# Conservation of Coppice and High Forest Management within the Natura 2000 Network – A Review

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## Abstract

The Natura 2000 network protects some of the most threatened species and habitats in the European Union, of which forests account for about 50% of the total designated area. This paper examines the broad habitat preferences of the terrestrial species listed in Annexes of the Birds and Habitats Directives, of which a majority are associated with non-forest habitats. By comparison, European red lists and the various country and regional level lists of species of principal importance contain many more species and species groups than the Directive Annexes. Foresters are likely to use a much narrower suite of species, often based only on the Annexes, when setting practical conservation targets for woodlands.

Achieving the objective of 'favourable conservation status', as required by the Directives, should apply equally to the designated forest habitat types and their listed specialist species. European Commission literature describes these habitats in terms of their typical tree, shrub and herbaceous species, although in practice a mixture of iconic and specialist Annex species may be used for making conservation assessments. Recognising the value of traditional coppice and its long anthropogenic history can be considered a valid reason for conservation in itself, but this form of management is now in serious decline all over Europe. High forests and old growth habitats, together with their associated species, also have equal claims for protection under the Natura 2000 network. Given the difficulty of simultaneously achieving species and habitat targets in the context of both early and late-successional aspects of forest conservation, we consider different silvicultural strategies that may achieve wider biodiversity benefits in the forest environment.

### Key words

Natura 2000, Birds and Habitat Directives Annex species, forest habitat type, indicator species, coppice, silvicultural system

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# Introduction

Some of the most valued and threatened species and habitats in Europe are protected within the Natura 2000 network under the Birds Directive (European Commission 1979) and the Habitats Directive (European Commission 1992). The latter Directive targets more than 230 'habitat types' and 1500 animal and plant species for conservation in its various Annexes, many of which are rare, threatened or endemic. They include 303 animals, 586 plants (Habitats Directive Annex II, HDII) and more than 190 birds (Birds Directive Annex I, BDI). For a further 400 species and sub-species listed in Annex IV of the Habitats Directive (HDIV), which includes many that are also listed in HDII, a strict protection regime must be applied across their entire natural range in the European Union (EU), both within and outside Natura 2000 sites.

Approximately 375,000 $km^2$ of forests are included in the Natura 2000 Network, representing around 50% of its total area and 21% of the total forest resource in the EU (European Commission 2015). A large proportion of this forest would undoubtedly have been coppiced in the past: based on the average of 24 European countries, up to 15% of the area is presently classified as coppice, together with a probably much greater extent of neglected or converted former coppices (Buckley and Mills, 2015). Considering the large protected area and the strong emphasis given to conserving the threatened biodiversity of forest ecosystems within the EU, one would anticipate that a high proportion of Directive-protected species would be found in, or be dependent on, forested habitats. To discover whether this is the case, the habitat preferences of species listed in BDI and HDII were investigated. The contribution that the traditional forestry techniques of coppicing and pollarding can bring to the protection of biodiversity in Natura 2000 sites was also considered.

Many of the species on the BDI and HDII lists are species of conservation concern, judged as vulnerable or under threat by the International Union for Conservation (IUCN). We consider the composition of different taxa making up these lists, their endemicity, threat status, and their preferences for forest habitats or other, more open ones. In the case of forest and woodland habitats, the definition of 'favourable conservation status', as applied by the Bird and Habitat Directives to both habitats and species, especially more 'typical' species as well as the Natura 2000 species, depends on the ability of different forest management regimes to conserve them. Here we focus initially on traditional coppice forest management, a widespread but now rapidly disappearing silvicultural practice in Europe, and the implications that abandonment or conversion to high forest might have for protecting habitats and species. At the same time we consider what additional protected species niches high forest systems might provide. Finally, we discuss management strategies that might deliver combinations of both early and late-successional growth stages, and which may serve to increase species diversity in forested landscapes.

## METHODS: ALLOCATING BROAD HABITAT PREFERENCES TO SPECIES

Using the HDII and BDI Annexes, each protected species was allocated to one or a number of broad habitat types, using the hierarchical classification proposed by the European Environment Agency (EUNIS) (European Environment Agency n.d.). The EUNIS species browser (http://eunis.eea.europa.eu/species.jsp) lists the 'most preferred habitats' in its quick facts for nearly all of these species. These, excluding fish, were allocated to the 10 EUNIS hierarchical habitats (http://eunis.eea.europa.eu/habitats-code-browser.jsp) described in Table 1. If no habitats were listed for a species on the EUNIS database, the world IUCN Red List species details (http://www.iucnredlist.org/details/) were consulted. When not listed in either database, it was recorded in the 'Insufficient data' column, except for fewer than 10 cases where information was taken, for example, from Wildscreen ARKive (http://www.arkive.org), EEA Eionet (https://www.eionet.europa.eu), Joint Nature Conservation Committee (http://jncc.defra.gov.uk), Environment Directorate General of the European Commission (http://ec.europa.eu/environment/index_en.htm) and Birdlife International (http://www.birdlife.org)

While recording this data, it was also noted if a species was on the IUCN Red List and if it was an endemic.

