alter the balance between pathogen/pest and native host species. For example, the planting of exotic pine stands in the UK appears to have facilitated the introduction of two exotic races of *Dothistroma septosporum* into Scotland which now pose a threat to native Caledonian pines (Piotrowska *et al*., 2017).

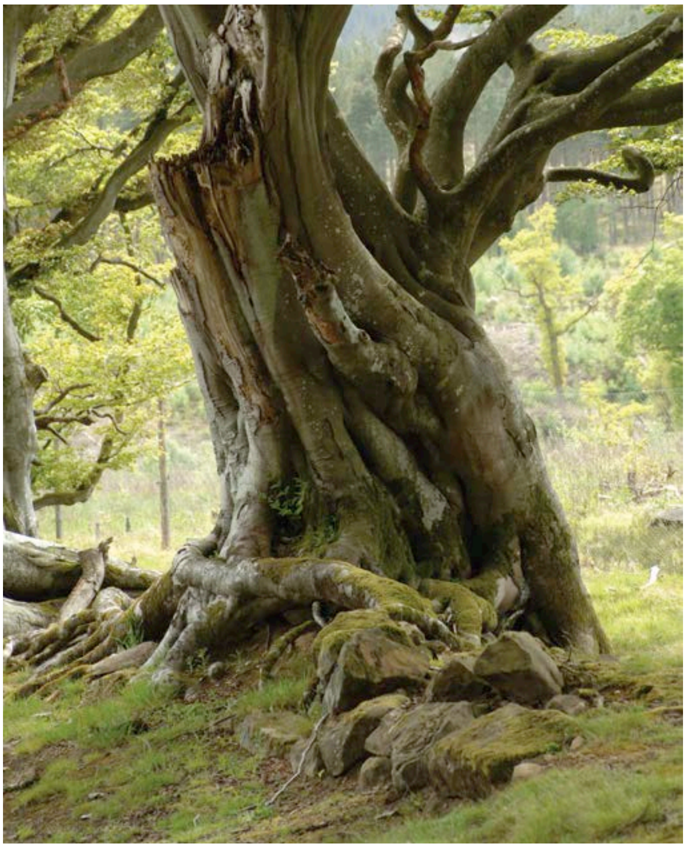
Which environmental and woodland features influence biodiversity and resilience at different spatial scales?

As outlined above, woodland biodiversity and resilience tend to be positively interrelated across multiple levels of organisation. Many of the drivers of biodiversity also positively influence resilience (directly or indirectly), and vice versa. Management efforts aimed at improving either biodiversity or resilience are therefore likely to be synergistic.

Tree- and stand-scale features

Environmental heterogeneity encourages biodiversity, and this diversity can be detected and measured in environmental conditions at the small scale of a stand, or even a single tree. Well-established older trees known as veterans tend to be rich in a diversity of microhabitat types such as water pools in tree crevices, moss-covered branches, or holes in the trunk; these serve as shelter, provide areas for recruitment, and act as sources of food for wildlife (Michel and Winter, 2009) (Figure 4). Protecting veteran trees as important woodland structures that support disproportionately high levels of biodiversity is thus recognised as highly valuable to enhance biodiversity in woodlands (Tews *et al*., 2004). Other similarly important woodland structures include deadwood, in the form of stumps, snags, fallen dead trees and branches. These structures are a key source of nutrients, growing substrate and shelter for a myriad of woodland species; recognition of their importance in woodlands is reflected by numerous guidelines on the recommended volumes of deadwood that should be retained to enhance biodiversity in woodland stands (Humphrey and Bailey, 2012). Another management-related activity that can enhance within- and between-stand environmental heterogeneity and related levels of biodiversity is the creation of open habitat, including rides and glades.

Figure 4 Veteran trees such as the beech pictured here tend to be of high biodiversity value because of the rich variety of microhabitats they provide.



In some cases, environmental heterogeneity is intrinsic to a stand, providing a diversity of conditions in support of enhanced levels of biodiversity regardless of any management intervention. For instance, the presence of wetland habitats (e.g. temporary pools of water, ponds and streams) or rocky habitats (e.g. caves, rocky outcrops, areas of scree and stone walls) generally has a positive influence on levels of woodland biodiversity. Similarly, variations in soil type, geology and topography can contribute to overall levels of heterogeneity within and between stands, thereby supporting higher biodiversity (Burnett *et al*., 1998).

