Research Report

The role of trees outside woods

in contributing to the ecological connectivity and functioning of landscapes

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Contents

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Summary

- Trees outside woods (TOWs), such as copses, hedgerows, scattered trees and orchards, make important contributions to the connectivity and ecological functioning of rural and urban landscapes, in particular through reducing the impacts of habitat fragmentation. Studies from the UK, taken together with evidence from other countries, suggest the contributions of TOWs within the landscape to be overwhelmingly positive. The nature and extent of their effects differ depending on the species or landscape being considered, and attributes of the TOWs themselves.
- TOWs can facilitate local movements of species as well as longer distance dispersals. For example, in the UK, TOWs, in the form of treelines, riparian woodland, hedgerows and hedgerow trees, are known to be important for the daily movements of several bat species, providing foraging habitat and increasing habitat connectivity between foraging and roosting areas (Frey-Ehrenbold et al., 2013; Murphy et al., 2012; Zeale et al., 2012). Outside the UK, pollen movement studies have revealed that single trees and small woods can have key roles as stepping stones over longer distances between larger patches of wooded habitats (Lander et al., 2010).
- Few studies have quantified the impact of TOWs on persistence of populations in the landscape. However, increased landscape connectivity, such as that achieved through hedgerow networks, has been shown to have positive effects on the maintenance and growth of populations of invertebrates, such as carabid beetles (Benjamin et al., 2008; de la Pena et al., 2003).
- The type and quality of TOWs, and the quality of the landscape matrix within which they are embedded, affects how well they function as connecting structures. For example, hedgerows with more connections have been shown to have more pollinator activity, increased pollen receipt and higher subsequent seed set (Cranmer et al., 2012). Some studies (largely from outside Europe) have shown that the extent to which species use wooded corridors will vary depending on the attractiveness or hostility of the surrounding landscape matrix.
- TOWs may help preserve the genetic integrity of woodlands by maintaining genetic connectivity between woodland patches. Trees outside woods may facilitate gene flow across fragmented landscapes, helping trees to overcome the problems associated with small populations (Breed et al., 2011). Scattered trees are potentially important in helping trees, and the fauna that depend on them, adapt to climate change (Manning et al., 2009).
- It is possible that increasing landscape connectivity may have undesirable consequences for the spread of tree pests and diseases. Studies that have investigated the impacts on habitat connectivity of tree damage or death, and how connectivity affects disease spread, reveal

complex interactions between local and landscape factors (Holdenrieder et al., 2004). In the case of ash dieback, one study by Rosenvald et al. (2015) found that disease progression was greatest in retained trees in dense stands, whereas those trees in open or more isolated conditions tended to be healthiest. It is possible that TOWs may have a greater chance of survival against ash dieback and be important suppliers of seed in the future.

- A variety of types and configurations of woody habitat elements within the landscape is important for biodiversity conservation (Mallinger et al., 2016). The restoration and conservation of TOWs, such as scattered trees and hedgerows that function as corridors and stepping stones, should be implemented alongside the preservation of the larger habitat patches that they connect (Schippers et al., 2009).
- TOWs have different effects depending on the taxonomic group under consideration. For example, Burgio et al. (2015) studied the relative impacts of vegetation and landscape connectivity (length of hedgerow network) on a range of invertebrate groups; each group exhibited different responses to the measured environmental variables.
- The extent to which TOWs facilitate movement of different species/groups varies in complex ways, often depending on their life history traits. Work on moths in the UK has shown that wingspan, wing shape and adult and larval feeding attributes are related to moth mobility, and that the impacts of forest fragmentation differ depending on a species' mobility and its affinity to forest (Slade et al., 2013). As taxa differ widely in their mobility, TOWs need to be implemented across a range of spatial scales to maximize their effectiveness (Merckx et al., 2012).
- From a policy perspective, the evidence strongly suggests that conservation and persistence of biodiversity is likely to be fostered by maintaining and enhancing the quality and quantity of TOWs in the landscape, as well as by preserving and augmenting the larger patches of habitat that they connect. More research is needed on how most effectively to optimise the contribution made by TOWs to their ecological connectivity and functioning in the UK landscape.

Introduction

Trees outside woods (TOWs) bring a range of benefits to the environment, in the UK and elsewhere (Alessandro and Marta, 2012). These benefits have been summarised in an earlier report to the Woodland Trust (Brown and Fisher, 2009) and include their roles in providing wildlife habitat, ecosystem service delivery and ecological connectivity. The aim of this report is to update and expand on the role of TOWs in contributing to the ecological connectivity and functioning of landscapes through a review of recent literature. Much work on this topic has been conducted in other countries, and this is reported in the review where the results provide evidence that is likely to be relevant to the UK situation. The overall objective is to provide an evidence base that will help inform efforts to protect, manage and restore TOWs in the UK landscape.

For the purposes of this review, TOWs include hedges and hedgerow trees, field trees in arable and pasture fields, small copses, orchards and agroforestry systems, open grown parkland and wood-pasture trees, trees along roadsides, trees in towns, gardens and urban parks, scrub, and riverside trees. Some literature from other countries refers to TOFs (Trees outside Forests) and other terms such as scattered trees, paddock trees, live fences and green-veins, remnant forest and veteran trees. A range of terms was used during the literature search for this review, which covered the roles of different types of TOWs in the landscape, as well as the wider impacts of local and landscape-scale processes relevant to the ecology and functioning of TOWs.

Image: Ruth Feber

Trees outside woods in the landscape

Over recent years there has been an increasing wealth of studies investigating the potential for landscape connectivity to help conserve and protect biodiversity. The literature summarised in this review features a range of terms, which are briefly defined here. First, what is meant by 'landscape connectivity'? Precise definitions differ, but, broadly speaking, there are two types of connectivity that are widely referred to in the literature: 'structural connectivity', which describes the physical relationship between landscape elements, and 'functional connectivity', which describes how well genes, propagules, individuals or populations move or are distributed through the landscape. Functional connectivity results from the ways that the ecological characteristics of the organism, such as habitat preference and dispersal ability, interact with the structural characteristics of the landscape. Structural connectivity does not always result in functional connectivity and, usually, the general term 'connectivity' refers to the latter definition (see review by Baguette et al. (2013)). 'Habitat fragmentation' is the process by which habitat loss results in large, continuous habitats being divided into smaller, more isolated remnants. Another term commonly used in the literature is 'corridors'. This has generally come to mean components or elements of the landscape (often, but not necessarily, linear) which facilitate the movement of organisms and processes between areas of intact habitat. Non-linear, small patches of habitat, which have a similar function, are sometimes referred to as 'stepping stones'. Lastly, the landscape in which larger patches of intact habitat, corridors and stepping stones are embedded is often described as the 'matrix'.