Table 1. Summary of 10 broad habitat types and their descriptions, based on the hierarchical classification proposed by the European Environment Agency (EUNIS)

| | | |
|---|---|---|
| 1 | **Marine** | Marine habitats: fully saline, brackish or almost fresh. Includes marine littoral habitats including tidal saltmarshes; marine littoral habitats and strandlines; waterlogged littoral saltmarshes and associated saline or brackish pools. |
| 2 | **Coastal** | Habitats are those above spring high tides, including coastal dunes and wooded coastal dunes, beaches and cliffs. Supra-littoral habitats include strandlines, moist and wet coastal dune slacks and dune-slack pools. |
| 3 | **Inland surface waters** | Non-coastal fresh or brackish waterbodies (rivers, streams, lakes and pools, springs), including their littoral zones. Also constructed waterbodies (canals, ponds, etc.) supporting semi-natural communities and seasonal waterbodies. |
| 4 | **Mires, bogs and fens** | Wetlands, with the water table at or above ground level for at least half of the year, dominated by herbaceous or ericoid vegetation. Includes inland saltmarshes and waterlogged habitats where the groundwater is frozen. |
| 5 | **Grasslands** | Dry or only seasonally wet land with >30% vegetation cover. Dominated by grasses and other non-woody plants, including mosses, macro-lichens, ferns, sedges and herbs. Includes semiarid steppes, successional weedy vegetation and managed grasslands (e.g. recreation fields and lawns). |
| 6 | **Heathland** | Dry or only seasonally inundated land with >30% vegetation cover. Includes tundra; heathland dominated by shrubs or dwarf shrubs not above 5m tall. Also shrub orchards, vineyards, hedges, climatically-limited dwarf trees (krummholz) >3 m high, *Salix* and *Frangula* carrs. |
| 7 | **Woodland** | Dominated by trees over 5m, with a canopy cover of at least 10%. Includes lines of trees, coppices, tree nurseries, plantations and fruit and nut tree orchards. Includes *Alnus* and *Populus* swamp woodland and *Salix*. Excludes *Corylus avellana* scrub and *Salix* and *Frangula* carrs. |
| 8 | **Sparsely vegetated** | Habitats with less than 30% vegetation cover which are dry or only seasonally wet. Includes caves and passages including underground waters and disused underground mines, and habitats with permanent snow and surface ice. |
| 9 | **Cultivated** | Habitats maintained solely by frequent tilling or recently abandoned arable land and gardens. |
| 10 | **Constructed** | Primarily human settlements, buildings, industrial developments, transport networks and waste dumps. Includes artificial saline and non-saline waters with wholly constructed beds or heavily contaminated water, virtually devoid of plant and animal life. |

# Results

## Species groupings

We calculate that 80-90% of BDI and HDII species are also registered on the International Union for Conservation of Nature Red List of Threatened Species (IUCN 2015), which classifies species on the basis of their relative extinction risk, consistent with their need for protection (Fig. 1). Relative to their species numbers, plants, birds and mammals are well represented, but some taxa, such as the arthropods, have received less attention, with under 50% of HDII species recorded on the world Red List, perhaps reflecting the relative scarcity of specialists dealing with this numerous group. Moreover, the species chosen for protection under HDII and HDIV are subject to taxonomic, geographic and aesthetic bias, with preferences given to larger, iconic species, but also including many that are widespread (Cardoso 2012). This bias is evident in the relative dominance of vertebrates compared with very few in the arthropod group, which in turn is biased towards Lepidoptera and Coleoptera, while completely lacking large insect Orders such as Diptera and Hymenoptera. Although plant species make up the largest group in HDII, only 32 bryophytes and no fungi or lichens are included (Orlikowska et al. 2016).

## Endemicity and threat status

Listing of HDII species is heavily influenced by their endemic status. Overall, 415 primarily terrestrial species or subspecies (41.7%) are strict endemics, i.e. restricted to one EU country or to Macaronesia. Plants and molluscs have the highest share of endemic taxa (63.8% and 48.3% respectively), with reptiles and amphibians intermediate and breeding birds

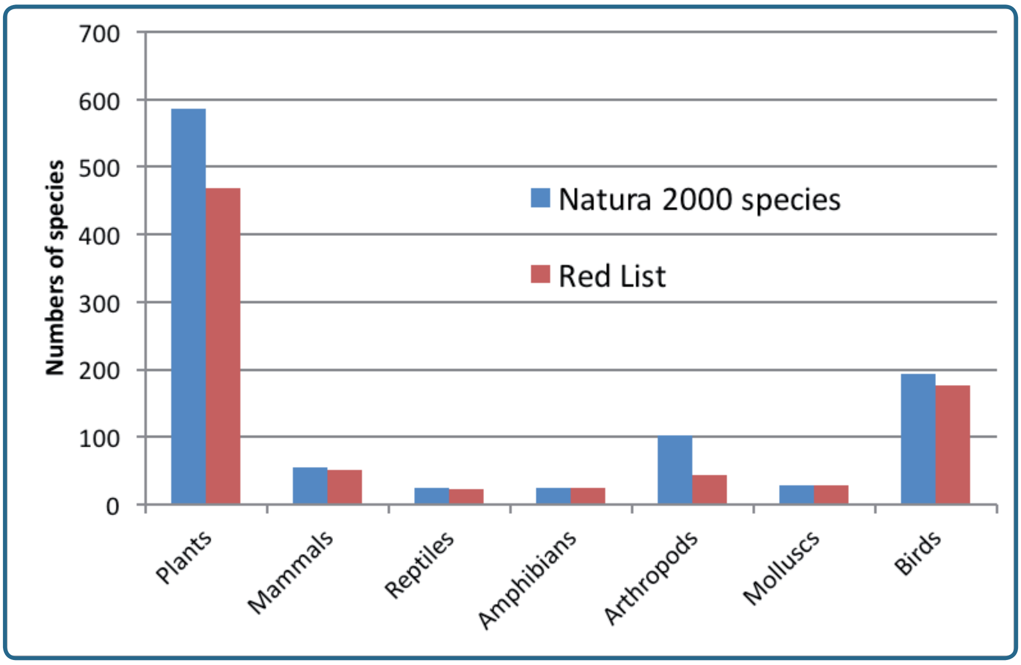


Figure 1. Numbers of BDI and HDII species and on the world IUCN Red List present in each taxonomic group, excluding fish

the lowest (4.9%) (Fig. 2). The low number of arthropods (8.3%) almost certainly reflects an incomplete assessment of this very diverse group. Macaronesian plant species, being by definition full endemics, make up over a quarter of all HDII plants, while of the non-Macaronesian plants, 55.9% are also strictly endemic.

While reptiles, molluscs and plants were relatively more threatened, many mammals, amphibians and birds were of 'least concern' on the IUCN World Red List, but when viewed in a narrower European context, several species may be perceived as more threatened.

