How Can Research Help Deliver A
‘Coherent & Resilient Ecological Network’?

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Summary

Lawton et al. (2010) reviewed the status of England's ecological network and concluded that we require 'More, bigger, better, and joined'. Here we comment on some of the key research questions emerging from this review, questions that will be crucial towards delivering a 'coherent and resilience' ecological network. The Lawton Review focused specifically on England, yet the principles and conclusions contained within it are relevant to many cultural landscapes where human impacts have greatly reduced or degraded habitats of value for wildlife. We highlight some key areas for future research below.

1. We must be careful in defining the terminology associated with ecological networks, such as habitat quality and connectivity, and account for scale in our definitions. Resource- and trait-based frameworks for defining these terms in reference of a particular species are needed, and such frameworks could help land managers target management at the correct scales for a range of biodiversity.

2. Improved understanding of the relative contributions of habitat extent, habitat quality and habitat connectivity to population persistence is needed. Much conservation research at landscape scales has emphasised the spatial aspects of habitat i.e. patch size, patch dispersion and linkages between patches. However, habitat quality has a crucial function, being closely linked with the provision of critical resources determining whether species can colonise and establish source populations. Habitat quality is a species-specific attribute, implying that some degree of habitat heterogeneity is required to maintain diverse species assemblages. More attention should be given to the definition, measurement and scales of measurement of habitat heterogeneity in different contexts.

3. When considering connectivity (landscape vs. functional) it is important to appreciate the importance of other factors (e.g. availability of food, predation risk, population pressure) in influencing animal movements. Research into functional connectivity needs to adopt better experimental approaches in order to separate the effects of landscape permeability from these other factors affecting movement. Translocation, play-back and food provisioning experiments could all be used to quantify the ease and costs of movement.

4. More basic research at smaller scales (e.g. field / natural experiments, behavioural studies) is required in order to develop a fine-scale understanding of how individuals interact with the landscape and how these interactions are affected by environmental change.

5. Agri-environment management is a key tool for delivering a ‘coherent and resilient’ ecological network, yet few studies have looked at the effectiveness of management in softening the matrix and effectively increasing connectivity. There is a need for finer-scale experimental studies to determine the most effective way to deploy management options within a landscape for these purposes.

6. We need to move beyond agri-environment management into other habitat types, e.g. woodland, heathland, wet grassland and interfaces/gradients. There is a serious knowledge deficit for many taxa as to what constitutes high quality within many of these habitat types.

7. The intersection of climate change, increasing land-use intensity and development pressures will put extreme pressure on England’s protected areas. However, predicting the combined effects of these changes is difficult due to the many possible scenarios that might emerge. Consequently, it will be informative to identify simple trait-based methods for classifying species that will be at risk under different scenarios.

8. Predicting the effects of climate change on communities and individual species is difficult. More use should be made of studies across altitudinal or longitudinal gradients (i.e. substituting space for time) to look at how gradual changes in climate conditions affect biodiversity.

9. Managing for habitat heterogeneity should be an important element of conservation strategies that aim to buffer biodiversity against the uncertain effects of changing climate.
Research can help to inform these strategies about the nature and scale of heterogeneity that is required.

10. There is a tendency to generalise ecological findings from regional (or global but thinly sampled) analyses. However, local conditions (e.g. evolutionary history, landscape history, competition and more) need to be considered before assuming that results are transferable. It is important to develop an understanding of the most important processes driving population changes in response to environmental change as this knowledge can help assess transferability of results between regions.

11. More intensive demographic monitoring would be valuable (e.g. measures of productivity and survival) in habitats exposed to human-modification and climate change in order to detect ecological traps, extinction debts and other subtle but important drivers of population decline. This is important in order to reduce the likelihood of management having unintended negative consequences.

12. We require flexible long-term monitoring of habitat creation schemes that are cost-effective, make best use of existing monitoring data where appropriate, and meet the information needs for conservation management. Within sites, the data must be gathered in a consistent or sufficiently-standardized way to ensure that trends and patterns are based on comparable data over any defined time period, ideally within an adaptive management framework. The sooner data collection starts the better, establishing baseline information for as many sites as possible before habitat restoration or creation commences.
1. INTRODUCTION

Biodiversity is under increasing pressure across the world. The human population is predicted to reach 8.9 billion by 2050 (Cohen 2003), placing an ever increasing demand on land and resources. Furthermore, the mean global surface air temperature is expected to increase by between 2 and 4°C by mid-century (Meehl et al. 2007), with potentially catastrophic effects for biodiversity. Thomas et al. (2004) predicted that under a mid-range climate-warming scenario (1.8-2°C), 15-37% of species will be threatened with extinction by 2050.

Given these alarming predictions for the fate of global biodiversity there has been significant debate regarding the best approach to preserving biodiversity and stemming the loss of species (e.g. Stuart et al. 2010, Knight et al. 2010, Godfrey 2011). The traditional approach of protecting biodiversity within nature reserves is still central to conservation, with more than 12% of the Earth’s land area under some protected area designation (Jenkins & Joppa 2009) and the global area of land protected increasing annually by c. 2.5% (Butchart et al. 2010). Despite some notable successes (Soares-Filho et al. 2011, Singh & Gibson 2011), the protected areas approach alone is now acknowledged to be insufficient to prevent broad biodiversity losses (Mora & Sale 2011, Sohdi et al. 2011).

Thus, conservation strategies increasingly must focus on conservation in the wider environment in order to meet the spatial and resource requirements of the full range of biodiversity and to increase the conservation value of protected areas themselves (Sutherland et al. 2006). However, conservation approaches are not geographically uniform and the balance between the allocation of resources to conservation within protected areas versus the wider environment will differ, based largely on the extent of remaining ‘natural’ habitat (e.g. Green et al. 2005). The focus on landscape/habitat restoration, of which ecological networks are an integral part, is perhaps especially relevant in landscapes and regions such as Western Europe with very long histories of human impact, where most natural vegetation has long since disappeared. For example, England’s biodiversity has been affected severely by the pressures associated with population growth, agricultural intensification, changes in land management practices (e.g. grazing systems, woodland management), increased pollution (e.g. eutrophication, acidification), increased water abstraction and more (Robinson & Sutherland 2002, Fuller & Ausden 2008). Added to these, the signs that climate change is affecting biodiversity are already present, with many species showing range shifts that track patterns of warming (e.g. Hickling et al. 2006).

The National Ecosystem Assessment found that the broader services provided by the United Kingdom’s (UK) natural resources have enormous social and economic value, however, 30% of these ecosystem services are in decline (NEA 2011). The UK has commitments, both globally (COP10 – Nagoya) and within the European Union (EU Biodiversity Strategy), to protect natural resources and biodiversity. England’s biodiversity strategy ‘Biodiversity 2020’ (Defra 2011) builds on the output from several government commissioned reviews, including the National Ecosystem Assessment, to set a path for ensuring that England’s biodiversity and natural resources are protected into the future. Central to the Biodiversity 2020 Strategy is the ‘Making Space for Nature’ report (Lawton et al. 2010), commissioned September 2009 and colloquially known as the ‘Lawton Review’. It addressed the pressing question:

‘Do England’s wildlife sites comprise a coherent and resilient ecological network?’ and ‘If not, what needs to be done?’

Here ‘wildlife site’ refers to all sites managed for nature conservation, whether receiving full protection or not, and includes, for example, SSSIs, Local Wildlife Sites, National Parks and NGO-managed reserves (e.g. RSPB, Wildlife Trusts). An ecological network is defined as ‘...a network of core sites connected by buffer zones, wildlife corridors and smaller but still wildlife-rich sites that are important in their own right and can also act as ‘stepping stones’...’ (Lawton et al. 2010 (p. 14). The
resilience and coherence of the ecological network was assessed against the following criteria (paraphrased from p. 54):

1. The network supports the full range of England’s biodiversity.
2. The network and its component sites will be of adequate size.
3. The network sites will receive long-term protection and management.
4. Sufficient ecological connections will exist between sites.
5. Sites will be valued by, and be accessible to people.

The review concludes that whilst the existing wildlife sites substantially meet the requirement of supporting the full range of biodiversity (point 1) there are ‘serious short-comings in the network’ for each of the remaining criteria. Most notably the review comments that the existing wildlife sites are generally too small, insufficiently protected and are poorly connected. To address the shortcomings of the ecological network, the review highlights five options, including (paraphrased from p. 57):

1. Improving the quality of current sites.
2. Increasing the size of current sites.
3. Enhancing the connections between sites.
4. Creating new sites.
5. Reducing the pressures on wildlife by improving the wider environment.