The first section in this review gives an overview of evidence for the different roles and functions of TOWs in terms of their contribution to ecological connectivity and functioning. This includes, for example, species movements, gene flow and maintenance of populations, trees as corridors and stepping stones, configuration of TOWs in the landscape and variation in impacts of TOWs on different taxonomic groups. The second section summarises evidence as it relates to different types of TOWs, and their biodiversity and function within the landscape, including hedgerows and hedgerow trees, scattered trees, riparian woodland and urban and roadside trees. The final section draws overall conclusions and suggests some directions for future research.

Contribution of TOWs to connectivity and function in the landscape

Image: Nick Atkinson

Trees connecting woodlands across the landscape

Habitat fragmentation is known to be a major factor in biodiversity declines. Fragmentation, often together with poorer quality of remaining fragments, can reduce availability of resources for wildlife, alter community structure, cause shrinkage and/or genetic isolation of populations and make populations more vulnerable to extinction (see Bailey (2007) and references therein). For example, in the UK, Hinsley et al. (2008) investigated the consequences of habitat fragmentation on breeding success of great tits Parus major and blue tits Cyanistes caeruleus. These are adaptable bird species which breed in habitats ranging from larger "primary" woodlands to more fragmented "secondary" habitats such as parks, gardens and farmland. They showed the birds to have reduced breeding success and higher parental costs in secondary habitats due to fragmentation and gap effects. Important contributions of TOWs in the landscape include facilitating species movements, increasing the connectivity between habitat patches and reducing some of the negative effects of fragmentation.

Facilitating species movements

There is strong evidence from the literature that TOWs have roles in facilitating day-to-day movements of species, such as for foraging or commuting, and some evidence for longer-distance dispersals across the landscape, which may help species' colonisation of new habitat patches. In the UK, Murphy et al. (2012) showed that the foraging activity of brown long-eared bats was positively related to hedgerow presence, especially in late summer and autumn, and that hedgerows provided habitat connectivity for bats moving between woodland patches. Similarly, in southern England, barbastelle bats, which prefer to forage in riparian and broad-leaved woodlands, will preferentially travel along hedgerows and treelines when moving between their foraging and roosting habitats (Zeale et al., 2012). High bat activity levels were observed by Fuentes-Montemayor et al. (2013) in small and isolated woodland fragments, and in sparsely wooded landscapes; they suggest this may reflect more intensive use of woodland in landscapes where this habitat is scarce. In a study in Estonia, bat activity was highest in woodland, followed by treelines (double treelines having higher activity than single treelines) and solitary trees (Kalda et al., 2015). Although single treelines and solitary trees were used less for foraging than woodland, they may have acted as stepping stone habitats and improved the connectivity between the larger habitat patches (Kalda et al., 2015).

Hedgerow trees (open-grown standard trees within hedgerows) are important for facilitating moth movements in farmed landscapes (Merckx et al., 2009; Merckx et al., 2010b). The presence of hedgerow trees significantly increased the abundance and species-richness of moths and, perhaps most interestingly, this positive effect of hedgerow trees was greatest when they were situated in more "joined-up" landscapes – landscapes with a higher uptake of agri-environment scheme options, such as hedgerow management, and which were considered to have higher habitat connectivity. The reasons for the beneficial effects of hedgerow trees on moth numbers and diversity included provision of food resources and structural diversity as well as a more sheltered microclimate. Merckx et al. (2009) suggested that hedgerow trees may act as 'stepping stones' for some species and could be important in adaptation to climate change, as they may provide more opportunity for movements through open agricultural landscapes. A landscape-scale, mark-release-recapture study of moths by Slade et al. (2013) also found that solitary trees and small forest fragments functioned as stepping stones for moths, especially when they were more connected within the landscape, through being located in hedgerows or in a more hospitable landscape. To sustain populations of species with high forest affinities, though, the forest fragments needed to be larger than five hectares and to have interior forest more than 100m from the edge. Moths are a diverse and species-rich group and an important food source for bats and birds, for whom the benefits of hedgerow trees have also been demonstrated (eg. Linton et al., 2015).

Further afield, translocation experiments in tropical habitats have highlighted the importance of trees outside forests in facilitating movements of birds. For example, Gillies and St Clair (2010) translocated 60 individuals of two species of birds with differing forest dependency in a highly fragmented, tropical dry forest landscape and followed their return movements. Both species used treelines, stepping stone habitats and riparian corridors to differing extents and used these habitats more than pasture.

Corridors, connectivity and stepping stones

TOWs as hedgerows and other linear landscape features can function as habitat corridors between larger expanses of semi-natural habitat. Gilbert-Norton et al. (2010)'s meta-analysis of nearly 80 studies concluded that habitat corridors were able to promote movement and dispersal between habitat patches. Sixty experiments showed positive effect sizes, suggesting corridors increased movement between habitat patches, and 18 experiments showed negative effect sizes. Overall, the positive effect of corridors on movement was highly significant. Although most of the studies were conducted over the short term, corridors generally increased migration between habitat patches by 50%. The importance of TOWs in increasing landscape connectivity, for example, by acting as corridors or stepping stones, is supported by the results from a UK study by Frey-Ehrenbold et al. (2013), who developed a connectivity index for rural trees and hedgerows, and modelled bat activity in both rural and urban landscapes. They identified a positive association between connectivity and activity patterns for three bat guilds, with shorter-range echo-locating bats being particularly sensitive to habitat fragmentation. Their study demonstrated the value of both linear and patchy habitat elements as foraging habitats and stepping stones for bats, and highlighted the importance of restoring a diversity of structural wooded elements across the landscape for bat conservation. While the presence of even a single tree to a highly connected hedgerow or forest was potentially of benefit to bats, the best connected elements were most valuable, particularly for some of the most threatened species. In urban areas too, a connectivity measure used by Hale et al. (2015) found a significant positive effect of connected urban tree cover on bat activity.