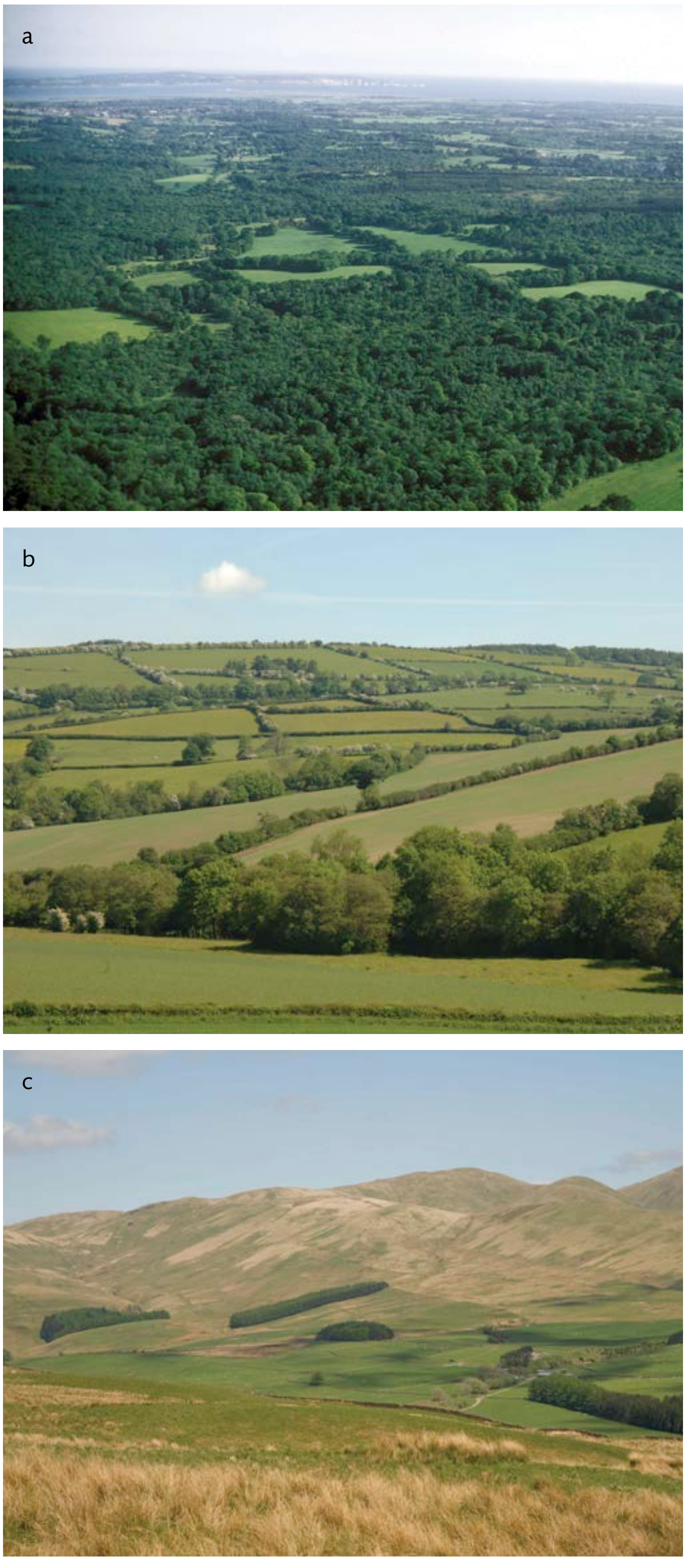
Woodland-scale features

The size of an individual woodland will have a major influence on the biodiversity it contains and therefore its potential resilience through the well-established species-area relationship (Connor and McCoy, 1979). In general terms, larger woodlands have the ability to capture greater environmental heterogeneity, provide more ecological niches, support larger populations, suffer less from genetic drift and experience lower levels of extinctions. The size of some woodlands may be greater than the scale of certain disturbance events such as frosts or the strongest winds within storms, thereby offering greater protection. The impact of woodland area can also be mediated by the shape of the woodland, with more compact shapes (that are closer to a circle, rather than being long and thin or complicated in shape) generally suffering from lower disturbances due to edge effects and adjacent land uses (e.g. intensive agriculture or urbanisation; see Murcia, 1995). Historical factors such as previous land use can also influence the current biodiversity value of a woodland (Hermy and Verheyen, 2007; Watts, Fuentes-Montemayor *et al*., 2016); ancient, semi-natural woodlands tend to support higher species richness and provide habitats for a number of rare, specialist species (Goldberg *et al*., 2007; Peterken, 1993). Environmental heterogeneity within and between woodlands, and in the surrounding landscape, promotes the development of distinct communities. Increases in diversity between woodlands can ensure that the compositions of species within each woodland are all slightly different (this is known as beta diversity) and are therefore more resilient than woodland communities in a more uniform landscape.

Landscape-scale features

At the broadest scale, the species that colonise woodlands are influenced by the landscape within which those woodlands occur. The frequency of successful colonisation events is affected by landscape connectivity, which is dictated by a woodland's proximity to source or founding populations and the permeability of the intervening matrix. Each of the illustrative wooded landscapes shown in Figure 5 will support different woodland communities. In principle, a well-connected, heavily wooded landscape will support higher levels of woodland biodiversity (Figure 5a). Woodlands within this type of landscape are generally more resilient and better able to recover from environmental disturbances than those landscapes containing small, isolated woodland fragments (Figure 5c) (Fischer, Lindenmayer and Manning, 2006; Ziter, Bennett and Gonzalez, 2013; Craven *et al*., 2016; Hansen *et al*., 2018). Hedgerows and trees outside of woodlands can also make an important contribution to landscape connectivity by providing corridors and stepping stones between woodlands that would otherwise be isolated (Figure 5b).

Figure 5 Contrasting wooded landscapes in the UK highlighting variations in woodland cover, spatial configuration, connectivity and landscape type: a) a landscape which contains a large amount of well-connected woodland, b) a landscape which contains small blocks of broadleaved woodland that are connected by hedgerows within an agricultural matrix, c) an upland landscape containing small, isolated patches of coniferous woodland.