The Lawton review summarises the solution as, ‘more, bigger, better and joined’, but stresses that priority should be given, where possible, to habitats that have suffered the greatest degradation and loss (p. 62). Although the Lawton Review was conducted in an English context, the broad conclusions and options will have wide relevance to landscapes that have been heavily modified by humans.

Given these conclusions, it is appropriate to ask what further research is required in order to improve the performance of wildlife sites, transforming them into a coherent ecological network and increasing their capacity to protect biodiversity in a changing environment. Fundamental research is crucial to guiding effective conservation management; without understanding ecosystems we cannot hope to preserve our biodiversity into an increasingly uncertain future. Ecosystems are complex, involving the interactions of multiple species and abiotic variables, and consequently, predicting the responses of an ecosystem to future environmental change with any certainty is problematic. However, primary research into components of ecosystem function, demographic trends or behavioural responses of species can provide insights into potential effects of environmental change, and have been used successfully to guide conservation management decisions (e.g. West et al. 2003, Newton 2004, Goulson et al. 2011).

The idea of creating ecological networks developed from island biogeography (MacArthur & Wilson 1967) and meta-population theory, which showed the potential negative effects of increasing habitat fragmentation (i.e. reduced patch area and increasing isolation). Generally, populations in smaller and more isolated patches are more susceptible to local extinction due to lower carrying capacity of small patches, reduced exchange of individuals between patches (lower genetic diversity, lower recruitment and re-colonisation potential) and the greater susceptibility to stochasticity in population dynamics. However, the relationships between characteristics of habitat fragments (e.g. patch size, isolation) and species richness, abundance, resilience or persistence are not simple and easily predicted. For example, the relationship between population size and habitat extent is not necessarily linear (Bellamy et al. 2000), and many species benefit from the habitat heterogeneity found at the edge of patches (Fuller 2012a). The relative densities of many common woodland birds are proportionally higher in smaller woods (Bellamy et al. 2000), perhaps exploiting habitat heterogeneity at the edge of woodland or preferring the denser vegetation at the periphery, although dispersal limitation is also possible in isolated patches.
There has been considerable debate about the balance between collecting more data and implementing conservation action (Stuart et al. 2010, Collen & Baille 2010, Knight et al. 2010), however, it is clear that we still lack important fundamental knowledge that would help inform conservation management (e.g. Fisher et al. 2011a,b). It is clear from several recent commentaries and reviews that each of the five options highlighted by Lawton et al. (2010) for creating an ecological network is still the subject of considerable research and debate. Examples include the relative merits of increasing connectivity versus area of habitat (Hodgson et al. 2009, Hodgson et al. 2011, Doerr et al. 2011) and the removal of underperforming protected areas and the optimum selection of new sites (Fuller et al. 2010). Whilst Lawton et al. (2010) make some suggestions, the purpose of their review was not to identify knowledge gaps and direct future research potential. Here we highlight some important areas of research that would help inform decisions regarding ecological networks, especially in regard to the five options for rebuilding nature (above) and the 24 recommendations given in the report (Lawton et al. 2010).
2. QUALITY, QUANTITY AND CONNECTIVITY

The five options suggested by Lawton et al. (2010) for addressing the shortcomings of England’s ecological network (i.e. improving the quality of current sites, increasing the size of current sites, enhancing the connections between sites, creating new sites and improving the wider environment) are all highly interconnected, with improvements in all five components required for the network to function effectively.

2.1 Quality

In relation to the effective management of wildlife sites, Lawton et al. (2010) commented that:

‘In many areas it will be the single most important requirement’.

As of 2012, 59.5% of SSSIs were classified as in ‘unfavourable recovering’ condition, meaning that the sites were currently unfavourable but that plans have been implemented to move these sites into a ‘favourable’ condition (www.sssi.naturalengland.org.uk). Currently 37.2% of sites are classified as in favourable condition. Lawton et al. (2010) recommend that progress in improving the management of SSSIs be sustained (recommendation 11) and comment that whilst the Public Service Agreement (PSA) of 95% of SSSI in ‘unfavourable recovering’ condition or better is likely to be achieved, the majority of sites are still not in a favourable condition (Note: the PSA was achieved as of 2012). Lawton et al. recommend that monitoring and management of Local Wildlife Sites should be continued and improved, and should be the responsibility of the local authorities (recommendation 12).

2.1.1. Defining habitat quality

Habitat quality is conventionally assessed in terms of individual fitness. In practice a range of surrogate measures can be employed to assess fitness of organisms in particular habitats (Johnson 2007, Fuller 2012b). Density of a species is by far the most frequently employed measure and is widely considered to be positively correlated with habitat quality (Hodgson et al. 2009) though this may not be justified in all cases (Van Horne 1983). Nonetheless, quality can usually be assessed through measures of density and abundance (Bock & Jones 2004). This is an indirect way of assessing whether the focal area contains the necessary resources to support a population, assuming that high densities of a species correlate positively with the presence of required resources. The latter assumption may be violated where, for example, predation risk is high or there are insufficient social stimuli from conspecifics (Fuller 2012b). Effects such as source-sink dynamics and ecological traps can also disconnect species density from habitat quality. Issues of scale can be resolved by considering population traits when determining the area over which a species’ population density should be measured.

In practice for much conservation work, evaluations of ‘habitat quality’ are often based on broad measures of vegetative structure and composition, often without reference to the needs of specific organisms. For example, favourable condition attributes for lowland dry heath SSSIs include, ‘Between 1% and 10% bare ground’ and ‘Less than 25% common gorse’ (Natural England 2008). This approach to habitat quality assumes that once these targets are met the site will be in a ‘favourable’ condition. A problem with judging site quality in this manner is the high likelihood that the site will effectively only be managed in ways that meet the resource needs of a few species (these may or may not be ‘key target species’), which, by definition, can become regarded as indicators of management success. Many other species, however, will not be catered for by this management approach to habitat quality. In particular, small scale habitat structure and heterogeneity is often ignored because management tends to favour more conspicuous species (e.g. birds, butterflies) that may require relatively coarse structures.
An alternative approach is to measure habitat quality using a resource-based framework, assessing how well the resource requirements of a target species, or even a wide suite of species, are met within a defined area (Dolman et al. 2011, 2012). With this approach the judgement of quality is based specifically on meeting species requirement, rather than reaching a somewhat arbitrary quota for habitat structure and composition perceived to be appropriate for the habitat type in question. Thus, the term ‘habitat quality’ can be applied in different contexts and its use is potentially misleading where one is interested in matching the species’ specific requirements to the available resources and characteristics of a defined area. By defining quality in terms of the specific requirements of species, the emphasis is placed on the traits of species rather than just perceived associations with broadly defined ‘habitat’ categories. The scale at which habitat or patch suitability is measured for any species will vary depending on the requirements of a species, but by matching the management specifically to the requirements of each species the scale will be explicitly considered. By taking a more species-focused approach to the definition of habitat quality, more subtle distinctions are likely to be made between suitable and unsuitable habitat, providing better estimates of available habitat, and the choices of target species are more likely to cover a diverse array of spatial scales. The difficulty, of course, is that the requirements of species are diverse, even conflicting, so that rarely will it be possible to manage particular locations for a full complement of species that might occur in the habitat type concerned. This is a particular problem in cultural landscapes, such as those of Britain, where habitat patches of high conservation value tend to be rather small.

2.1.2 Management for habitat quality

The importance of habitat heterogeneity has been discussed frequently in regards to species conservation and resilience of landscapes to environmental changes (e.g. Benton et al. 2003). Heterogeneity is scale-dependent (Benton et al. 2003, Vickery & Arlettaz 2012) with both spatial and temporal dimensions (Lindenmayer et al. 2006) and again should be defined in terms of the resource requirements of a species. Laca et al. (2010) showed experimentally that body mass affects the grain at which herbivores exploit food resources, with larger species exhibiting a coarser-grained use of food resources i.e. ranging more widely and feeding less selectively. Multi-scale heterogeneity will be needed where management is based on consideration of species’ specific traits. Research would help to inform appropriate management techniques for creating such multi-scale heterogeneity.

One of the most important management approaches for improving the average habitat quality (i.e. through increasing the diversity and quantity of resources) of agricultural land across England, and outside of protected areas, is agri-environment schemes, specifically, Environmental Stewardship (ES; see recommendations 15, 16 & 23). ES was designed using the best available evidence for effective management practices, albeit based on a limited range of taxa. However, ES is very much a structural-based management tool, designed to deliver multi-scale heterogeneity, often requiring minimal input from landowners (e.g. hedgerow management is reduced to the frequency of hedgerow cutting).