Image: Durham Hedgerow Partnership/Hedgelink

Hedgerow re-establishment

The extent of habitat connectedness has been shown to influence other taxonomic groups, such as bumblebees and beetles, in a variety of ways. In the UK, Cranmer et al. (2012) found that when there were more connections between habitat patches, there was increased pollinator (bumblebee) activity, increased pollen receipt and higher subsequent seed set. Pterostichus melanarius is a carabid beetle often used as an indicator of habitat change. When Benjamin et al. (2008) modelled its population dynamics, they found that population growth increased significantly with increasing landscape connectivity. For forest carabid beetles in France, de la Pena et al. (2003) showed that populations were maintained where hedgerow networks were dense and connected, with good quality vegetation, while in landscapes with lower hedgerow quality and increased habitat disturbance there were fewer forest species. Other work has demonstrated positive impacts on birds of "live fences" (or hedges) through increasing the connectivity of a landscape where large forest tracts had been lost (Pulido-Santacruz and Renjifo, 2011). In Spain, a study of mongoose and genet home ranges showed that they regularly used hedgerows for movement, with individuals making up a continuous population. The results suggested that well-distributed hedgerow networks could help prevent fragmentation of their populations in agricultural areas (Pereira and Rodriguez, 2010).

Landscape-scale attributes (such as area of woodland patches and distance to other patches) may also influence the ability of some woodland bird species to withstand weather-mediated population declines (Newson et al., 2014). In northern Spain, Saura et al. (2014) modelled the expanding range of the black woodpecker and their results suggested that increasing the size or quality of the source habitat patch, or the population of a species in that patch, would not be sufficient compensation for a lack of stepping stones to other habitats, with the caveat that stepping stones did need to be of sufficient size and quality to be of conservation value. Further afield, Perez-Hernandez et al. (2015) showed that stepping stone habitats were even more important than corridors for promoting functional connectivity for the lingue, a tree endemic to southern Chile and Argentina, whose seeds are bird-dispersed, and which does not readily grow in corridor habitats. Thus the quality, size and degree of isolation of habitat patches are all important factors when thinking about ecological networks (Humphrey et al., 2015) and the effectiveness of corridors and patches for promoting connectivity and dispersal is landscape and species specific.

Species dispersal

In fragmented landscapes, TOWs in the form of hedgerows have been shown to facilitate the dispersal of plants, such as forest plant species on farmland (Roy and de Blois, 2008). In Germany, Wehling and Diekmann (2009) found that hedgerows had over three-quarters of the plant species (including some endangered species) that were in adjacent forests, with species richness declining with distance from the forest-hedgerow transition zone (reduced recruitment and poor persistence of forest species in hedgerows may hamper migration along hedgerow corridors (Schmucki and de Blois, 2009)). A positive relationship between the richness of some non-animal-dispersed species and the connectedness of hedgerows to forest patches was found by Oliveira et al. (2015), highlighting the importance of hedgerows for biodiversity conservation in fragmented landscapes, where spillover of forest species may help retain connectivity between populations of species which cannot readily disperse through the agricultural matrix.

This process, by which populations from woodland or forest fragments spill over into other areas, may help retain connectivity between populations of species which cannot readily disperse through the agricultural matrix. Gray et al. (2016) tested whether riparian forest fragments were sources of dung beetles within oil palm plantations in Malaysia: dung beetle species richness, abundance and diversity declined with distance from the riparian fragments, suggesting that contiguous habitat corridors were important for maintaining connectivity of invertebrate populations. Hedges and tree islands contribute to forest bird conservation and tree biodiversity by facilitating the spillover of forest birds and the functions they perform, including tree seed dispersal (Muñoz et al., 2013).

Riparian forests can act as important corridors through unsuitable habitats for dispersal of forest dependent species. Many of the studies on ecological processes in riparian corridors have been conducted in tropical habitats, but the results are relevant to other situations. In fragmented tropical landscapes, riparian corridors provide critical habitat and connectivity for common seed-dispersing forest understory birds (Sekercioglu et al., 2015). Remnant forest patches in rural landscapes may be important for maintaining viable populations of forest species, especially when these remnant habitats maintain connectivity through riparian vegetation strips. In the rural landscape of the Chilean Lake District, Smith-Ramirez et al. (2010) showed that narrow riparian forest strips, in a highly inter-connected mosaic of remnant forest patches, may be as important as large patches and continuous forests for sustaining viable populations of a threatened, arboreal, marsupial.

While fostering habitat connectivity is likely to yield benefits for populations, there is a paucity of evidence on the extent to which connectivity affects species' long-term population persistence in the landscape (see Davies and Pullin (2007) for a review of hedgerows as corridors). Despite a lack of evidence, it is possible that restoration/management of TOWs could potentially have a role in tackling extinction debt (the time lag before local extinction of species following habitat loss or degradation (Kuussaari et al., 2009)).

Gene flow and adaptation

Image: Nick Atkinson

In-field trees provide 'stepping stones' to allow wildlife to travel across the landscape

The importance of landscape connectivity for maintaining genetic diversity has been highlighted in reviews by Pautasso (2009) and Sork and Smouse (2006). Breed et al. (2011) consider that trees outside forests, in the form of scattered trees, may facilitate gene flow across fragmented landscapes, assisting the trees to overcome genetic problems associated with small populations. They recommend that conservation and restoration of scattered trees should be undertaken to increase their population sizes and to connect them with genetically diverse fragments. At the same time, though, scattered trees should be avoided as sources of seed for re-vegetation, as they may produce genetically poorer stock. Their conclusions fit with those of Manning et al. (2009), who conclude that scattered trees are potentially important in helping adaptation to climate change of the trees themselves, and their dependant fauna, in human-dominated landscapes. Increasing the long-term resilience of trees in the face of challenges from climate change and tree pests and diseases is a concept that has gained prominence in recent years (eg. Cavers and Cottrell, 2015); models to predict the abilities of species to migrate need to account for dynamic processes, such as dispersal, mortality and reproduction, as well as landscape characteristics, such as extent of habitat connectivity. Renton et al. (2012) showed, using modelling, that even if the landscape is fully intact, only just over a third of all simulated species groups had a good chance of successfully tracking climate change, but that corridors which linked habitat fragments increased species persistence rates by up to 24%. However, the lowest persistence rates were found for trees.

Several research projects have revealed the importance of single trees and small woodland sites acting as stepping stones for long-distance pollen dispersal. In a study focusing on an endangered tree species in a fragmented landscape in Central Chile, pollen was shown to move, sometimes large distances, from small patches and single trees into larger woodland patches, as well as the other way round (Lander et al., 2010). Ripperger et al. (2015) radio-tracked a frugivorous bat species that is a valuable seed disperser in degraded ecosystems in Costa Rica. Day roosts and the main foraging areas of radio-tracked bats were within mature forest fragments, but wider-ranging bats also travelled from natural to degraded forest sites in order to forage, traversing the matrix over distances of up to 300m. The bats were functionally connecting fragmented areas by dispersing seeds between natural and degraded sites, highlighting the need for conservation of natural habitat patches within agricultural landscapes.