Nearly half of BDI and HDII species (48%) fell into the threatened categories (critically endangered, endangered, vulnerable and near-threatened) on the world Red List.
The figures were (Fig. 3):

- 87% for reptiles,
- 68% for molluscs,
- 55% for plants,
- 52% for amphibians
- 43% for mammals,
- 36% for arthropods
- 21% for birds.

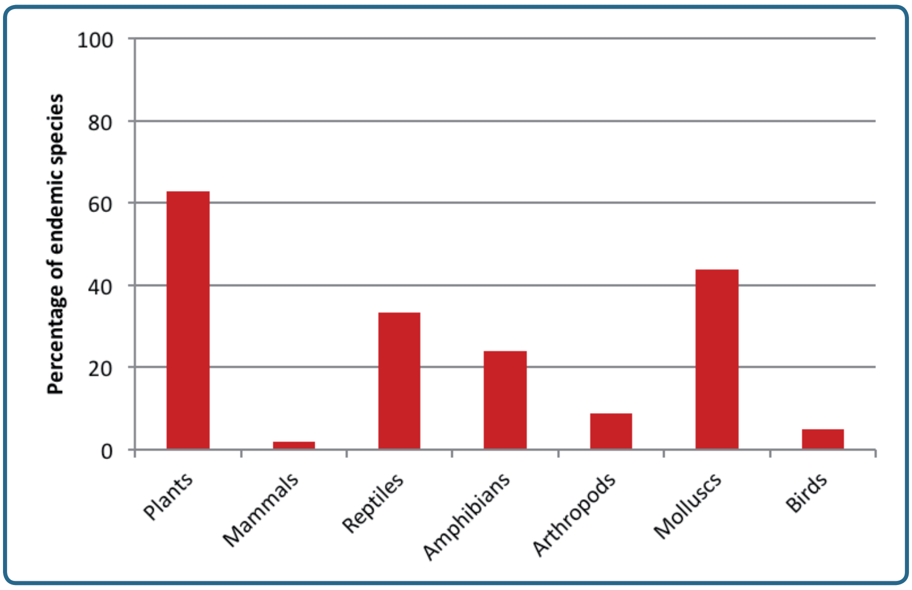


Figure 2. Percentage of BDI and HDII endemic species, by taxonomic groups (excluding fish)

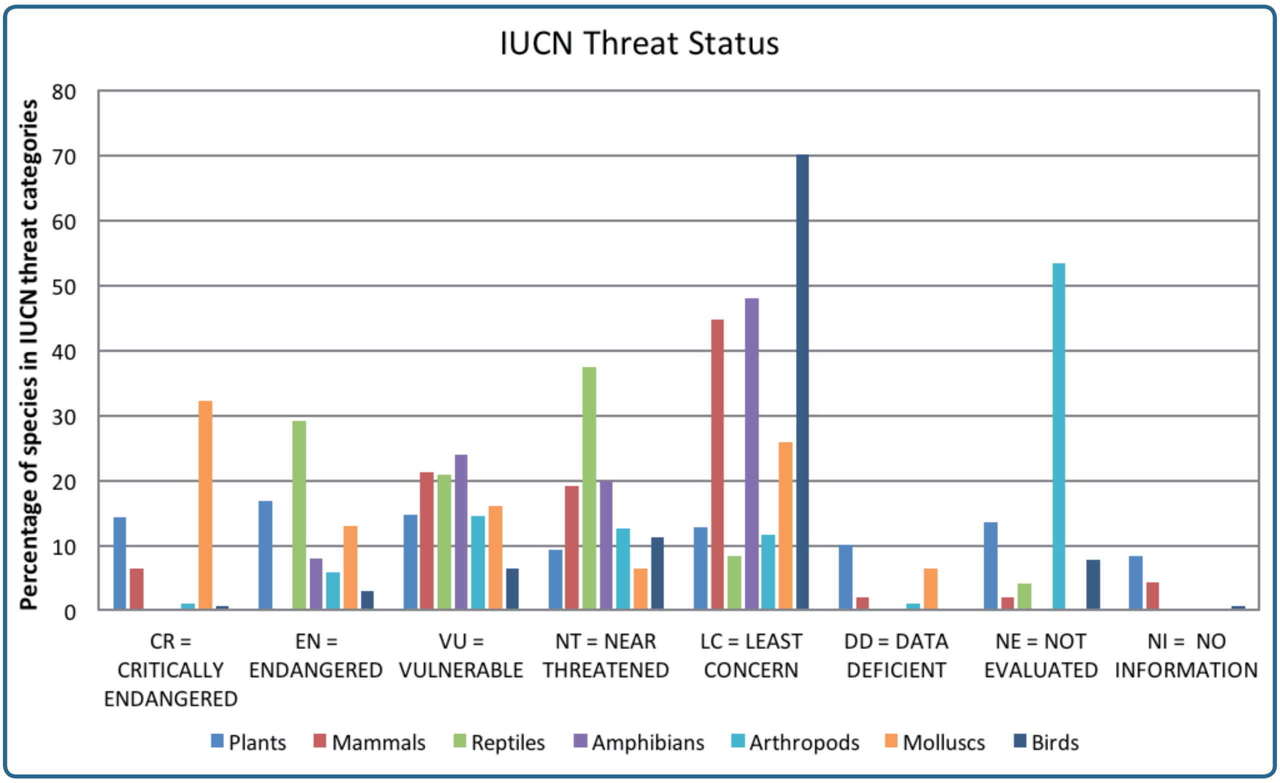


Figure 3. Percentage of BDI and HDII species from different terrestrial taxonomic groups in the IUCN world list categories