Connectivity between woodlands ensures a regular exchange of species and genes between populations occupying areas of the landscape which differ in the conditions they provide. Where species are unable to persist or to adapt locally, this connectivity may allow them to shift their range to more suitable conditions, possibly in response to climate change or other drivers. This exchange may allow the recolonisation of woodlands that have lost particular species, for instance, following a severe disturbance (e.g. a disease or pest outbreak). It also enables some species to operate effectively as metapopulations* across a number of spatially discrete but genetically connected woodlands. The exchange of genes through this flow of individuals, pollen or seeds between connected woodlands is also important in maintaining genetic diversity within species and reducing inbreeding and genetic bottlenecking. Adversely, connectivity may sometimes increase pressures on woodlands and lead to ecosystem disservices when it facilitates the successful establishment and spread of a pest, pathogen or invasive species (e.g. Condeso and Meentemeyer, 2007; Maguire *et al*., 2015). The advantages of enhancing woodland connectivity for woodland species should therefore be weighed up against their possible disadvantages, especially where the potential negative impacts may be severe.

Woodland specialist species tend to be more at risk of genetic drift and local extinctions in response to landscape characteristics compared to the tree component of a woodland ecosystem. This is particularly true for those woodland species with small population sizes, isolated patchy distributions, exacting ecological requirements, low rates of reproduction, and/or poor abilities to disperse. An extreme example of such a species is the twinflower (*Linnaea borealis*), an iconic plant of the Caledonian pinewoods that is currently exhibiting acute genetic effects of the chronic fragmentation of its habitat in the Scottish Highlands (Figure 6). It is self-incompatible and its poor pollen dispersal ability has resulted in a lack of mate availability and consequent poor seed set as it exists mostly as single clone patches, which are separated by distances that exceed those of pollinator movement (Wilberg *et al*., 2016). Another woodland specialist, the wood cricket, survives in large populations within a highly fragmented landscape. However, it is a poor disperser and rarely moves beyond its woodland habitat, which has resulted in high genetic differentiation between isolated populations on the Isle of Wight (Watts, Vanhala, *et al*., 2016). Although these wood crickets are not currently showing signs of inbreeding or genetic bottlenecking, individual populations are vulnerable to extinction as the large number of highly suitable, yet unoccupied woodlands on the island points to a limited recolonisation ability (Brouwers and Newton, 2009).