For other species, habitat corridors have been shown to function more effectively in terms of facilitating gene flow when they are continuous, with few or no gaps. In the US, populations of a forest-dependent species, the black-capped chickadee, were genetically structured as a result of natural breaks in continuous habitat at small spatial scales, with gene flow being restricted by breaks in cover (Adams and Burg, 2015). When Cushman et al. (2014) evaluated the effects of river network connectivity and climatic gradients on gene flow of a riparian tree species, they concluded that ongoing fragmentation of riparian habitats would lead to a loss of landscape-level genetic connectivity, leading to increased inbreeding and a concomitant loss of genetic diversity, with knock-on effects for wider biodiversity.

Spread of pests and diseases

The evidence for the contribution of TOWs to landscape connectivity and functioning is strongly positive. Nonetheless it is possible that increasing landscape connectivity may potentially have undesirable consequences for the spread of tree pests and diseases, as well as pests and diseases that attack crops (Avelino et al., 2012) and non-native or invasive species (Bonnington et al., 2014). This topic is considered in detail by Holdenrieder et al. (2004) who consider evidence for the effects of landscape fragmentation on pathogen spread and whether the value of connectivity for biodiversity can be outweighed by its potentially negative pathological effects. They review studies that have looked at the impacts on habitat connectivity of tree damage or death and how connectivity affects disease spread, revealing complex interactions between local and landscape factors. For example, both landscape-scale configuration and local composition of host habitat were related to the severity of sudden oak death, an emerging and destructive forest disease caused by Phytophthora ramorum, with greatest disease severity found within contiguous woodlands (Condeso and Meentemeyer, 2007). Ellis et al. (2010) found that connectivity was important in determining the spatial pattern of sudden oak death, but relatively less so than environmental variables, such as canopy cover and relative humidity.

The fate of ash (Fraxinus excelsior) in Europe is of major concern due to the spread of a fungal pathogen (Chalara fraxinea), first observed to kill trees in Poland in the 1990s (Boyd et al., 2013). Ash trees (mapped in Britain by Maskell et al. (2013)) are known to support 953 species: 12 birds, 28 mammals, 58 bryophytes, 68 fungi, 239 invertebrates and 548 lichens. Forty-four species are obligate: 11 fungi, 29 invertebrates and four lichens, and 62 are 'highly associated' species (Mitchell et al., 2014). Ash trees are a particularly important species on farmland, for example, as scattered standard trees, and trees within hedgerows. In the UK, local spread of Chalara is likely to be by wind and, over longer distances, spread is most likely to be through the movement of diseased ash plants. One study by Rosenvald et al. (2015) found that, within felled woodland plots, disease progression was greatest in retained trees in dense stands, whereas those trees in open or more isolated conditions, such as those on the edge of the plots, tended to be healthiest. It is possible therefore that TOWs may have a greater chance of survival against ash dieback and be important suppliers of seed in the future.

Quality of landscape matrix

A number of studies (largely from outside Europe) have shown that how well wooded corridors function in terms of species movements and dispersal is also affected by the quality of the matrix in which they are embedded. The matrix can help mitigate the effects of isolation and habitat loss: Zapponi et al. (2014) studied the effect of habitat patches and attributes of the matrix on bird communities in a fragmented landscape of central Italy. The distribution of bird assemblages was strongly influenced by tree diameter and configuration of the matrix, whereas parameters describing patch composition and structure had relatively minor effects. Vergara (2011) showed, using modelling, that the effectiveness of corridors for movement is a matrix-dependent process, because the extent to which species use them will vary depending on the attractiveness or hostility of the surrounding landscape. In line with these findings, Lander et al. (2011) used paternity analysis of seeds and data modelling to analyse the pollen flow through the matrix. They demonstrated that pollinators may be waylaid in resource-rich areas between habitat patches, which thus hinder, rather than promote, movements. Uezu et al. (2008) assessed the influence of agroforest woodlots on bird distribution and diversity in the Atlantic Forest region (South East Brazil), testing how birds used different types of connection elements (eg. large/small patches, riparian corridors), and whether this was influenced by the distance to large forest patches. Generalist and open-area species were frequently recorded in the agroforest system or other connection elements, whereas only a few forest species were present in these elements. For the latter species, the distance of woodlots to large patches was an important determinant of their richness and abundance. In line with Vergara (2011) and Lander et al. (2011), they suggested that there is an optimal relationship between the permeability of the matrix and the efficiency of stepping stones, which occurs at intermediate degrees of matrix resistance, and which is dependent on the species under consideration. However, there are considerable challenges in disentangling the relative influences of habitat loss, fragmentation and connectivity on species distributions (Mortelliti et al., 2010).

Amount, quality and configuration of TOWs in the landscape

In Britain, non-cropped habitats on farmland are primarily made up of trees, hedgerows and grassy margins (O'Connell et al., 2015) and their amount, quality and spatial configuration can affect their functioning within the landscape. In the UK, Boughey et al. (2011) showed that linear woody features of all types were associated with an increase in common pipistrelle bat P. pipistrellus incidence, but incidence of soprano pipistrelle P. pygmaeus depended on tree density within the hedge and the distance to woodland. Only linear features containing trees were associated with increases in soprano pipistrelle. Studies suggest that a range of configurations of linear, small wooded elements and larger patches of woodland is important. Tattersall et al. (2002) compared small mammal communities in non-linear and linear habitats. They found no evidence that specialist species avoided linear habitats. Indeed, the field boundary was the most species-rich habitat surveyed, and bank voles were more abundant in linear hedgerow than in non-linear woodland.

In regions where woodland is not a dominant habitat type, its presence within the landscape may increase landscape diversity and provide complementary floral resources, supporting a more diverse wild bee community. Mallinger et al. (2016) showed that different habitat types within diverse landscape mosaics, particularly those that provided early-season (orchards and woodlands) and late-season (grassland) flowers, together resulted in overall greater resource diversity and temporal continuity for bees. Schippers et al. (2009) investigated whether mixtures of large, small and linear habitat elements were better for population performance than landscapes that comprised only large elements, and concluded that a mixture of habitat elements were best, because small linear elements increase habitat connectivity and facilitate dispersal, while larger habitat patches secure populations over the long term due to reducing extinction risk.