The effectiveness of ES management aimed at improving existing habitat quality is probably hampered two-fold. Firstly, management is likely to be implemented where the habitat is approaching the minimum satisfactory condition, because restoration of highly degraded sites is costly (Littlewood et al. 2012). For example, the restoration of poor-quality grassland into a floristically diverse habitat can be difficult due to the closed sward, which limits colonisation and establishment potential of new species (Edwards et al. 2007). Secondly, the broad management

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1 Note that ES is funded through the Rural Development Programme for England (RDP). Transition arrangements are currently in place leading up to the next RDP starting in 2015 (www.naturalengland.org.uk/ourwork/farming/funding/es/)
prescriptions of ES are not tailored towards the resource requirements of species that are present or likely to recolonise a particular patch and, therefore, many opportunities will be missed through inappropriate or ineffective implementation. Higher Level Stewardship (HLS) contains management options designed to restore highly degraded habitat, (including woodland, scrub and grassland) to some perceived generalised state of ‘high quality’; this is likely to provide a better mechanism for creating a range of habitats in agricultural landscapes.

Woodland improvement grants have been a mechanism through which forested habitat is managed (Forestry Commission 2010). The delivery of a diversity of age structures, foliage structures and tree species compositions, will be necessary in order to meet the resource requirements of a wide range of woodland biodiversity (Hewson et al. 2011, Fuller 2013, Fuller et al. 2007, 2012). The dominant tree species will have complex and diverse effects on the resources available to wildlife, ranging from gross effects on understorey and canopy structures to more subtle effects such as the nutrient availability of the litter with consequences for biodiversity at higher trophic levels (Hobbie et al. 2006, Barbier et al. 2008). Thus, decisions concerning choice of tree species and subsequent management regimes will have an enormous influence on the resource availability within a landscape and, thus, the biodiversity of a region (Bibby et al. 1989, Gabbe et al. 2002, Hewson et al. 2011, Fuller et al. 2012).

It is government policy in Scotland, England, Wales and Northern Ireland to increase the total extent of tree cover substantially, and tree planting will form a major component of landscape restoration in many regions. The emphasis of these policies, and of those promoted by, for example, the Woodland Trust, is on quantity of forest. There is little discussion of what form these forests will take, yet this will be fundamental to whether they deliver biodiversity benefits. There is a need to develop a more comprehensive view of how forest management systems affect biodiversity and the contribution they can make to delivering appropriate habitat heterogeneity (Fuller 2013). There is an important issue of what are the optimum scales and balances between different structures that could be provided through productive management (Hewson et al. 2011, Fuller et al. 2012). There needs to be a focus on resource requirements across a range of biodiversity so that we can begin to understand the scales at which species respond to structure and composition of forests and forest networks (i.e. patches of fragmented forest within a landscape). Fuller et al. (2007) suggest that management approaches that increase both young- and old-growth habitats are likely to be beneficial and that a range of management techniques will be required. Research into the effectiveness of a range of techniques, from minimum intervention to clear felling, is required to provide an evidence-base for managing diversity at multiple scales within forests. Similar issues are found across the breadth of broad habitat categories (e.g. heathland, upland forest, wetlands), where managing for heterogeneity with a resource-based focus will be required in order to improve the availability of a range of habitats to support high biodiversity, i.e. a range of niches.

The value of experimental studies in guiding management prescriptions is enormous and has the potential to produce large improvements in the efficacy of management for a broad range of biodiversity. For example, Staley et al. (2012) found that extending the hedgerow cutting regime from a 2-year interval to 3-years would increase the berry biomass by c. 40%. Within ES, Entry Level Stewardship (ELS), hedgerow options mandate at least 2-years between hedgerow cutting; increasing this minimum interval would probably have a large positive effect on hedgerow quality for biodiversity. Unfortunately, experimental studies of management techniques are frequently (even typically?) not conducted or are poorly conducted, and where experiments are conducted there is often no translation of the results into practice (Pullin et al. 2004, Sutherland et al. 2004). Thus, there is a need for more field-scale experimental studies of management techniques and options in order to ensure that guidance on management are evidence-based and effective.

2.1.3 Measuring habitat ‘quality’
Managing land using resource-based approaches goes some way to ensuring that management delivers the ‘required quality’ for a range of biodiversity. However, there is still a need for more traditional assessments of habitat quality through demographic monitoring in order to detect unintended effects on populations. Johnson (2007) recommends the priority use of demographic measures as metrics of habitat quality. There is great potential for using multiple demographic measures for detecting source-sinks and ecological traps, e.g. combined measures of population density and productivity in different habitat types.

Ecological traps are poor quality habitat that is preferentially selected by individuals, usually due to a mis-match between habitat selection cues and habitat quality (Kristen 2003, Battin 2004). Ecological traps appear to be most frequent in human-modified landscapes and have the potential to drive populations towards extinction (Battin 2004, Gilroy et al. 2011). For example, Bro et al. (2004) suggested that cover crops designed to provide winter food and shelter for grey partridge Perdix perdix were acting as ecological traps by attracting high densities of predators and, thus, this conservation measure was ineffective. In order to identify ecological traps, multiple demographic measures are required from several selected habitat types and, thus, few studies have provided good evidence for their presence and effect (see Battin 2004). For example, a measure of density is required in order to indicate preferential selection of a patch and a demographic measure is required to indicate a reduction in fitness from selection of this patch (e.g. lower reproductive output or juvenile survival).

Thus, there is a need for the establishment of more rigorous demographic monitoring within rapidly changing landscapes, including those affected by climate change, as well as human-impacted environments. This could be especially important in habitats modified through agri-environment management and those areas selected as Nature Improvement Areas. Such monitoring will reduce the likelihood that management aimed at protecting biodiversity does not inadvertently have negative consequences.

2.1.4 Conclusions: research needs relating to quality

1. 'Quality' needs to carefully defined in reference to the resource requirements of exemplar species and ensure that management considers exemplar taxa that function over a range of spatial scales in the context of different broad habitat types.
2. Resource- and trait-based frameworks should be developed for assessing rapidly the most important resources to manage within a site and the most appropriate management options in different contexts. More field-scale experimental research is required on the efficacy of management techniques and options to ensure that conservation measures are evidence-based. Carefully designed comparative studies of different management treatments may also give valuable insights. The provision of different successional stages within landscapes would theoretically encompass a range of niches: research to assess optimum balance of stages would be valuable. It is possible that analyses of existing field-scale data may give useful insights (e.g. of any long-term monitoring data sets gathered on reserves; although no national repository or register of such studies appears to exist, Natural England is exploring how to make better use of records collated across the National Nature Reserve network (Tim Hill pers. comm.)). Larger scale data should also be considered (an example being Baker et al. 2012) but such data rarely allow tests of the efficacy of particular management interventions due to the difficulty of matching the scales of data collection with the scale of intervention. The issue of monitoring is discussed further in section 4.
3. More demographic monitoring would be valuable in human-modified landscapes and in those experiencing climate-change impacts in order to detect and understand ecological traps, and other important processes that could drive populations towards extinction. We need to move beyond agri-environment management into other habitat types e.g. woodland, heathland, wet grassland and interfaces/gradients. For many taxa there is a
knowledge deficit for these habitat types, although for many taxa knowledge is lacking even in farmland environments. Careful identification of exemplar taxa would be necessary, representing a range of resource and spatial scale requirements.

2.2 Quantity

Increased fragmentation is usually associated with a reduction in species diversity (Fahrig 2003) due to the species-area relationship, where larger areas contain more species. This can be explained by increased extinction rates (i.e. due to small populations having reduced resilience to stochasticity), higher disturbance and lower habitat heterogeneity (i.e. fewer niches) in smaller areas. Lawton et al. (2010) commented that ‘77% of SSSIs and 98% of LWS [Local Wildlife Sites] are smaller than 100 ha’ and that several BAP priority habitats have a median patch size of less than 2 ha. Thus, the review concluded that the ecological network does not meet the requirement of adequate size in relation to the component parts (e.g. wildlife sites). The objective of increasing the size of current wildlife sites would be met through the implementation of several of the 24 recommendations. Recommendations 1-3 would encourage the identification, creation/restoration and protection of potential wildlife sites, whilst recommendations 15, 16 and 19 suggest the creation of new habitat via agri-environment management, or through collaborations between the public and private sectors. In the following sections we focus on the research requirements for creating new habitat.