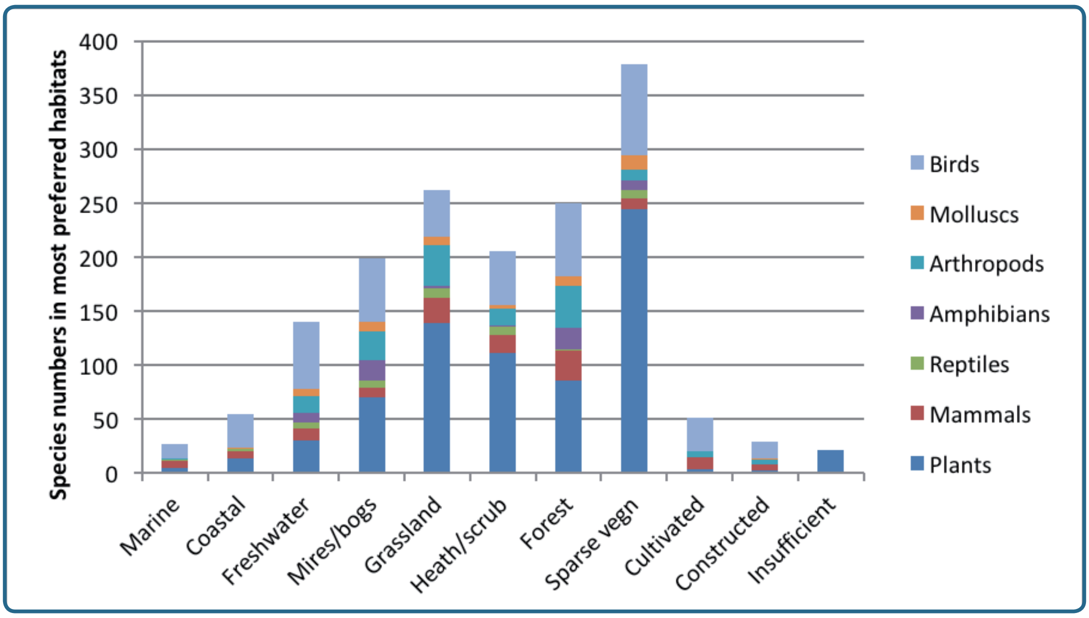


Figure 4. Numbers of BDI and HDII species occurring in different EUNIS habitat types

## Habitat distributions of protected species

The most frequent preferred species habitats were in sparsely vegetated habitats, with grasslands, forests, heathlands and wetlands intermediate, and relatively few in marine, coastal, cultivated and construction sites (Fig. 4). Several plant species were given preferred habitat status in sparse vegetation, although many could also be categorised more specifically as species of sand dunes, cliffs, tundra and alpine habitats. Of particular interest was the 'forest and woodland' category, which contained relatively balanced proportions of the different taxonomic groups compared with other categories, including a comparatively high number of arthropods, amphibians and mammals, although relatively fewer plants and reptiles than in other open habitats. As forests cover such a large part of the Natura 2000 network, it is not surprising that they shelter a large number of Directive-protected species. Collectively, however, the great variety of more open habitats (e.g. sparse vegetation, grassland, heath, etc.) contain significantly more. The vast majority of these BDI and HDII species appeared to be associated with non-forest or relatively open conditions.

## Spatial hierarchies of protected species

Lists of rare species tend to become more refined as the area of interest narrows. A hierarchical gradient taken from the IUCN world perspective, diminishing in scope for Natura 2000 and the European Red Lists, and further to the more localised level of countries and regions, shows that species lists of principal conservation importance often tend to become more focused and lengthier (Table 2). In separate European countries and regions, protected species lists are generally focused more at this level than at the BDI and HDII Annex level: those species relatively widely distributed at a European level effectively become 'rarer' at a local level, and therefore more notable. Compared with the BDI or HDII species annexes, European Red Lists contain many more species, often more than three times the number. This is particularly obvious for invertebrate Red Lists of dragonflies (Kalkman et al. 2010), saproxylic beetles (Nieto and Alexander 2010), non-marine molluscs (Cuttlelod et al. 2011), butterflies (van Swaay et al. 2011) and bees (Nieto et al. 2014). At a national level the picture is even more variable: in Britain, for example, as would be expected from this country's size and its history of glacial impoverishment, the numbers of vascular plants, mammals, reptiles and amphibians were lower than the equivalent BDI and HDII annexes and European red lists, but a greater effort has been made to cover non-vascular plants, invertebrates, fungi and lichens. In other countries and regions, such as France, Estonia and Flanders, the same tendency to specialise within some of the broader taxonomic groups is seen (Table 2).

Table 2. Numbers of terrestrial species (mostly terrestrial or freshwater) selected at different spatial levels for biodiversity conservation: the IUCN world red list, the BDI and HDII, the IUCN European red lists, UICN French red lists, the UK Biodiversity Action Plan, Estonian protected species and Flanders red lists

| Taxonomic group | HDII and BDI species on IUCN world red list[1] | HDII and BDI species (Natura 2000)[2,3] | European red list (EU27) | France red lists | Britain – species of principal importance[4] | Estonian protected species[5] | Flanders red lists |
|---|---|---|---|---|---|---|---|
| **Vascular plants** | 412 | 554 | *1750[6] | 1018[7,8] | 382 | 215 | 1152[9] |
| **Non-vascular plants** | 1 | 32 | * † | | 552 | 46 | |
| **Mammals** | 45 | 47 | 179[10] | 99[11] | 25 | 18 | 65[12] |
| **Total invertebrates** | 75 | 135 | | | 597 | 52 | |
| Dragonflies | 11 | 11 | *134[13] | | 3 | 5 | 64[14] |
| Saproxylic beetles | 9 | 17 | *408[15] | | 10 | 3 | 19[16] |
| Molluscs | 31 | 31 | *1805[17] | | 29 | 4 | |
| Lepidoptera | 14 | 38 | 421‡[18] | 253‡[19] | 195 | 10 | 72‡[20] |
| Bees | 0 | 0 | 1900[21] | | 44 | 18 | |
| **Reptiles** | 23 | 24 | 128[22] | 35[23] | 6 | 5 | 6[24] |
| **Amphibians** | 25 | 25 | 82[25] | 35[23] | 4 | 11 | 16[24] |
| **Fungi/lichens** | 0 | 0 | 0 | | 782 | 97 | |
| **Birds** | 150 | 162 | 399[26] | 345[27] | 105 | 93 | 200[28] |