Woodland patch configuration (shape and size) is a strong determinant of moth abundance in non-urban landscapes (Merckx et al., 2012; Slade et al., 2013), and isolated trees, hedgerow trees and small woodland patches all function as 'stepping stones' for macromoths (Slade et al., 2013). The debate over land-sharing and land-sparing is relevant here: Benayas and Bullock (2012) suggest "woodland islets" as an intermediate approach between land abandonment and farmland afforestation, for ecological restoration in extensive agricultural landscapes. Grashof-Bokdam and van Langevelde (2005)'s review highlights the difficulties in quantifying the relative impacts of spatial structure (amount and spatial configuration) and management intensity of "green veining" networks (non-cropped linear features such as field margins, ditch banks and hedgerows, and patches such as woodlots) on biodiversity. Modelling can be a useful approach for understanding how potential trade-offs between agriculture and woodland might impact on landscape connectivity (Gimona et al., 2012) and how best to mitigate the impacts. Horst and Gimona (2005) developed a GIS-based method to map the potential biodiversity benefits of new woodlands in Scotland. They found that the creation of small woodlands on the (marginal) edges of agricultural areas would provide greater biodiversity benefits than the creation of similar woodlands in the middle of areas of arable land: the more isolated the new farm woodlands, the more difficult it would be for species to colonise them and sustain viable populations, while the more marginal lands were better connected to existing habitats. Tools such as GIS can be effective for informing ecosystem restoration designs and for modelling possible future outcomes (Welsch et al., 2014).

Variation in impacts of TOWs on biodiversity

TOWs influence species in different ways and at different spatial scales, such that woody habitat restoration aimed at benefitting one taxonomic or functional group will not inevitably benefit others. For example, Burgio et al. (2015) looked at the influence of vegetation and landscape structural connectivity on a range of groups: butterflies, carabid beetles, syrphids and sawflies in farmland in northern Italy. They found that carabids showed the most positive response to landscape connectivity, but each group exhibited different responses to the environmental factors under consideration (eg. floristic richness, vegetation pattern and landscape connectivity). In their meta-analysis, Gilbert-Norton et al. (2010) found that there was no difference in the amount of movement through corridors for invertebrates, non-avian vertebrates and plants, but all three taxa showed more movement through corridors than birds. Pocock et al. (2012) looked at multiple ecological networks in an agroecosystem and modelled how the networks interacted. They concluded that management targeted to benefit one animal group did not result in multiple benefits for many different groups.

Jamoneau et al. (2011) quantified relative importance of direct and indirect effects of local, landscape and historical processes in explaining observed species composition in local plant communities. The importance of each factor varied with species group: forest herbs were more responsive to patch age and landscape connectivity than other species, whereas non-forest and woody species were more influenced by agricultural intensity. Even within just one taxonomic group, spiders, Herrmann et al. (2010) showed different responses to fragmentation: spider species associated with the meadow habitat within Swiss apple orchards were affected by local plant diversity, but not by fragmentation of orchards, while those spider species associated with tree canopies responded both positively and negatively to isolation from other woody habitats, depending on their ecological requirements. Thus the picture that emerges from the literature is a complex one, with TOWs influencing species in different ways and at different spatial scales.

An important aspect of understanding the contribution of TOWs to landscape connectivity and functioning, and their differing effects on species of taxonomic groups, is a consideration of species mobility and dispersal behaviour (Baguette and Dyck, 2007). For example, large, low mobility, forest carabid beetles were less abundant in intensively farmed landscapes with poor networks of permanent habitat elements (Aviron et al., 2005). Small-scale habitat restoration may be particularly helpful for pollinator species more vulnerable to habitat degradation (Kremen and M'Gonigle, 2015). They found that as hedgerows matured, they had a greater positive effect on species that were more specialized in their floral and nesting requirements, and which were smaller and less mobile. Fuentes-Montemayor et al. (2013) demonstrated that the responses of bats to the surrounding landscape depended on their mobility. For relatively low mobility species (eg. soprano pipistrelle), the local woodland characteristics were more important than the landscape context, whereas the opposite was observed for higher mobility species (eg. common pipistrelle). Slade et al. (2013)'s citizen science study found that wingspan, wing shape, adult feeding and larval feeding guild predicted macro-moth mobility, although the predictive power of wingspan and wing shape depended on the species' affinity to the forest. Mobile forest specialists were most affected by forest fragmentation as, despite their high intrinsic dispersal capability, these species were confined mostly to the largest of the forest patches due to their strong affinity for the forest habitat, and were also heavily dependent on forest connectivity in order to cross the agricultural matrix.

Within an intensive agricultural landscape, Merckx et al. (2010b) investigated the relative effects of hedgerow trees on moths. Numbers of shrub/tree-feeding individuals were higher at sites with hedgerow trees, as were less mobile species. The authors suggest that hedgerow trees increased adult moth numbers because they provided shelter in typically exposed agricultural landscapes. The presence of hedgerow trees can also benefit some rare or endangered moth species on farmland (Merckx et al., 2010a). A wide range of other taxa feed on macro-moths and may also benefit from these features, but, as taxa differ widely in their mobility, measures mitigating biodiversity loss may need to be implemented across a range of spatial scales to maximize their effectiveness (Merckx et al., 2012). New modelling techniques are proving valuable in providing new insights into the understanding of dispersal behaviour, by providing information on how inter-patch movement of organisms and potential connectivity between habitat patches can be estimated (Bergerot et al., 2012). A multi-function, multi-taxon approach is most appropriate when considering indicator species, to ensure a range of responses is being included to adequately represent the system under study (Gerlach et al., 2013).

Image: Guy Riddoch

Buff arches *Habrosyne pyritoides*

Contribution of different types of TOWs in the landscape

Hedgerows and hedgerow trees

Image: Ruth Feber

A mature hedgerow tree

Hedgerows are vital providers of shelter, food (eg. nectar provision; Baude et al., 2016) and breeding habitat (eg. nesting habitat and song-posts; Siriwardena et al., 2012) for many wider countryside species. The importance of hedgerows in supporting biodiversity in the landscape is affected by their species composition and structure as well as the surrounding landscape. Walker et al. (2005) measured bird occurrence on green lanes (farmland tracks with unsealed surfaces, bordered on each side by hedgerows) and paired single hedgerows in Cheshire, UK. While green lanes had higher abundance and species richness of birds than single hedgerows, bird abundance on single hedgerows increased with the number of trees and amount of hawthorn in the hedge.