2.2.1 Planning habitat creation

There has been considerable interest and research activity in the area of optimal planning of reserves and ecological networks (Margules & Pressey 2000, Naidoo et al. 2006, Carvalho et al. 2010), including the design of marine protected areas (Leslie et al. 2003, Klein et al. 2008). Recent approaches to the planning of protected areas and ecological networks have mainly adopted an optimisation approach, using algorithms to select the best strategy weighed against ecological benefits and practical constraints (e.g. cost, land availability). An example of such a decision support tools for guiding conservation planning is Zonation (Moilanen 2007, Moilanen & Kujala 2008), which has been used to guide practical management decisions and explore theoretical issues, such as the effective use of indicator species (Franco et al. 2009).

However, there are substantial differences between designing an ecological reserve network from scratch and adding to an existing reserve network in order to improve its performance. Meir et al. (2004) found that when conservation action is spread over a number of years, comprehensive reserve network design may not produce an optimal solution, especially when habitat is continuing to degrade and there is considerable uncertainty in site selection. It is suggested that simple heuristic rules, such as protecting sites with the highest species richness or protecting the most extensive sites, might be more effective in these circumstances. Franco et al. (2009) showed that it is important to base conservation solutions on data for multiple species, and especially those with narrow niche breadth. Thus, there is a strong need for multi-taxa monitoring data in order to make effective decisions.

The process of identifying sites in order to extend ecological networks is known as gap analysis (Jennings et al. 2000). Although the concept of gap analysis is simple, i.e. identify which aspects of biodiversity are not captured within the existing ecological reserve network, the process is data intensive, requiring good quality species distribution data, and, potentially, access to landscape data (e.g. land classification, elevation). Applying gap analysis to England’s protected area network, Thomasina et al. (2004) found that lowland areas were under-represented (3.5%, compared to 65.8% for upland areas), with most types of natural areas under-protected. Maiorano et al. (2006) used gap analysis to evaluate the effectiveness of existing protected areas in Italy to conserve terrestrial vertebrates, showing that the existing network was not fully representative of species diversity. Regional gaps in the network were identified, providing a strategy for improving the
network: however, the authors caution that the results were highly dependent on the quality of the dataset and the conservation targets.

Thus, all robust approaches towards planning ecological networks require high quality ecological data (e.g. species distributions, traits concerning resource use, habitats) preferably on multiple taxa (see Carvalho et al. (2010) for effects of incomplete data). Because distribution data across a range of taxa are often not available, even in well surveyed countries such as England, umbrella or indicator species/groups for which there is good available data are frequently used to select priority sites for protection and management. This approach assumes that protecting the distribution of a species with the greatest requirements, or that is representative of a range of species, will provide protection for a broad range of biodiversity. Whilst there is some suggestion that umbrella species can increase species richness and abundance of co-occurring species (Branton & Richardson 2011), such approaches have often been shown to be inadequate at provisioning habitat where the requirements of species are very different (Minor & Lookingbill 2010). However, it is likely that for practical reasons the use of umbrella or indicator species/groups will continue, though in many cases it will be unclear how well these species represent the requirements of wider taxa and, especially, rarer species (Rodrigues & Brooks 2007, Eglington et al. 2012).

### 2.2.2 Mechanisms for delivering new habitat

Several funding streams are likely to be important for creating new habitat. In recent times the most relevant have been Environmental Stewardship and Woodland Creation Grants; the latter aim to ‘create woodlands that generate public benefit’ (Forestry Commission 2010). As well as modifying existing habitat, Environmental Stewardship (ES) has the potential to generate new habitat, with options that include planting grass and wild flower margins and the creation of wood pasture, scrub, wet-grassland and more (Natural England 2010a,b). Much of the new habitat created through ES encompasses only small patches e.g. field margins or beetle banks, but nonetheless can provide important habitat for invertebrates and plants with small area requirements.

Whilst the Higher Level Stewardship (HLS) component is targeted towards high-value objectives (including biodiversity), the Entry Level Stewardship (ELS) component is open to all farmers with no top-down placement of management within the landscape. Thus ELS, the major component of ES, is not optimally designed to target habitat creation towards priority sites, and HLS currently represents only a small area of land managed for biodiversity. Lawton et al. (2010) recommended the creation of a new type of ES (recommendation 16) that would be targeted towards creating buffer zones and stepping stone sites. However, the government response to Lawton et al.’s recommendation stated a desire to improve the existing scheme first, before devising a new scheme.
2.2.3 Conclusions: research needs relating to quantity

1. There is a strong need for multi-taxa monitoring data, both spatial and temporal, to ensure that the creation of new wildlife sites meets the requirements of a broad range of taxa. This is important in two respects. First in the optimum targeting of protection of wildlife sites and creation of new habitats where greatest biodiversity gains may be expected (e.g. Franco et al. 2009). Second, to assess the success or otherwise of creating new habitat and managing habitat to improve its quality. The latter needs to be designed in such a way that responses of taxa are measured in relation to changes in habitat and resources at appropriate scales (see section 4).

2. Because this is often difficult there will be some need to use surrogate, indicator or umbrella-species to signal high priority sites for habitat creation. It is therefore imperative that we understand how well rarer species and habitats are represented by the needs of more common and conspicuous species. In selecting such species account should be taken of the extensive literature on this subject that is beyond the scope of the current review. Alternatively it may be necessary to define the specific needs of rare species and provide these through targeted management at specific locations, while managing wider areas for diverse assemblages of commoner species.

3. Land management and creation schemes will be crucial to the creation of new habitat within the wider countryside, and there is potential to use species distribution data and gap analysis approaches in order to place this management in areas of greatest need.

4. Ecotones and habitat designed to act as ‘stepping stones’ will be important for softening habitat edges and connecting existing components of the landscape. Resource complementation (Dunning et al. 1992) is a critical feature of many species in long-fragmented landscapes; understanding the implications for planning the creation of habitat and its subsequent management is extremely important.

2.3 Connectivity

Lawton et al. (2010) concluded that movement of organisms between wildlife sites has become harder in England’s increasingly fragmented landscape, with the degradation of linear habitat features (e.g. hedgerows and river corridors) and the loss of many small habitat patches and features (e.g. ponds) that presumably for many organisms acted as stepping stones between more extensive habitat. One of the main outcomes of the Lawton Review (recommendation 3) has been the establishment of Ecological Restoration Zones (ERZ), renamed as Nature Improvement Areas (NIAs) on implementation. The recommendation is that within these areas, “significant enhancements of ecological networks are achieved, by enhancing existing wildlife sites, improving ecological connections and restoring ecological processes”. Although individually large, the impact of NIAs will be restricted to a relatively small proportion of England’s land surface. Perhaps the greatest potential for improving connectivity lies in the effective implementation of agri-environment management, with improved targeting of options in areas with low connectivity (following recommendations 16 and 23). Lastly, habitat creation measures could be partly focused in areas where connectivity between existing patches is low, thus providing stepping stone habitat between current wildlife sites. There is a need, however, to assess the relative benefits derived from habitat creation of increasing potential connectivity rather than expanding the area of existing habitat patches (see section 2.4 and Figure 1).

2.3.1 What is connectivity and why is it important?

Connectivity is a central component of an ecological network, and broadly refers to the ‘degree of movement of organisms or processes’ (Crooks & Sanjayan 2006). Connectivity potentially has multiple functions (Bennett & Mulongoy 2006), including: providing access to a larger area of habitat; facilitating migration; preserving genetic diversity through exchange of individuals between
spatially separated populations; increasing the probability of a patch being recolonised after a local extinction event; and, allowing a population to shift its distribution in response to a reduction in the suitability of their current range (e.g. through habitat degradation or climate change). However, connectivity is not a simple concept to apply to network design, as the functional definition of connectivity changes dramatically depending on the mobility of the focal species and resource availability within patches (i.e. food, mates, territories). Minor & Lookingbill (2010) found that protected areas in North America were well connected for large mammals but not for small mammals, probably because the latter have lower dispersal rates and are more likely to be influenced by fragmentation effects within a protected areas, and not just between sites.

Connectivity is often defined as either physical connectivity or functional connectivity. The former refers to the physical connectedness of patches with a landscape, whereas the latter is defined by the observed ability of organisms to move between patches. Physical connectivity is more easily measured, at least at coarse scales, but often provides limited information about the actual effect of the landscape configuration on species' movement potential. Functional connectivity is far more difficult to measure, usually requiring experimental approaches (see section 2.3.2), but when combined with appropriate spatial habitat data can provide a more nuanced measure of connectivity. Functional connectivity is somewhat related to physical connectivity, although it takes into account species-specific (or other taxonomic or functional groupings) interactions with the landscape.