*to be completed by 2018 † bryophytes only ‡ butterflies only

[1]IUCN (2015) [2]European Commission (1992) [3]European Commission (1979) [4]Natural Environment and Rural Communities (NERC) Act (2006a, 2006b), Nature Conservation (Scotland) Act (2004) [5]Riigi Teataja (2014a, 2014b) [6]Bilz et al. (2011) [7]UICN France et al. (2012) [8]UICN France et al. (2009) [9]Van Landuyt et al. (2006) [10]Temple and Terry (2007) [11]UICN France et al. (2009) [12]Maes et al. (2014) [13]Kalkman et al. (2010) [14]De Knijf (2006) [15]Nieto and Alexander (2010) [16]Thomaes et al. (2015) [17]Cuttelod et al. (2011) [18]van Swaay et al. (2010) [19]UICN France et al. (2014) [20]Maes et al. (2011) [21]Nieto et al. (2014) [22]Cox and Temple (2009) [23]UICN France et al. (2015) [24]Jooris et al. (2012) [25]Temple, Cox (2009) [26]Birdlife International (2015) [27]UICN France et al. (2011) [28]Devos et al. (2004).

At forest species protection level, Britain's state forestry service (the Forestry Commission) has produced a web-based decision support system for its managers dealing with Habitats and Rare, Priority, and Protected species (HaRPPS). This provides information on about 123 woodland species, including:

- 25 mammals,
- 37 birds,
- 4 herptiles,
- 21 invertebrates,
- 13 vascular plants and
- 23 fungi and lower plants (Forest Research 2011),

allowing forest managers to predict which species might be present in a given area and to test the impact of forest operations on them.

Although the British lists of species of principal importance for conservation cover all habitats, including forests (NERC Act 2006a,b; Nature Conservation (Scotland) Act 2004) there are big disparities with HaRRPS for different taxonomic groups: mammals, birds and herptiles are well covered, whereas vascular plants, bryophytes, liverworts and invertebrates are not (Fig. 5). Practising forest managers should be able to identify iconic animals and birds in their well-protected groups, but are less likely to have specialist knowledge of some invertebrates, fungi, vascular and non-vascular plants.

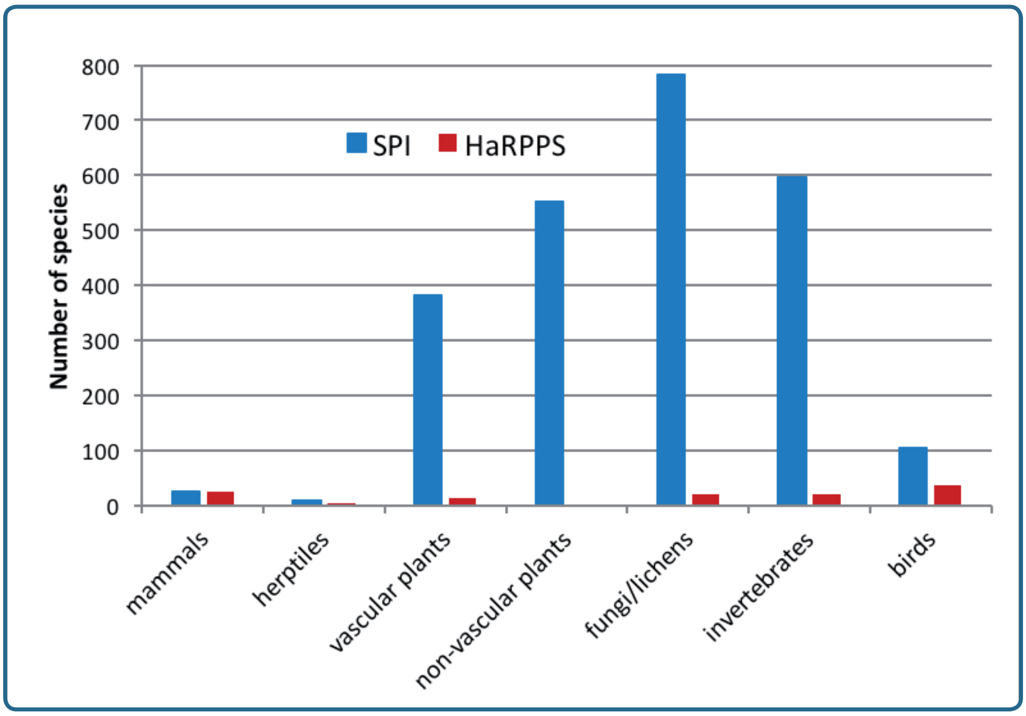


Figure 5. Numbers of species of principal importance (SPI) in Britain by taxonomic group, relative to that of the Forestry Commission's information system for use in woodland habitats (Habitats and Rare, Priority and Protected Species HaRPPS) (Forest Research 2011)