Hedgerow height and volume had a positive influence on numbers of great tits (Redhead et al., 2013), and more structurally heterogeneous hedgerows had higher numbers of common and lesser whitethroats (Szymański and Antczak, 2013). The total amount of hedgerow habitat available (hedgerow width, height and length) was also a positive indicator of total small mammal biomass in Gelling et al.'s (2007) study of 180 English farm hedgerows. Species that are mainly associated with a non-woodland habitat, for example grassland butterflies, may also benefit from conservation management that maintains hedgerows and treelines (Kati et al., 2012).

As summarised earlier, TOWs in the form of hedgerows have an important role in facilitating species movements across the landscape. In the UK this is particularly well documented for bats, several species of which use hedgerows for foraging and as commuting routes between roosting and foraging sites (Boughey et al., 2011; Frey-Ehrenbold et al., 2013; Murphy et al., 2012; Zeale et al., 2012). As well as structure and species composition, the extent of connectivity of hedgerows affects their function within the landscape. For example, Gelling et al. (2007) found that hedgerow connectivity was a positive predictor of wood mouse Apodemus sylvaticus abundance, and hedgerow gappiness was a negative predictor of bank voles Clethrionomys glareolus (although this contrasts with Michel et al., (2007)'s study in Brittany, where local habitat features , such as the width of hedges and tree species richness, were more important for explaining small mammal communities than land cover and connectivity). Effects may be related to the wider impacts of agricultural intensification; nonetheless, hedgerows should be managed to reduce gappiness, leading to better continuity and quality of habitat (Staley et al., 2013). Populations of forest carabid beetles in France were maintained where hedgerow networks were dense and connected, with good quality vegetation, while in landscapes with lower hedgerow quality and increased habitat disturbance there were fewer forest species (de la Pena et al., 2003). Using a combination of light-trapping and mark-release-recapture studies, Merckx et al. (2009, 2010b) demonstrated the importance of hedgerow trees for moths, which may act as 'stepping stones' across the landscape.

Other less obvious, but potentially important, roles of hedgerows have been shown by Dulaurent et al. (2012) and Thiel et al. (2015). Dulaurent et al. (2012) found hedgerows to reduce infestation of pine stands by pine processionary moths in France: the presence of a non-host broad-leaved hedgerow in front of the edge of the pine stand resulting in lower pine processionary moth infestation, reducing the risk of defoliation in the crown of mature host trees. In Thiel et al. (2015)'s study, the diversity of hedgerow shrubs and trees was significantly correlated with soil carbon, suggesting that planting more biodiverse hedgerows may have a positive effect on their greenhouse gas mitigation potential on farmland.

Scattered trees

Mature or veteran TOWs support a rich and diverse flora and fauna and are considered to be keystone structures (Hall and Bunce, 2011). Attributes of veteran trees that are important for supporting biodiversity include hollow or split trunks (Muller et al., 2014), partially dead canopies, rot holes and dead wood (Hall and Bunce, 2011). Tree species in Chillingham Park in North East England differed with respect to their veteran attributes, with alder and ash having the most attributes (Hall and Bunce, 2011). Furthermore, lone trees or trees in linear features had more veteran attributes than trees in groups, most likely because of higher exposure to weather elements, such as wind. Openness surrounding veteran trees has been shown to affect the abundance of some endangered species that depend on open-grown veteran trees, such as the great capricorn beetle Cerambyx longicorn (Albert et al., 2012). Saproxylic (dead-wood dependent) beetles are a species-rich and functionally important group associated with forests and scattered trees outside forests, such as parks (eg. Jonsell, 2011); they are sensitive to trunk diameter and exposure to the sun, and also to the extent of tree isolation (Buse et al., 2015). Saproxylic beetle communities were affected by patch quality and small-scale patch connectivity, with increased connectivity between oak trees having a positive effect on predatory beetle abundance, but a negative effect on abundance and species richness of wood-feeding beetles (Buse et al., 2015). Moreover, threatened species were more abundant with decreasing connectivity. Plausible explanations could include different microclimates on isolated trees or differences in their connectivity.

Image: Jim Smith-Wright

Veteran wild pear

Sun exposure was also a significant predictor for the occurrence of exit holes of the marbled jewel beetle on aspen (Astrom et al., 2013), for which clear-cuts and aspen standing along roads can offer favourable conditions. Horak and Rebl (2013) showed that solitary trees in sun-exposed habitats were preferred to shaded trees in closed canopies by a range of groups, including click beetles, emphasizing the importance of maintaining spatial and temporal continuity of sun-exposed veteran trees. Paltto et al. (2011) found species richness of red-listed lichens on ancient oaks in secondary woodland to be half of that compared with oaks growing in open conditions, perhaps because the lichens were adapted to desiccating conditions making them more competitive, or because the open, windy conditions enhanced their colonisation rate. Keeping a balance between mature trees and open habitat requires active management (Kirby, 2015).

Even in heavily fragmented landscapes, isolated individual trees can enhance biodiversity. Higher mite species abundance and richness were found under isolated trees compared to treeless open wet heath in the Scottish uplands (Brooker et al., 2008). Studies in tropical and Australian agricultural systems have shown that isolated remnant trees provide many ecological functions important to birds, including landscape connectivity for woodland species (Fischer et al., 2010). An individual tree's ecological influence could be considered to be disproportionate to its actual physical footprint; DeMars et al. (2010) showed that bird species richness generally decreased with increasing tree cover, and the number of species using individual trees increased with increasing tree isolation, suggesting that an isolated tree can become a 'habitat magnet' for tree-dependent species in the landscape. Similarly, for birds and bats in an Australian landscape, the marginal value of individual trees was highest when trees occurred at low densities (Fischer et al., 2010). Although specialist species were found only in large areas of dense tree cover, scattered trees had moderate levels of bird and bat activity when they were in cleared landscape areas. A SLOSS (single large or several small) analysis revealed a complex pattern in which, in some situations, several small and medium trees supported similar numbers and species richness of individuals as a single large tree, but in others, many small or medium trees had fewer species than large trees (Le Roux et al., 2015). As is the case for other TOWs, an important potential function of scattered trees is that they could help adaption to climate change (Manning et al., 2009) by facilitating movement of species through intensively managed landscapes.

Scattered trees in agricultural landscapes and open woodlands are declining due to intensive land use (Gibbons et al., 2008; Miklin and Cizek, 2014). Historical maps of scattered trees and orchards in southern Germany reveal major losses in scattered trees, mainly due to urbanization, agricultural intensification and land abandonment (Plieninger, 2012). Scattered trees are often perceived by farmers as having negative impacts on agricultural production; however, Rivest et al. (2013) found that, across four tree functional groups, mature scattered trees did not lower pasture yield. In fact, Rossetti et al. (2015) modelled the effects of isolated trees on soil properties, plant and soil fauna assemblages and found topsoil C to be 50% higher under the tree canopy in comparison with the areas beyond the tree canopy. Plant diversity was lower under the tree canopy, but enhanced the total species richness of the grassland, and collembolan diversity was higher under the tree canopy.