The notion that landscape connectivity is important for the maintenance of healthy and resilient populations has been frequently advocated (Damschen et al. 2006, Brudvig et al. 2009, Minor & Lookingbill 2010), and is underpinned by a strong body of ecological theory (including island biogeography and metapopulation dynamics). Heller & Zavaleta (2009) found that increasing the amount of connectivity in a landscape was the most frequently proposed adaptation under climate change. Research on habitat corridors has shown significant biodiversity benefits, such as a 20% increase in plant species diversity in directly connected patches (Brudvig et al. 2009), although research has also shown that connecting patches with corridors is less effective at increasing population size than increasing patch area (Falcy & Estades 2007) and there are taxa-specific variations in use of corridors (Gilbert-Norton et al. 2010).

However, it has been argued that the role of connectivity in driving population declines is often applied too broadly (Schmiegelow & Monkkonen 2002), and that the importance of connectivity in planning for future climate change scenarios is overemphasized. Hodgson et al. (2009) argue that using connectivity as the primary conservation metric is dangerous given uncertainties in the estimation and effect of connectivity. They suggest that habitat area and habitat quality are more reliable metrics for conservation planning in the face of climate change, especially when the resources available to conservation are limited. Nonetheless, with an increasing body of research on behavioural ecology, there may be improved understanding of functional connectivity. Incorporating connectivity into conservation planning, alongside area and quality variables, may then become more tractable (Doerr et al. 2011). It is important to recognise that the relative benefits of enhancing connectivity, quality and quantity will almost certainly vary according to taxa and landscape context.

2.3.2 Measuring connectivity

Measuring connectivity in an ecologically meaningful way is crucial for assessing both the full effects of habitat fragmentation on biodiversity and for monitoring the effectiveness of schemes designed to increase connectivity. Bruckmann et al. (2010) note that the reason many studies have failed to find effects of connectivity on species diversity might be the use of unreliable connectivity measures. They showed that incorporating both patch area and distances between patches into indexes of connectivity improved the estimates of this parameter, over metrics such as nearest-neighbour distance and percentage habitat cover. However, the general focus on structural, rather than
functional, connectivity is also relevant; we must be careful to separate landscape connectivity (i.e. the physical connectivity in the landscape) from functional connectivity, the latter being of greater relevance to species conservation.

Functional connectivity is often quantified based on the probability of moving between points or the amount of movement (see Crooks & Sanjayan 2006). However, Belisle (2005) criticised this approach because the likelihood of moving between patches is dependent on more than simply the physical connectivity and the movement potential of the species. The motivation to move might be linked to differences in resource availability between patches, or the density of individuals on a patch, ideas that are central to foraging theory, i.e. ideal free distribution theory and marginal value theorem. Integrating foraging and behavioural theory into models of landscape connectivity is likely to improve estimates of functional connectivity. Quantification of movement costs, motivation (i.e. purpose of movement) and species traits that affect movement potential would require research. It is also possible that changes in predation risk may generate increased or decreased levels of movement between patches.

Belisle (2005) highlights the use of translocation, playback and food provisioning experiments for quantifying landscape permeability and the costs of movement. Such approaches have been used to measure the gap-crossing ability of species (Creigan & Osborne 2005, Robertson & Radford 2009), as well the use of linear features (Gilles & St Clair 2008). Additionally, individual-based modelling approaches could be used to explore the theoretical implications of movement decisions within a multi-patch network, and potentially they could be developed to predict the likely functional connectivity of a future landscape, thus informing both planning and theory (Tracy 2006, Pe’er et al. 2011).

2.3.3 Creating connectivity

Connectivity within a network is usually increased through either the creation of physical ‘corridors’ between patches or stepping stones, i.e. smaller patches that reduce the distances between neighbouring patches. We use the term ‘corridor’ for convenience to denote linear or other connecting features. Corridors can substantially increase movements between patches, especially of invertebrates, non-avian vertebrates and plants (Gilbert-Norton et al. 2010). Translocation experiments combined with radio-telemetry have shown that many species of birds prefer to move through corridors (Gilles & St Clair 2008) although, overall, birds benefit less than other taxa due to their relatively high mobility (Gilbert-Norton et al. 2010). It should be noted that although individuals may prefer to use corridors, this does not prove that their movements will be substantially impeded or reduced in the absence of such features.

Similarly, stepping stones may facilitate movement across a landscape, such as scattered trees assisting the movement of birds across farmland (Guevara & Laborde 1993, Fischer & Lindenmayer 2002) or small meadows aiding the migration of butterfly populations (Neve et al. 1996). Stepping-stones can have effects across quite large spatial areas, including trans-continental migration routes, whereas corridors function over relatively short distance. The matrix can also affect the movement of individuals between patches, with movements increasing where the matrix was more similar to patch habitat (Eycott et al. 2010). The efficacy of corridors and stepping stones has also been linked to matrix quality (Baum et al. 2004).

Several key questions regarding corridor design and implementation have yet to be addressed adequately. Most importantly, under what circumstances are corridors likely to be effective in increasing a population’s persistence and preventing extinction? Western European landscapes have been highly fragmented for much of recent history and, consequently, many populations will have adapted to cope with such conditions. Fragmentation will affect species that have highly specialised resource requirements more than generalists, as the latter can make use of a broader range of
habitat types in order to move through the landscape (Gilles & St Clair 2008). Understanding potential limits on dispersal requires detailed behavioural studies and habitat manipulation experiments, but methodologies exist and have been successfully used to explore such questions (Gilles & St Clair 2008).

Gilbert-Norton et al. (2010) were unable to analyse the effects of corridor length or width in their meta-analysis because too few studies had attempted to test these variables in relation to corridor function. Haddad (2008) suggested that identifying the optimum width of habitat corridors is the most important guidance required by land managers. Several authors have commented on the requirements of trait- and phylogenetic-based frameworks for assessing species likely to benefit from corridors and stepping stones (Haddad 2008, Gilbert-Norton et al. 2010), and such an approach would be of great practical conservation benefit. Relevant traits (including dispersal distances, main predators, gap-crossing potential and habitat preferences) could be used to create an index of connectivity requirements. The main limitation in adopting this approach is that for many species the critical metrics have not been systematically measured. Dispersal is difficult to quantify (Paradis et al. 1998, Bullock & Nathan 2008, Tittler et al. 2009). Experiments are required to determine gap-crossing ability (e.g. Desrochers & Hannon 1997, Creegan & Osborne 2005) and perceived habitat associations are context-dependent, frequently not representing the full spectrum of potential habitat of an organism (Fuller 2012b). The latter point is important because for some species, habitat needs during dispersal may be very different to those required for breeding or overwinter survival.

The Environmental Stewardship scheme contains many options that could increase connectivity though the wider countryside. Options include hedgerow and margin management that creates or restores linear habitat features, and potentially grassland and arable options that could function as stepping stones through otherwise hostile habitat where such features are rare. The role that agri-environment management will have in restoring the quality of the habitat outside of protected areas will be crucial in increasing connectivity for many species, often referred to as 'softening the matrix'. However, once again there is a lack of field-scale experimental research on the effectiveness of this management in increasing connectivity through the landscape for any organism. It is possible that the lack of a coherent top-down planning strategy could hamper the effectiveness of ES in delivering increased connectivity, but without experimental studies such questions cannot be addressed. Even if it were possible to introduce any such strategy, the design would be challenging because ‘connectivity’ and ‘landscape permeability’ mean such different things to different organisms. Here the trait-based approach outlined above is relevant. It may be necessary to establish approaches that, as far as current knowledge permits, satisfy requirements of selected target species which could be specific to particular landscape types or act as exemplars of defined suites of traits.

2.3.4 Conclusions: research needs relating to connectivity

1. As with habitat quality and quantity, there is a requirement for behavioural and field experiments to determine species’ connectivity requirements and to identify the factors that make corridors and stepping stones effective. Such approaches, including, translocation experiments, would be feasible for many species, especially birds where tracking technology could also be employed. Experiments are the ideal approach for testing specified hypotheses about the effects of different kinds of connectivity on movements, colonisation and population persistence. Nonetheless, carefully designed comparisons of the occupancy of habitat patches differing in structural connectivity may also provide useful insights. The main difficulty to be surmounted with such comparative work is that it may be difficult to control for variation in patch and matrix quality.

2. Because it will only be possible to apply these approaches to a small number of species, trait-based frameworks should be developed for assessing the connectivity requirements of species and habitats. Such frameworks could enable land managers to assess rapidly the
level and type of connectivity required within a landscape for species known to be present, and this could incorporate guidance on the physical properties of corridors. Ideally these frameworks should be informed by detailed research designed to fill in critical knowledge gaps, but, in practice, it will be necessary to build on the inevitably incomplete knowledge we already possess and to refine the frameworks as knowledge improves.

3. More research is required the ability of agri-environment management to deliver connectivity and how such management should be deployed to optimise any effects.