Figure 6 The twinflower is an example of a woodland specialist species that is highly sensitive to woodland fragmentation at the landscape scale.

Implications for forest management

Although providing a comprehensive set of advised management actions is beyond the scope of this Research Note, the implications for forest management at tree to landscape scales are briefly discussed, based on the links found between biodiversity and resilience at different levels of organisation.

Taking action on the ground

It is not feasible to convert all the evidence synthesised into practical action. For instance, the geology, soils and topography of a site cannot be changed for biodiversity gains. However, by targeting efforts to protect or provide woodlands in an effort to harness the rich tapestry of environmental conditions and habitat types (e.g. rocky outcrops and ponds) provided by the UK's often diverse and topographically complex landscapes, a wide array of genotypes, species and woodland communities can be supported and encouraged. Heterogeneity can also be created within a woodland and shaped by management actions in support of biodiversity and resilience. This can be achieved at the level of individual trees, but also by providing and maintaining key microhabitats and favouring a diversity of species, structures, age classes and silvicultural approaches across woodlands (Figure 7).

* A metapopulation is a set of sub-populations that are dynamically connected through a flow of individuals or genes between them. The regular movement of individuals between discrete woodlands helps to ensure the persistence of the metapopulation as a whole by recolonising locally extinct patches and rescuing small populations from local extinction (Hanski, 1998).

Figure 7 Various woodland management actions can be carried out in support of biodiverse, resilient woodlands, including strategic tree planting to improve woodland connectivity.

Woodlands also have a large capacity to evolve if regular cycles of successful regeneration, providing large numbers of individual young trees on which natural selection can operate, are encouraged through forestry management. Greater use of methods such as continuous cover forestry, using single or group selection approaches, need to be more widely considered if the objective of promoting adaptation to novel conditions, as well as increasing the age structure and species diversity of future woodlands in the UK, is to be achieved.

The objective of maintaining or increasing the adaptive genetic capacity, species diversity and age structure of future woodlands should, however, be tempered by the need to grow appropriately adapted material and to develop suitable silvicultural techniques for the establishment of mixed age and mixed species stands. When aiming to plant material which contains the appropriate type and level of diversity at the gene or species level, the need to grow tree material suited to site conditions must be recognised, and potential changes in climate must also be considered. This is particularly important on sites which present a specific challenge (e.g. sites that experience early or late frosts or sites that are especially wet or dry). If the difference in the phenology of seed source and planting site is too great it can lead to reduced survival, slow growth or poor formation. Growers need to weigh up the potential benefit of planting material from further south as a strategy to preadapt woodlands to climate change against the risk of that material being poorly adapted to current conditions (Barsoum, 2015).

Diversification may not always be appropriate as some trees, stands, woodlands and wooded landscapes support unique woodland communities and rare or restricted species that require conditions which are not compatible with diversification (e.g. Atlantic oakwoods and Caledonian pinewoods support unique species assemblages). The UK is at the northwestern distribution limit of several native tree and woodland species and as such may contain a unique complement of the adaptive genetic diversity present in these species at a European scale; this merits conservation through mechanisms such as the European Forest Genetic Resource network (EUFORGEN; see de Vries *et al*., 2015).

At the landscape scale, despite current land cover and land use constraining changes to woodland cover to some extent, there are nevertheless opportunities to improve woodland biodiversity and resilience; new woodlands can be strategically planted to improve connectivity, habitat restoration and management can provide new habitats and soften the permeability of the landscape matrix, and features such as hedgerows and individual trees can be targeted to provide linkages between woods. For example, reforestation in the Loch Lomond & The Trossachs National Park and conifer expansion in the North York Moors National Park were both found to benefit wood ants by connecting formerly fragmented isolated populations (Vanhala *et al*., 2014; Proctor *et al*., 2015). This reforestation has also enabled wood ants to expand their range into novel plantation forest habitats from previously isolated ancient woodland fragments (Proctor *et al*., 2015).

Table 1 frames the important principles for forestry management according to the spatial scales and levels of biological organisation set out in this Research Note. More comprehensive management advice is given in the UKFS, which advocates measures to reduce pressures on woodland ecosystems such as controlling herbivores and invasive species, and outlines additional steps for protecting and enhancing woodland biodiversity and resilience (Forestry Commission, 2017); further work is required to suggest how more practitioners could be encouraged and better equipped to implement these actions more widely.