# Discussion

## Favourable conservation status

The emphasis placed on rare or iconic species is not always effective in promoting species diversity, as the overriding issue for forest species is fundamentally the protection of their habitat and its quality. However, when compiling the Standard Data Forms for the designation of Natura 2000 sites, agencies tend to focus on rare species, irrespective of whether they are only a fraction of a metapopulation that extends beyond the boundary of the protected area (Battisti and Fanelli 2014). In fact, in terms of ecological integrity, achieving a 'favourable conservation status', a legal requirement of Natura 2000 designation, applies to any 'typical species' of a HDI habitat (Rees et al. 2013). The Directive applies equally to the habitat, which must be stable or increasing and likely to sustain its structure and function for the foreseeable future. The reality is that only 15% of the protected forest habitats in the EU are reported as being in a favourable condition due to multiple factors, such as fires, disease, browsing, pollution, urbanisation, etc., but mainly to forest and plantation management, such as the removal of dead and dying trees (European Commission 2015). Among the human activities reported on Standard Data Forms, agriculture and forestry were associated with more than 86% of a sample of Natura 2000 sites, of which forestry activities affected 59% (Tsiafouli et al. 2013). Many broadleaved forest HDI habitats described as 'Temperate Forests of Europe' in the European Commission's Interpretation Manual of European Union Habitats EU28 (European Commission 2013) have the potential to be coppiced, based on the re-sprouting potential of the dominant trees (Mairota et al. 2016), although most is now high forest. The summary descriptions of each forest habitat type are of essentially widespread or characteristic plant species (Table 3), including several relatively common herbs and grasses, which depend on the forest margins and the more frequently open canopies that could be provided by coppice management. Very few HDII species (i.e. rarities and endemics) are listed. When this suite of 'typical', widespread species is present, it follows that a 'favourable conservation status' is more likely to be achieved for rarer ones.

To support the regular monitoring of Natura 2000 sites a range of species specialists associated with long-term anthropogenic management of their forest habitat could be identified, as recognised by the Habitats Directive (Epstein et al. 2015). Such 'indicator species' would not necessarily be rare endemics or HDII species, but could represent several taxa, including vascular plants, bryophytes, wood-decaying fungi, epiphytic lichens, saproxylic beetles and land snails (Nordén et al. 2014). Some of these are more properly indicators of traditional high forest or old growth, but many ancient woodland 'indicator plants' with limited dispersal characteristics (sensu Hermy et al. 1999; Verheyen et al. 2003; Kimberley et al. 2013) are also associated with former coppice habitats; Decocq et al. (2005) even suggested that they might be better labelled 'coppice-woodland species'. In northwest Germany, Schmidt et al. (2014) listed 67 ancient woodland indicator plants, most of them typical of closed forests, but with 13% preferring forest edges and clearings, while Pellisier et al. (2013) identified 40 'core' and 38 'periphery' forest species based on a large database of over 1800 forest patches in northern France.

Aesthetic as well as biodiversity criteria can be taken into account in species protection. In the Zurich Canton of Switzerland, aesthetic criteria were involved in an action plan to restore the typical flora (from a target list of 172 species) associated with 'light' or open-canopied forests, which was carried out on a portion of the total forest area of 47,500 ha (Bürgi et al. 2010). The areas selected were based on an analysis of the target species and forest management practices, recognising not only anthropocentric history but also the ecological continuity of coppice habitats within the region, much in the spirit of the Habitats Directive.

## Provision for coppice specialists

Traditional coppice management, often based on regular short rotations over centuries, has produced a habitat for species that are adapted to the dynamic of rapidly altering light, temperature and hydrological regimes (Peterken 1993, Rackham 2003, Szabo 2010). These regular, intense pulses of disturbance tend to boost the diversity in both the ground flora and shrub layers (Ash and Barkham, 1976; Decocq et al. 2004; Brunet et al. 2010; Verheyen et al. 2012; Campetella et al. 2016). The transient woodland structure produced is important for many songbirds that forage and nest in young growth, as well as for other open-ground

Table 3. Species with frequencies of 10% (2/20) or more that are named in the summaries of 20 different forest habitat types from the 'Forests of Temperate Europe' (Annex 1 code 9100); the list is based on 26,433 Natura 2000 sites where at least 100 sites are devoted to each forest habitat type

| **Trees** | /20 | | /20 | | /20 |
|---|---|---|---|---|---|
| *Quercus petraea* | 8 | *Acer tartaricum* | 3 | *Ilex aquifolium* | 2 |
| *Fagus sylvatica* | 6 | *Betula pubescens* | 3 | *Populus nigra* | 2 |
| *Quercus cerris* | 6 | *Fraxinus angustifolia* | 3 | *Populus tremula* | 2 |
| *Quercus robur* | 6 | *Fraxinus excelsior* | 3 | *Quercus pyrenaica* | 2 |
| *Carpinus betulus* | 5 | *Euonymus verrucosus* | 3 | *Sorbus domestica* | 2 |
| *Acer campestre* | 4 | *Picea abies* | 3 | *Taxus baccata* | 2 |
| *Sorbus torminalis* | 4 | *Quercus pubescens* | 3 | *Tilia tomentosa* | 2 |
| *Tilia cordata* | 4 | *Acer pseudoplatanus* | 2 | *Ulmus glabra* | 2 |
| *Abies alba* | 3 | *Alnus glutinosa* | 2 | *Ulmus minor* | 2 |
| **Shrubs** | /20 | | /20 | | /20 |
| *Euonymus verrucosus* | 3 | *Frangula alnus* | 2 | *Vaccinium myrtillus* | 2 |
| *Ligustrum vulgare* | 3 | *Pyrus pyraster* | 2 | | |
| *Buxus sempervirens* | 2 | *Ruscus aculeatus* | 2 | | |
| **Herbaceous Species** | /20 | | /20 | | /20 |
| *Carex montana* | 4 | *Anemone nemorosa* | 2 | *Hieracium sabaudum* | 2 |
| *Dentaria* spp. | 4 | *Buglossoides purpurocaerulea* | 2 | *Lathyrus niger* | 2 |
| *Festuca heterophylla* | 3 | *Carex michelii* | 2 | *Luzula forsteri* | 2 |
| *Knautia drymeia* | 3 | *Cyclamen purpurascens* | 2 | *Molinia caerulea* | 2 |
| *Potentilla micrantha* | 3 | *Galium schultesii* | 2 | *Potentilla alba* | 2 |
| *Pteridium aquilinum* | 3 | *Galium sylvaticum* | 2 | *Pulmonaria mollis* | 2 |
| *Tanacetum corymbosum* | 3 | *Helleborus odorus* | 2 | *Tamus communis* | 2 |

foragers (Camprodon and Brotons 2006; Fuller 2012). After coppicing, the resulting sunny and warm miocroclimate creates suitable conditions for a range of butterflies, macromoths and other invertebrates (e.g. Sparks et al. 1996; Fartmann et al. 2013; Horák et al. 2014), which take advantage of increased understorey flowering and abundant sources of pollen and nectar.