2.4 Interactions Between Quality, Quantity and Connectivity

Hodgson et al. (2009, 2011) have argued that habitat area and quality are more important than connectivity in maintaining and enhancing biodiversity because carrying capacity always increases with area or quality, but not necessarily with increasing connectivity. Thus, increasing the size of suitable patches of habitat is expected to result in a larger population, but the effect of increasing the connectivity between suitable patches of habitat is largely unknown (Hodgson et al. 2011). Whilst this is likely to be broadly true, there is much nuance in these terms (quality, quantity, connectivity) that makes the interactions complex.

We have emphasised the importance of habitat quality, defined in terms of resource-provision and individual fitness (see above), in the development of conservation strategies. It is especially relevant, therefore, to consider if and how habitat quality may be affected by habitat quantity and connectivity. Figure 1 summarises how habitat fragmentation (involving both reduction in quantity and dispersion into increasingly disconnected fragments) is expected to affect population viability under low and high habitat quality. One would expect the importance of connectivity in maintaining viable populations to be greater where average habitat quality is low rather than where it is high. For high quality habitat, quantity and connectivity are relatively less important as viable populations can persist in smaller fragments than is possible in low quality habitat. A key issue here is that low quality patches are more likely to function as sinks than high quality habitat, and that occupied low quality habitat might only appear viable because of immigration from source patches (i.e. larger patches and/or higher quality). Once the level of connectivity has decreased to a level where colonisation is a rare event, low quality patches will be unable to sustain viable populations for a given area of continuous habitat quantity. (This assumes, of course, that linkages between habitat patches do actually affect dispersal and potential colonisation). Populations in high quality patches are likely to persist longer, and to be able to withstand greater loss of habitat and connectivity, before the population is no longer viable. Thus, the extent to which connectivity and quantity affect populations is likely to depend very much on the quality of patches involved.

In England, one would expect most protected areas to be situated in landscapes in the lower part of Figure 1 i.e. where habitat quantity is low and habitat fragmentation is relatively high. The implication is that declining habitat quality in this context would have severe consequences for the survival of many populations at a patch scale. Increasing connectivity would probably have rather little effect on population survival if habitat quality and habitat quantity was low. Increasing the quantity of habitat (by increasing patch size) may only be beneficial if it resulted in an increase in extent of high quality habitat.

Hodgson et al. (2009) argue that ‘...uncertainty associated with connectivity is generally higher than uncertainty about habitat area and quality...’. However, habitat quality can be equally difficult to define and exactly what constitutes ‘high quality’ will vary greatly between species and seasonally (see above).

Many of these arguments about the relative importance of habitat quality, quantity and connectivity gloss over the issues of scale, which is central to defining each of these terms. Figure 2, therefore, takes these concepts one step further by considering how different processes affecting colonisation
and population persistence, two key parameters in population conservation, are scale-dependent. All three aspects of landscape variation (quality, quantity and connectivity) are important in their relationships with population processes, but they are not independent. Nor are the scales independent – there are several cross-scale interactions. Whilst quality operates mainly at patch scales, it is relevant to landscape scales through its effect on regional population size, the link being the amount of good quality habitat available at the landscape scale.

Quality, quantity and connectivity represent three conceptual parameters for visualizing biodiversity responses to landscape variation. We have outlined above their interdependence in terms of ecological processes. It is important, however, to recognize that the physical reality of landscapes can be exceedingly complex and that some habitat features may serve multiple functions for organisms. For example, linear semi-natural features may not only enhance connectivity through dispersal but, depending on their width and quality, may support populations of some species. Even if they act as population sinks they will, nonetheless, add to the population reservoir. Where such ‘corridors’ do not support year-round populations, they may provide food resources at certain times of year for mobile and wide-ranging species, for example seed and fruit-eating birds.

### 2.4.1 Climate change, resilience and range-shifts

The selection of protected areas is usually based on the resources that they currently protect (Araujo et al. 2004). Thus, there are serious questions as to the ability of current protected areas to provide continued protection into the future as climate change alters the distribution of species. Araujo et al. (2011) predicted the likely distributional changes for a range of European species and found that c. 58% of species would no longer be protected by current protected areas under a c. 3°C temperature increase scenario. However, Hole et al. (2009) conducted a similar analysis of sub-Saharan Important Bird Areas (IBA) and suggested that whilst there would be considerable changes in communities, a range of climate-spaces was likely to persist and c. 90% of priority species will still be protected. Of course, the novel ecosystems that might result from such climate-induced distributional changes could have unexpected consequences for species occupancy and persistence, and consequently alter species-specific responses to climate-change beyond the range of our current models (Hobbs et al. 2009). Mountain areas have considerable potential to inform us about the processes by which climate change affects biodiversity by monitoring altitudinal shifts in species distributions (Chamberlain et al. 2012).

Clearly, there is a need to assess the ability of protected areas to protect the full range of biodiversity under different climate-change scenarios in the UK (Gaston et al. 2006). There are several potential options for addressing inadequacies in the current network of protected areas, including selecting new sites based on future climate projection or allowing biodiversity within a protected area to change but facilitate range shifts by increasing connectivity. Into this debate comes the controversial issue of abandoning protected areas that are ‘underperforming’ (Fuller et al. 2010). Climate-induced changes are likely to reduce the importance of some protected areas (or shift the biodiversity they contain to something different but potentially valuable) and increase the value of currently unprotected areas. Recent research indicates that protected areas act as focal points for species colonisation (Thomas et al. 2012, Hiley et al. 2013) and will retain conservation importance in the future (Johnston et al. 2013). The optimal solution will probably involve a combination of approaches, but a coherent ecological network building on the sites that are already protected will be crucial. There are two additional elements of future change which are exceedingly difficult to predict. First, how might communities change as a result of climate-change induced changes in species distribution and how these changes may affect persistence within protected areas? Second, will habitat associations of some species shift? This appears already to be happening with some invertebrates in Britain (Davies et al. 2006), presumably a response to interactions between climate-change and microclimate in different vegetation types.
Much discussion of climate change adaptation for biodiversity has emphasised the importance of connectivity in allowing species to shift their distributions allowing them to effectively track their climate envelopes. In practice this will be exceedingly difficult to achieve; the scale of habitat creation required is enormous. Two additional components of conservation strategy seem at least as important. First, maintaining large areas of high quality habitats within the existing ranges of many species is important to minimise, or at least to delay, local extinctions. This aspect of strategy embraces the maintenance of existing protected areas, improving their quality where necessary and taking opportunities to create new habitat. Second, species need the opportunity to colonise new habitat types if climate change causes microclimates to become unsuitable, or food supplies to diminish, within currently occupied habitats. This implies that high levels of habitat heterogeneity need to be maintained on different scales (Fuller 2012d). Given the uncertainties surrounding the responses of wildlife to climate change, it is crucial that all options are kept open for species to change their distributions at different scales and for new assemblages to develop.

2.4.2 Conclusions: research needs relating to climate change resilience

1. Assess the performance of protected areas under a range of climate-change scenarios building on recent work on this topic.
2. Novel ecosystems could have important effects on communities undergoing climate induced changes. More consideration of the impact of these novel ecosystems is required and, although difficult, could be explored using experimental approaches and simulations.
3. Further work on relationships between climate and habitat occupancy are desirable across a range of taxa with altitudinal shifts having considerable potential to inform us of species sensitivities to climate change.
4. Development of conservation strategies with respect to habitat quality and heterogeneity that may help to buffer biodiversity against the uncertainty of how species and assemblages will respond to climate-change.
3. IMPROVING THE WIDER ENVIRONMENT

Whereas Island Biogeography emphasised a clear distinction between exploitable habitat and non-exploitable matrix, this distinction should be avoided when considering the relationship between terrestrial protected areas and the surrounding land in which they are embedded. Most species are capable of exploiting some habitat outside protected areas, with substantial populations of many species existing entirely outside of these protected sites (e.g. woodland bird and butterfly species). Thus improving opportunities for wildlife in the wider environment will reduce the pressure placed on protected areas and effectively increase the connectivity of the ecological network (Baum et al. 2004, Donald & Evans 2006). Lawton et al. (2010) comment that:

‘the more we improve the wider environment within which wildlife sites sit, the less we will have to do of the other options to establish a coherent and resilient ecological network’.