Orchards

Image: Judith Parry

TOWs in the form of traditional orchards can provide important habitat for a range of species, including invertebrates dependent on dead wood, such as saproxylic beetles (Horak, 2014). The benefits obtained are affected by their size and connectivity within the landscape. In Switzerland, Bailey et al. (2010) studied a range of taxonomic groups in traditional apple orchards, finding, overall, that the extent of isolation of habitat was more important than amount of habitat. High habitat connectivity benefited wood-preferring birds, spiders and beetles, with the strongest and more consistent responses for birds. The type of landscape surrounding an orchard, and the amount of woody elements within that landscape, may also affect an orchard's biodiversity. For example, Saunders (2016) showed that unmanaged vegetation (grassland and woodland) within orchards was important for wild pollinators in simple landscapes (characterised by monoculture almond plantations), but not in complex landscapes (which had a heterogeneous mosaic of crops, semi-natural grassland and natural woodland). In Italy, local species richness of wild bees in intensive apple orchards was greater when the surrounding landscape was dominated by forest compared to grassland (Marini et al., 2012). Wild pollinators which frequent orchards tend to be found in those areas that are close to semi-natural habitat, including woody habitats such as flowering hedgerows, which may help provide resources when the orchard trees are not in flower (Klein et al., 2012; Marini et al., 2012). Diversification with native trees can increase landscape connectivity (Gonzalez-Valdivia et al., 2014).

Riparian trees

Riverside, or riparian, trees have a range of benefits, and the loss of riparian woodland to other land uses, such as pasture, can have impacts on a number of community structure and ecosystem functioning attributes of streams (eg. Hladyz et al., 2011b). Riparian trees provide habitat for biodiversity through their structure, for example, providing shelter, food resources and nesting sites (Harper et al., 1999), and riparian corridors are particularly important for bats (eg. Zeale et al., 2012). Riparian shade has a moderating influence on stream and river temperatures (Hannah et al., 2008; Malcolm et al., 2008), with benefits for heat-sensitive fish such as brown trout (Broadmeadow et al., 2011). Riparian woodland improves water quality, as measured by numbers of pollution-sensitive invertebrates, and, depending on the area, can have a greater effect than organic farming (Poole et al., 2013).

Impacts of riparian woodland or forest vary with width and tree type. In eastern England, UK, river width was the most significant factor explaining bird distributions, followed by presence of floodbanks, riparian tree cover and amount of thick marginal vegetation (Mason et al., 2006). Also in the UK, Thomas et al. (2016) found macroinvertebrate biomass in deciduous woodland streams to be around twice that in moorland streams, and lowest of all in streams draining non-native conifer woodland. In their study, the effects of riparian buffers of 15–60m width were insufficient to mimic the effects of more extensive riparian woodlands. Wahl et al. (2013) showed that patchy forested riparian corridors may not be sufficient to restore stream condition in intensively managed, degraded catchments. In the tropics, Valle et al. (2013) assessed the connectivity between forest patches, the influence of protected areas and riparian width on stream ecological condition, using the macroinvertebrate fauna as bio-indicators, in a river basin in Brazil. They observed a continuous decrease in a range of sensitive biotic indicators from the upstream protected area to highly deforested sites and recommended that widening and lengthening the riparian zones would increase the connectivity of macroinvertebrate populations between fragmented patches of vegetation.

Image: Michael Cooper Photography

Riverside trees

Riparian zones can be an important component of the mosaic of urban habitats. In Sheffield, UK, species richness of several taxonomic groups varied markedly in relation to distance from the urban core, and trends differed both between taxonomic groups and between rivers (Dallimer et al., 2012); river corridors were shown to be important elements in the urban mosaic, although they did not disproportionately support tree and Natural Surface Cover when compared to non-riverine urban areas. The authors suggest complex patterns of environmental variation associated with cities. Threlfall et al. (2012) examined the response of insectivorous bat species to urbanization. Their study suggested that bats would benefit from the conservation of suburban bushland remnants and riparian habitats, especially if connectivity to these areas, via the maintenance of tree cover across the matrix, could be improved.

Riparian invasive species, for example Rhododendron ponticum, can have significant impacts on ecosystem processes in streams (Hladyz et al., 2011a) through poor quality litter and densely shaded canopy suppressing decomposition rates and algal production, and the availability of resources to consumer assemblages. Riparian connectivity can also be affected by the presence of non-native tree species. For example, in a study in South East Australia, riparian transects through native vegetation had more birds, bird species and foraging guilds than transects dominated by non-native willow Salix rubens or cleared transects (Holland-Clift et al., 2011). Habitat complexity increased from cleared to willow-invaded to native riparian transects, as did abundance of native and woodland-dependent birds. Native shrub and tree species had more foliage and branch-associated arthropods than did willows. The authors concluded that willow invasion in the native riparian zone, through decreasing food resources and altering habitat, was likely to reduce native bird biodiversity and disrupt riparian connectivity.

Urban and roadside trees

Image: WTML David Rodway

Roadside trees deliver a range of ecosystem services

Urban trees support rich and biodiverse communities, deliver a range of ecosystem services and are often the most prominent green features within cityscapes (Weber et al., 2014). Trees are found in a variety of urban environments. In Greater Manchester, for example, surface area mapping found tree cover to be highest in woodlands (70%), followed by formal open space (28%), remnant countryside (28%), low density residential (26%) and cemeteries and crematoria (25%) (Gill et al., 2008). Town centres had only 5% tree cover. Urban trees are diverse: of 6560 urban trees added to the Tree Register, nearly 3000 records were classified as of 'nationwide interest' for size, rarity or historic importance (Johnson, 2005). Across the UK, gardens contain 28.7 million trees (54% of gardens containing one or more trees taller than 3m), which is just under a quarter of all trees occurring outside woodlands (Davies et al., 2009), a potentially rich resource for biodiversity and connectivity in the urban landscape. Urban parks are among the most species rich urban green spaces (Nielsen et al., 2014) and large trees, often considered keystone structures in rural landscapes, may be particularly important as habitat, as well as stepping stone structures. In urban parks in Canberra, Australia, large native trees had a consistent and positive relationship with five measures of bird diversity, the effect increasing as trees became larger (Stagoll et al., 2012).