While many thermophilic and opportunistic species are cosmopolitan, others are more restricted to the coppice habitat. They include many vascular plants tolerant of intermittent shading, accompanied by a large insect biomass dependent on flowers and young foliage (Warren and Key 1991; Greatorex-Davies and Marrs 1992). In order to maintain viable populations, sufficient canopy openings and forest margins must be present, whether created anthropogenically or by a natural disturbance dynamic. Some beneficiaries that are specialists of the coppice habitat are considered of high conservation value: there are examples of conservation coppicing carried out expressly to support a single species or group of species. Examples are rare butterfly populations such as the Scarce Fritillary (*Euphydryas maturna*) and many others that are not necessarily listed in HDII and HDIV (e.g. van Swaay et al. 2006; Kobayashi et al. 2010; Fartman et al. 2013; Dolek et al. 2018). Very low densities of standards in coppice, covering as little as 10-15% of the stand, have been recommended in order to maintain open conditions for butterfly conservation (Clarke et al. 2011). Coppicing may also be maintained specifically for other iconic species such as the hazel grouse (*Bonasa bonasia*), where coppice provides a substitute for its optimum forest habitat of shrub layers in gaps of old-growth forests (Kajtoch et al. 2012), for migrant songbirds that nest and forage in scrub (e.g. *Sylvia* species), and small mammals such as the hazel dormouse (*Muscardinus avellanarius*) (Ramakers et al. 2014; Sozio et al. 2016).

Many other species also benefit from the openings created by coppicing. However, in long-neglected or converted coppice stands, plant species diversity and some red-listed herb layer species tend to diminish rapidly (Van Calster et al. 2008a; Kopecky et al. 2013; Vild et al. 2013; Müllerová et al. 2015). In formerly grazed and coppiced sub-continental oak forest in the Czech Republic, these declining and endangered species tended to persist in locations with high light availability and relatively higher pH (Roleček et al. 2017). Similarly, in comparing vegetation data from still-active selection coppices with beech-dominated high forests in the Banat region in Romania, the coppices were slightly more diverse, containing thermophilous and non-forest species more typical of more open grassland habitats, although they were similar in herb species richness to high forests (Šebesta et al, 2017). The re-application of traditional forest management practices may be able to reverse successional tendencies in long-abandoned or converted former coppices. In lowland thermophilous oak forest, restoration of a litter-raking treatment effectively increased the richness and cover of both forest and dry grassland species over a 5-year period (Douda et al. 2017). The restoration of canopy thinning, analogous to coppicing, in a long abandoned ancient coppice-with standards woodlands, has been shown to potentially support and revive light-demanding woodland floras (Vild et al. 2013) and also to increase the functional diversity responses of plant and ground-dwelling spider communities (Šipoš et al. 2017).

Several researchers have shown that vascular plants in the herb layer of beech forests were marginally more diverse in managed stands or after disturbance at the plot level, compared with unmanaged stands, later to decline with neglect (e.g. Schmidt 2005; Bartha et al. 2008; Garadnai et al. 2010; Mölder et al. 2014). At the patch level, Campetella et al. (2016) showed that a rich species pool of specialist plants associated with beech forest in the Central Apennines could be maintained under active management, i.e within a landscape mosaic comprising different woodland development stages. In the same region, Scolastri et al. (2016) found that beech forests, whether classified as old coppice-with-standards or as high forest, contained many heliophilous plants indicative of past light regimes, as well as many shade-tolerant, understorey species typical of 9210* Apennine beech forests with *Taxus* and *Ilex* recognised in the European Commission's Habitat Directive Interpretation Manual (European Commission, 2013). Cervillini et al. (2017) considered that with canopy cover stabilising between 10 and 16 years, approximately 10 years before coppice harvesting, many such specialists of shaded beech forests were able to persist.

## Conversion to high forest

Coppices gradually change their biological character when they are abandoned or are converted into high forests. Several long-term studies have investigated the vegetational and edaphic changes resulting from this transition in European forests (Debussche et al. 2001; Peterson 2002; Decocq et al. 2004, 2005; Van Calster et al. 2007, 2008b; Baeten et al. 2009; Verheyen et al. 2012; Kopecký et al. 2013; Verstraeten et al. 2013; Becker et al. 2016). Most of these recorded a decline in species-richness of the tree, shrub and herb layers, with homogenisation increasing under the shade cast by a developing canopy, together with increases in shade-tolerant, vernal and eutrophic species.

Changes in the vegetation, such as increasing tree cover, may be happening in parallel with coppice abandonment, frequently detected in signals of eutrophication and acidification resulting from increased atmospheric deposition (Verheyen et al. 2012), as well as potential climate change. Peterson (2002), investigating a chronosequence of sample plots in ageing coppice in Denmark (median age = 40 years), suggested that increasing shade, together with the build-up of acidifying litter, tended to reduce species density and to favour clonal forest species. In Belgium, Van Calster et al. (2007) also reported increases in soil acidity in coppice-with-standards undergoing conversion to high forest from 1967-2005, at least partly explained by the poor litter quality under canopies of *Fagus sylvatica* and *Quercus robur*. In recordings made over an interval of 50 years, Verstraeten et al. (2013) found that the species pool of understorey herbs in former coppice-with standards generally declined, as did Ellenberg light indicator values, while those for nitrogen availability increased. The high input of atmospheric deposition within this period shifted the plant community towards a more N-demanding and shade-tolerant type.