3.1 The Contribution of Agri-Environment Schemes

Most management schemes target protected areas (see Ausden & Fuller 2009), although by far the best funded conservation management scheme at the present time, Environmental Stewardship, is aimed almost exclusively at the wider countryside. The future of agri-environment schemes depends on outcomes from the CAP Review. Nonetheless, agri-environment management currently provides the most likely source of habitat creation to buffer wildlife sites (recommendations 15 and 16), although a more structured approach is likely to be needed in order to guide accurate placement of management (recommendation 22). Ecological restoration zones and other habitat creation measures (e.g. recommendations 3 and 19) will also be important in buffering existing wildlife sites.

Recent evidence suggests that ‘broad-and-shallow’ agri-environment management can positively affect bird populations across England (Baker et al. 2012). This suggests that the effective implementation of such schemes can improve the average quality of the wider countryside, outside of protected areas. Although Baker et al. (2012) reported evidence of local responses to management (i.e. increasing population growth rate where management occurred), national breeding bird trends do not reflect these positive trends. Therefore, perhaps the amount of management across England is not sufficient to affect the wider countryside as a whole, or perhaps the undirected delivery of ES has led to a patchy distribution of management (Figure 2). Alternatively, perhaps any local increase in habitat quality has been insufficient to benefit breeding productivity or survival to a level where surplus individuals are available for colonising wider areas and leading to measurable population increases at regional scales (Figure 2). Again, ES design could benefit from information derived from field-scale and landscape-scale experiments looking at the spatial scales over which individuals and populations interact with management (Figure 2).

There might be local density thresholds for food provisioning options, or combinations of options might be required in order to support populations, such as breeding habitat (e.g. hedgerows) with adjacent foraging habitat (e.g. grass margins). Perhaps hedgerow management should be contiguous between patches of woodland to create corridors without gaps for those species that are limited by gap-crossing potential. Such hypotheses need to be studied across multiple spatial scales in order to detect potential effects. For example, Baker et al. (2012) looked at the effect of winter food provision at different spatial scales on breeding bird abundance, to test the hypothesis that many species benefit from winter food provisioning over a large spatial scale during winter. Strong positive effects of winter food provisioning were found at 9 and 25km$^2$ scales for some species, but more research is required to determine whether there are important spatial and quantity thresholds in the delivery of this management.

3.2 The Role of Nature Improvement Areas (NIA) in Improving the Wider Environment
Nature Improvement Areas (NIA) are one of Government’s responses to the recommendations [3] of Lawton et al. (2010). NIAs are 'large, discrete areas that will deliver a step change in nature conservation' (Natural England – Nature Improvement Areas Criteria). These sites meet the major requirements of Lawton et al. (2010) for a coherent and resilient ecological network, where significant improvements are expected in the areas of ‘more, bigger, better, joined’. Twelve NIAs were initially selected, with potential for more in the future, based on the submission of a bid by local governments, NGOs or significant private landowners and were expected to comprise an area of between 10 000 and 50 000 ha. They were judged against the likelihood of achieving a significant improvement in the functioning of the ecological network and selected to ensure a diverse habitat coverage and geographic spread. Whilst NIAs include protected areas, one of the key criteria for the selection of a project was that ‘the surrounding land use can be better integrated with valued landscapes and action to restore wildlife habitats and underpinning natural processes helping to adapt to climate change impacts’. Thus, improving the wider environment is integral to the objectives of this scheme.

The monitoring of NIAs will be important in judging their success; however, many of the objectives of the schemes are difficult to assess (e.g. ecosystem services, connectivity), especially over the short initial period of this scheme (3 years). It is expected that much of the monitoring will be based on existing monitoring, surveillance and reporting schemes, with the objective of creating a flexible monitoring programme, but one that is still comparable nationally (see www.naturalengland.org.uk, NIA Monitoring and evaluation). Given the spatial scale of ecological restoration areas and the 3-year duration of the scheme it is unlikely that biological responses above background variations will be detectable. Any benefits of improved connectivity would be expected to materialise over considerably longer time periods. However, if the scheme continues long-term (or if initiatives set in place within the first three years are designed to have long-term benefits) then a variety of field and landscape monitoring could be used to assess the biodiversity benefits of these projects. However, it is unlikely that national surveys, such as the BTO/JNCC/RSPB Breeding Bird Survey (BBS), will be able to detect effects of these schemes on local abundance as few survey sites are likely to intersect with NIAs, and even supplementation with additional survey squares might struggle to achieve enough statistical power (DJB – unpublished data).

New approaches to monitoring biodiversity within NIAs that are tailored to particular landscapes and restoration initiatives may prove more appropriate. The approach currently being developed jointly by the British Trust for Ornithology and The Wildlife Trusts to monitor biodiversity responses to A Living Landscape (the Wildlife Trusts vision for landscape restoration) is designed to offer a multi-tiered framework providing the flexibility, breadth and depth required on an appropriate spatial scale and across a variety of taxa. This approach also aims to engage the public in monitoring biodiversity, a core aim of NIAs, through the collection of casual records or more systematic standardised repeatable surveys, but can also incorporate more intensive professional surveys where necessary (see section 4). Additionally, more research is required in order to identify good indicators of the ‘difficult to measure’ processes, such as ecosystem services and functional connectivity, across taxa and spatial scales. Such primary research will be important for ensuring that a range of species is monitored that is likely to act as early indicators of positive or negative changes in the wider environment. Monitoring is absolutely central to determining the performance of landscape-scale conservation initiatives in terms of wildlife responses, as well as understanding the dynamics of wider populations which will affect what happens within those areas selected for particular conservation measures. We therefore consider the requirements for monitoring in more detail in the next section.

3.3 Conclusions: Research Needs Relating to the Wider Environment
1. How much Environmental Stewardship or similar future management will be required to deliver widespread biodiversity benefits, and what options are most effective? Should the emphasis be more on HLS or equivalent, rather than ELS?

2. What are the best spatial scales on which to deliver ES management and how can we target management efficiently (i.e. towards priority species and areas)?

3. Which are the most appropriate ecological indicators for optimal monitoring, especially in regards to Nature Improvement Areas (NIAs)? Would such indicators need to be scale specific?

4. How can interventions delivered at a field scale, have influence at larger (i.e. population) scales?
4. MONITORING – VALUE AND REQUIREMENTS

Monitoring the responses of biodiversity to habitat creation and restoration at landscape scales fits closely with recent Government policy. These landscape schemes are clearly directly linked with climate change adaptation requirements. Will the new habitat initiatives provide enhanced permeability of landscapes to enable species to shift as their climate space moves? Will they provide a sufficient extent and diversity of habitat to enable species to occupy new niches that may be more favourable under a changed climate? The other relevant strand of policy is ecosystem services. Biodiversity is itself an important cultural service, but will the new habitat schemes provide additional services through, for example, carbon storage and flood control?

The reasons for monitoring the responses of wildlife to large-scale habitat creation schemes span across the three inter-related strands of conservation, education and science. It should be stressed that the scale of benefits that could be achieved from monitoring depends on implementing structured approaches that deliver reliable data and information. The most rewarding outcomes of monitoring will be realized over rather long timescales measured in several decades, though valuable information would be generated within the first decade. Co-ordinated monitoring of habitat creation schemes has the potential for learning lessons that are transferable between habitat schemes, for testing ecological theory and for linking with intensive studies of the effects of specific habitat management treatments.

The comments here relate mainly to monitoring biodiversity responses to the creation of new habitat. However, as discussed above (notably in relation to habitat quality, section 2.1) there is a need to develop monitoring frameworks that allow the tracking of biodiversity responses to habitat management interventions on fine scales that more closely relate to habitat quality and the provision of critical resources.

4.1 Adaptive Management and Setting Goals for Landscape Scale Management

Arguably the greatest value of monitoring lies in its feedback value for conservation planners and managers. Structured monitoring can provide reliable information of immense value to site managers who can use it to make informed adjustments to their management plans in specific ways to meet long-established or new goals. In view of the increasingly dynamic nature of ecosystems (see below) it will be increasingly necessary to manage with an expectation of change. Where the scale of change in species populations and biological communities is large, information derived from monitoring will provide the basis for rethinking conservation priorities. Figure 3 indicates how monitoring operated within an experimental design can feed into active adaptive management. In practice there are considerable potential gains to be made from simply monitoring how wildlife responds to management treatments that are not based on a strict experimental design, but knowledge would be advanced more surely by using an experimental structure. Broad questions where monitoring-based evidence could be used to inform decisions about the future direction of habitat management across suites of sites include:

- Which management systems and habitat configurations appear to benefit scarce species or ones with populations considered to be particularly vulnerable in the face of climate change?
- Are species changing their patterns of habitat use under climate change?
- Which species are expanding their range and what habitats are they colonising? This is likely to be very relevant under climate warming.
- Which types and scales of habitat mosaics maintain the most complex communities of plants and animals?
- What time lags are involved in the responses of different taxa to habitat creation and subsequent management actions?
4.2 Requirements and Benefits of a Wildlife Landscape Monitoring Programme

Hereafter, the term ‘habitat scheme’ is used to refer to any large-scale habitat creation initiative. This may cover a single large tract of land, a cluster of connected sites or other type of habitat network. We do not set a minimum size to these habitat schemes. By ‘wildlife’, we mean any living organisms easily identified and recorded live in the field and by ‘wildlife landscape monitoring’ we mean the (mainly) systematic measurement of changes in wildlife on individual or multiple habitat schemes. The following ideas were developed as part of the thinking underpinning the collaboration between the BTO and the Wildlife Trusts in developing a monitoring framework for *A Living Landscape*.