Non-native, or exotic, trees are common in urban environments, with consequences for biodiversity. For example, the proportion of native trees at roundabout and parkland sites in Bracknell, UK, was positively related to the abundance of both Hemiptera and Paridae (insect-feeding birds)(Helden et al., 2012). A study of trees on golf courses in Ireland found that native Irish species, such as Quercus, Salix and Betula, supported more than 200 insect species, while Fraxinus, Sorbus and Taxus support between 10 and 69 (Hunter et al., 2010). Urban environments often combine complex habitat mosaics with an abundance of non-native tree species, presenting challenges for species that need to find and benefit from isolated patches of native trees; blue tits, for example, may forage significantly more in native than non-native deciduous trees during incubation and when feeding fledglings (Mackenzie et al., 2014).

Trees can provide important connectivity between isolated pockets of fragmented habitats within the urban landscape (Morgenroth et al., 2016; Nowak et al., 2013). Hale et al. (2012) surveyed bats around urban ponds in the West Midlands, UK, and modelled bat presence and activity using land-cover and land-use data around each pond. They found that the presence of tree networks appeared to mitigate the negative effects of urbanization for bats and suggest that protecting and establishing tree networks may improve the resilience of some bat populations to urban densification. Dimming of lighting and reducing gaps in tree cover could also help bats in urban environments (Hale et al., 2015).

Preserving connectivity along corridors and other ribbons of natural vegetation, and minimizing gaps in vegetation throughout the urban landscape can make it more permeable for wildlife. Tremblay and St Clair (2011) conducted a series of translocation experiments within the urban landscape of Calgary, Canada, focusing on two bird species with contrasting ecologies – an adaptable urban resident and an urban-sensitive migrant. Birds were caught in riparian habitats and translocated either within the riparian corridor of origin or across the urban matrix. The presence of gaps in forest cover explained more variation in return time than the amount of forest cover for both species. Multiple gaps, in particular, resulted in significantly longer return times compared with continuous forest.

Increasing urban density has led to a loss of urban greenspace in many cities, particularly a loss of tree cover (Pauleit et al., 2005), with potential consequences for both the local quality of habitat and the extent of connectivity between habitats. Both factors are important for urban wildlife and may have differing influences compared to rural environments. For example, gardens in more urbanized locations were associated with lower moth species richness and abundance, where deleterious effects of habitat fragmentation, poor habitat quality and light pollution may be more severe than in rural areas (Bates et al., 2014). Species richness and diversity of moths in urban woodlands were found to be more affected by local site characteristics than the surrounding landscape (Lintott et al., 2014). Quality of habitat patches within urban environments may be particularly important for invertebrates such as butterflies and carabid beetles, while modelling and empirical data suggest that mammals such as dormice and water voles are particularly dependent on the connectivity of linear habitats (Angold et al., 2006).

Within both urban and more rural environments, some generalist species may be able to use roadsides for dispersal (Coffin, 2007). In Europe, E. ferrugineus, an endangered click beetle, often inhabits avenues of mature trees planted along roads; such avenues increase the connectivity between habitat patches, and may reduce the risk of local extinctions of the species (Oleksa et al., 2015). There is evidence for some positive effects of roadside vegetation on birds, particularly woody vegetation such as trees and shrubs, which can provide foraging and nesting habitat and possibly act as ecological corridors (Morelli et al., 2014). Roadside hedges can connect separated populations of mammals such as hazel dormouse, and roadside copses might be stepping stone habitats for individuals establishing new populations (Encarnacao and Becker, 2015). In fragmented agricultural landscapes, large perch trees play a role in the dispersal of vertebrate-dispersed seeds to nearby roadside environments (Coulson et al., 2014). De Torre et al. (2015) assessed the potential role of plantings on roadside embankments to attract frugivorous birds and to enhance wider seed dispersal; however, only seeds of the planted species were dispersed, perhaps because of the scarcity of seed-dispersing birds in the surrounding agricultural landscape. Other authors recommend refraining from planting fruit-bearing vegetation that attracts birds alongside roads to reduce vehicle-induced bird mortality (Kociolek et al., 2011). The challenge for management of roadside vegetation is to better quantify and understand its role and manage roadsides to enhance their positive impacts and reduce their negative effects (Milton et al., 2015).

Conclusions

The evidence from this review, drawn from studies within and outside the UK, shows strongly that trees outside woods (TOWs), such as small woodland patches, hedgerows and ribbons of riparian woodland, scattered rural and urban trees, make positive contributions to the ecological connectivity and functioning of landscapes. They provide a range of resources for wildlife including foraging habitat, shelter and breeding habitat, and may act as corridors or stepping stones for facilitating species' movements through the landscape. However, the picture that emerges is a complex one, and more research is needed in the UK as to how their benefits can be optimised, for example, in relation to their type (eg. species), patch size, configuration and location (eg. situation of small woodlands and connectivity to hedgerows) within the landscape.

The effects of TOWs vary depending on a range of factors such as species life-history traits and the quality of the wider landscape. For example, the importance of TOWs to a species depends on the ecological attributes of the species, such as its mobility or whether it is a habitat specialist or generalist. Species also require connectivity at different scales. For example, more mobile species, such as bats and birds, may need habitat patches to be connected at much larger landscape scales, while carabid beetles may be more sensitive to hedgerow connections at the scale of several fields. Understanding the factors that contribute to landscape connectivity for species, populations or communities, and disentangling the mechanisms underlying the observed effects of TOWs (eg. the relative effects of provision of resources, shelter or connectivity to other habitats), requires further research.

The contribution of TOWs to landscape functioning is also dependent on their quality and the context in which they are situated. For example, species or age of a single tree, size of a small area of woodland, or gappiness of a hedgerow will all influence their function within the landscape. The effect of distance between patches of habitat in a landscape assumes different importance depending on how hostile that landscape is. The relative importance of increasing the size and quality of protected areas versus the importance of conserving and enhancing landscape connectivity for species conservation is much debated (eg. Doerr et al., 2011; Hodgson et al., 2011), but in practice, approaches which consider all these aspects will be needed to protect populations of species and increase their resilience, especially in the face of a changing climate.

The overall findings from this review suggest that, to conserve biodiversity, priority should be given to increasing and strengthening habitat diversity within landscapes. Measures to manage and conserve different types of TOWs, from scattered trees to woodland patches and connecting hedgerows, alongside protecting larger habitat areas, will help achieve this. More research is needed on how most effectively to optimise the contribution made by TOWs to ecological connectivity and functioning in the UK landscape.

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