Table 1 Key steps to achieving a biodiverse wooded landscape in support of resilience. Actions that can be taken to enhance biodiversity are highlighted according to the spatial scale of implementation and the organisational level of biodiversity affected.

Level of biological organisation influenced	Spatial scale of action			
	Tree	Stand	Woodland	Landscape
Genes	Retain trees to sufficient age to reliably flower and set seed.	Create gaps to encourage young tree regeneration and promote adaptation to changing conditions. Control grazing and invasive species to encourage regeneration. Ensure planting material is appropriately adapted to planting site (i.e. the right tree in the right place).	Maintain and create large woodlands to support greater gene diversity, lower genetic drift and lower extinctions in species that are poor dispersers. Increase diversity between stands in terms of tree phenotypes and genotypes.	Enhance connectivity to promote gene flow between woodlands.
Species	Retain and maintain trees that provide diverse microhabitats (e.g. veteran trees and deadwood); some tree species will have a greater diversity of microhabitats than others.	Establish and maintain trees with a diversity of characteristics including a range of response and effect traits. Create and utilise existing environmental heterogeneity across the stand, including a variety of microhabitats (e.g. ponds).	Maintain and create large woodlands to support greater species diversity and larger populations. Create and maintain existing environmental heterogeneity across the woodland by increasing structural complexity (e.g. mixture of tree age classes) and by promoting a variety of microhabitats (e.g. ponds).	Enhance connectivity to promote recolonisation by woodland-dependent species and the movement of individuals between patches. Maintain semi-natural ancient woodlands that support specialist species. Utilise existing environmental heterogeneity across the landscape.
Communities	Same as species scale.	Where possible, maintain and plant native tree species suited to the site (considering future climates) to support complex networks of interactions.	Increase diversity between stands in terms of tree species and growth stages.	Increase diversity between woodlands across a landscape (beta diversity). Maintain semi-natural ancient woodlands that support complex networks of interactions.

Targeting action

To enhance the success and cost-effectiveness of the various management actions discussed, resources and effort need to be targeted. Knowledge, information and tools are required to inform this targeting and to monitor progress towards national woodland biodiversity objectives and obligations. Landscape ecology indicators and models can aid decision-making by providing valuable, quantitative information under different scenarios (Synes *et al*., 2016). Simple surrogate proxy measures, describing features such as the condition, composition, structure and spatial configuration of stands, woodlands and landscapes, can give a rapid indication of woodland biodiversity and resilience levels (Ferris and Humphrey, 1999). More complex models can be used to better understand and predict a wide range of issues such as the ecological suitability of a site for a tree species (e.g. Ray, 2001), the landscape genetics of a woodland species, or the likelihood of disturbance events. Long-term experiments (e.g. Barsoum, 2015; Watts, Fuentes-Montemayor, *et al*., 2016) are making important contributions to the evidence base; empirical data from large-scale surveys such as the National Forest Inventory are helping to monitor trends and are being used to develop powerful statistical frameworks for increasing our understanding of the context dependency of the drivers of woodland condition and functioning in order to better inform the spatial prioritisation of management actions (e.g. Spake *et al*., Forthcoming).

Conclusions

This Research Note outlines the theoretical basis supporting the assertion that 'Biodiversity is fundamental to resilience. Greater diversity of species, genetic variability and larger and less fragmented forest woodland habitats, better integrated with other habitats, all contribute to this objective' (Defra, 2013, p. 19).

It has been demonstrated that, rather than relying on specific components of woodland ecosystems to explain or predict relationships between biodiversity and ecosystem functioning and resilience, multiscale approaches need to be increasingly considered. Recent evidence reveals that the effects of biodiversity loss on ecosystem functioning become stronger at larger scales of space and time (Isbell *et al*., 2017). While these larger scales are the ones that are most relevant for policy and conservation to counter declines in woodland biodiversity, action should ultimately be taken collectively at the scale of single trees, stands, woodlands and landscapes. A single-scale focus or complete inaction risks further loss of woodland biodiversity, leading to substantial reductions in multiple ecosystem services, including the many intangible, cultural and well-being benefits which biodiverse woodlands provide.

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