Five fundamental points about establishing a programme for wildlife monitoring of habitat schemes are:

1. It must be conducted over a long period of time, though not necessarily annually. This means it should be as sustainable as possible, i.e. cost-effective and making best use of existing schemes and data where appropriate.
2. Within sites, the data must be gathered in a consistent or sufficiently-standardized way to ensure that trends and patterns are based on comparable data over any defined time period.
3. It must meet information needs for conservation management purposes as well as generating information of scientific relevance.
4. Periodic measures of environmental change are required, especially with regard to vegetation development.
5. The sooner data collection starts the better; establishing baseline information for as many sites as possible is important.

Specific desirable feature requirements for a wildlife landscape monitoring programme are:

- A sufficiently flexible structure is needed to cope with different types of habitat schemes in terms of habitat types, extent and spatial configuration and ideally also to accommodate much existing monitoring.
- Clear, easily understood, robust protocols are needed that allow capture of *systematic* data allowing long-term trends to be identified.
- Ideally there also needs to be a facility for capturing less systematic observations that may be of value in, for example, determining colonization events and identifying changes in non-target taxa.
- Capacity to record abundance (relative or absolute) of selected taxa, not just species presence.
- It needs to be multi-scaled allowing data capture at the level of the entire habitat scheme but also for specific areas or locations within it. Spatial referencing of data is important so that records can be related to particular locations.
- Capacity to record diverse taxa. Whilst there will probably be core target taxa, it is desirable to allow the collection of as wide a range of wildlife and habitat data as possible.
- Capacity to record essential features of habitat, especially with respect to vegetation type (floristics and structure) and hydrology, as needed.
- Allow the involvement of people with different skill levels.
- Online data capture and feedback facilities for both observers and managers.
- Dissemination and data supply facilities at both national and local levels.
- Robust database systems. The ability to interrogate the available data is essential for adaptive management applications and data dissemination / supply.
- Must be able to deduce real (or likely) absence of a given target taxon.
• Must have well-defined systems of validation/verification of records (can build on existing networks to some extent).

Lindenmayer et al. (2008) identified important issues in managing landscapes for conservation. Ideally, a wildlife landscape monitoring programme should be developed in an integrated way alongside the following four considerations to maximize feedback for habitat and landscape management.

1. **Manage in an experimental framework** - Our understanding about ecosystem dynamics and responses can be improved by applying an adaptive management experimental approach to different management treatments and options (Walters & Holling 1990). As far as we are aware, this is very rarely done on protected areas in the United Kingdom. The new generation of landscape-scale conservation initiatives represents a huge opportunity to undertake adaptive management experiments (Figure 3).

2. **Manage both species and ecosystems** - These are complementary approaches in that conservation management embraces a variety of strategies, some based on particular species or groups of species, others emphasising whole landscapes, habitat mosaics or ecosystems. This requires a multi-scale approach and the capacity to record diverse information.

3. **Manage at multiple scales** - Conservation strategies for the new habitat schemes will need to recognize that ecological processes and species operate on different spatial scales.

4. **Allow for contingency** - All habitat schemes are different to some degree and no single management strategy fits all. The specific context and conditions of each habitat scheme will determine how it proceeds, at the same time taking account of broad ecological considerations.

The above requirements cannot be met by one rigidly defined system. There is a clear need for flexibility to accommodate different types of habitat schemes and different types of data. Therefore a conceptual monitoring framework, rather than a system, is desirable that (a) can be adapted to the conditions of individual habitat schemes and (b) allows development of monitoring and experimentation over time, depending on available resources. It would also allow biological recording at different levels of precision which have different purposes.
5. OVERALL CONCLUSIONS

Lawton et al. (2010) summarise their review using the phrase ‘more, bigger, better, joined’. Hidden within that simple phrase there are many unanswered questions and much complexity. The most notable knowledge gap lies in the definitions of terms such as ‘habitat’, ‘quality’ and ‘connectivity’, and how we can define these terms meaningfully across multiple spatial and temporal scales. Resource- and trait-based frameworks provide an approach that moves beyond simple descriptions of physical properties e.g. structural connectivity or descriptive habitat definitions. Such trait-based frameworks could explicitly incorporate variation in resource requirements across species, including the scale at which these resources are exploited. Such approaches are likely to be useful for scientists and practitioners alike, and would help target management more effectively and across a range of spatial scales.

Whilst landscape scale approaches are useful and necessary, there is a need to understand the relationships of individuals with their environment at a finer-scale. Clearly this information cannot be acquired for all species. A realistic approach would be to establish an understanding of how individuals of exemplar species exploit their environment and how they respond to heterogeneity of resources at different spatial and temporal scales. This is intimately bound up with the notion of what constitutes habitat quality. Such an approach will be especially valuable in working out how to increase functional connectivity for a variety of taxa, which might respond to habitat structure at different spatial scales. We suggest that an assessment and gap analysis is needed to determine for which species such knowledge already exists and which traits are not well represented by these existing studies. This would help target future research at the species level. Demographic responses to environmental change also need to be measured in order to determine the mechanisms linking these changes to population level effects. Experimental approaches have proved effective in measuring functional connectivity and systematic demographic monitoring has been used to understand effects of climate and land-use changes on demography.

Conservation planning tools can help to design optimal ecological networks, although they function less effectively when building on an existing network. Thus, gap analysis approaches might be more useful, and would enable conservation planners to identify under-protected species/resources. There is also a need to continue work aimed at predicting the effects of climate change on ecological networks, taking account of new habitat creation and potential enhanced connectivity.

Significant quantities of data are required to address the above issues. Ideally, a multi-taxa perspective is needed, taken across a range of landscape types and spatial scales. In addition, general surveillance requires long-term data sets in order to measure population responses to a changing environment. Adaptive approaches to monitoring are required that can incorporate these requirements and engage the interests of scientists, conservation practitioners and the public.

Lawton et al. (2010) provide a conceptual framework for delivering a ‘coherent and resilient’ ecological network. However, there is much the scientific community can do to guide the realisation of this objective and help ensure that biodiversity is secured into an increasingly uncertain future.


Habitat quantity, and the extent to which it is fragmented, is expected to affect the viability of populations of all species. However, the quality of the available habitat is likely to alter relationships between habitat quantity, connectivity and population viability. Exactly what constitutes ‘habitat’, ‘quality’ and ‘connectivity’ will be species-specific.

Figure 1
In terms of population viability, parameters (or goals) of particular interest are (i) the capacity to colonise habitat patches and establish populations there and (ii) the long-term persistence of populations both at local and regional scales. Various processes affect these key parameters at patch and landscape scales. These processes are shown according to their relevance to quality, quantity and connectivity of habitats. Likely interactions between processes are indicated with broken lines. All three aspects of landscape variation (quality, quantity and connectivity) are important but not independent.
Adaptive management structures that could potentially be applied to habitat creation schemes. These could be undertaken within single habitat schemes, or within clusters of similar schemes. (a) Shows a simple non-experimental approach in which monitoring is used to assess biodiversity responses to a chosen management policy. (b) Incorporates an experimental component. Experiments could be used to compare different management treatments against specified objectives for wildlife, or to examine the potential causes of particular management problems (e.g. declines in species, loss of plant diversity) and how to overcome them. In some cases it may be appropriate to include replicates and controls outside the habitat scheme(s). This may be needed where one wanted, for example, to assess affect of size of site on the responses to the treatments. Where a sufficiently clear conclusion can be drawn from the experiment this can have an immediate influence on management policy, but where the response is unclear or ambiguous it may be necessary to revisit the hypotheses and to refine the experimental treatments. In reality it may be decided to both alter management policy based on available evidence and undertake further experimentation. The red lines indicate change in biodiversity that occurs as a consequence of external factors that are not controlled by the internal management. For example, changing climate may lead to new assemblages as a consequence of range expansion and colonization, and/or shifts in habitat use by species. These external changes may alter management objectives and the design of experimental management.