In Germany, similar observations were made by Becker et al. (2016) in coppice-with-standards woodlands which had been in conversion for c. 100 years. They recorded decreases in species richness, accompanied by increases in nitrophilic and shade-tolerant species over a recording interval of 41 years, although the legacy of coppicing was still evident in the composition of the tree, shrub and herb layers, suggesting that the influence of former management could persist for more than a century. In beech-dominated forest that had formerly been under a coppice-with–standards regime, Heinrichs and Wolfgang (2017) detected relatively more homogenisation over time in those understorey communities situated on dry, nutrient-poor and sun-exposed slopes, which tended to lose light-demanding, drought tolerant and oligotrophic species, compared with a more mesic forest community, which tended to gain in generalist species. A more recent resurvey interval, with a baseline set in the 1990s, detected similar increases in nitrophilous and mesotrophic light-demanding species in formerly coppiced thermophilous oak forests in SW Poland (Reczyńska and Świerkosz 2016). However, in this case an increase in plant biodiversity and an inferred decrease in soil pH occurred over the 20-year interval, coinciding with major reductions in sulphur emission levels between 1960 and 2000. Other drivers of change were declining soil moisture and increased ungulate grazing.

## Provision for other forest habitats

Notwithstanding the apparent lack of deadwood for saproxylic niches in coppices, it has been pointed out that some are capable of maintaining microhabitats such as dendrothelms and mould cavities in old coppice stools, pollards or standard trees (Lassauce et al 2012; Vandekerkove et al. 2016, Larrieu et al. 2016). Microhabitats in ageing stands of trees are key components of biodiversity – for example tree cavities will benefit several mammals, birds, arthropods, but also fungi, bryophytes and lichens, including several obligate saproxylic beetles listed in Annex II of the Habitats Directive such as *Limoniscus violaceus*, *Osmoderma eremitica, Cerambyx longicorn* and *Lucanus cervus*. As stands age and amounts of deadwood increase, old coppices may even have the potential to allow saproxylic species to re-colonise. In the medium term at least, they may favour species with a preference for sun-exposed wood (Vandekerkhove et al. 2016).

The reductions in herb-layer diversity commonly observed in unmanaged forests do not apply to many other species groups. A meta-analysis of European forest literature found a marginally wider species diversity in unmanaged forests compared with managed ones, the differences increasing with time since abandonment (Paillet et al. 2010). Management tended to favour light-demanding understorey vascular plants, ruderals and competitive species, whereas bryophytes, lichens, fungi, saproxylic beetles and carabids, more dependent on closed-canopy, benefited from abandonment. However, the way in which high forests are managed may considerably effect the biodiversity of species requiring longer rotations. A systematic Biodiversity Exploratory Project on beech high forests in Germany actually found a greater species diversity in managed forests compared with unmanaged ones, but the former contained higher average amounts of deadwood, possibly accounting for a higher diversity of specialist deadwood beetles, mosses and lichens (Müller et al. 2015).

Conversely, in three European biogeographical regions Zehetmair et al. (2015a,b) found no differences between commercially exploited Natura 2000 sites and matching non-Natura 2000 stands of 9130 *Asperulo-Fagetum* forest in terms of their densities of forest-dwelling bats or beetle diversity (including saproxylic species). This suggested Natura 2000 status alone would not make the stands more ecologically effective, especially for encouraging late succession species, and that additional conservation efforts were needed in these designated stands. This would require more deadwood, both standing and fallen, retention of 'habitat trees' with microhabitats such as cavities and bark pockets, and mature, living trees as potential recruits. Current forest certification schemes and local forest administration rules increasingly advocate such conservation measures, but non-selective and intensive harvesting practices in many forest types still tends to remove senescent trees and reduce deadwood (Larrieu et al. 2016). This is particularly the case in actively managed coppice woodland with few, if any, mature trees, except in ageing stands that are no longer exploited.

In another forest type, old thermophilic oak forests, canopy openness favoured saproxylic species (fungi, lichens, beetles, ants, bees and wasps), inferring that coppice and wood pasture could maintain their populations in more open conditions (Horák et al. 2014). Similarly, in lowland oak forest in southern Moravia, canopy openness favoured an optimum diversity of spiders (Košulič et al. 2016), although these authors suggested that small-scale disturbances created by conservation thinning and selective harvesting, rather than extensive coppicing, could adequately maintain the various successional stages required. In old-growth, predominantly beech forest in the Czech Republic Horák et al. (2016) also found that saproxylic beetle richness was positively influenced by canopy openness, as well as by the the quantity of deadwood, whereas saproxylic fungi species responded more to canopy closure, deadwood quantity and higher levels of humidity. The higher temperatures under more open canopies might also partially compensate for a lack of deadwood (Schulze et al. 2016). Deadwood and old-growth conditions equally benefit the diversity of bird and bat communities. Cavity-nesting birds, as well as gleaner bats, were positively associated with standing deadwood in a study comparing managed and unmanaged stands of both lowland and upland forests in France (Bouvet et al. 2016). More nesting and feeding opportunities were available when microhabitats such as cavities and cracks were abundant, but insectivore birds, which require more open forests with well-developed shrub layers, were negatively affected by high densities of living trees.

Clearly, a range of forest age-classes or patches at a landscape scale would help to optimise their species diversity. While British literature tends to emphasise the benefits of young growth associated with coppice for birds, both European and North American studies emphasise the merits of later stand development for this same taxonomic group, perhaps reflecting the fact that Britain has relatively fewer old-growth stands (Quine et al. 2007). Thus, some balance between the extent of open and closed forests should deliver the maximum biodiversity for all taxa.

## Strategies to increase biodiversity

What other forms of silviculture might mirror the biodiversity associated with coppice management? Clear-cutting routines, which create abundant open space after harvesting, have aspects in common with a coppice cycle, although in coppice the canopies generally recover faster through vegetative regeneration and are also harvested earlier. Contrasting with traditional coppice-with-standards, the more frequent harvests in forests undergoing selective cutting may actually disadvantage the ancient woodland flora by causing greater disturbance (Decocq et al. 2005). In another context, the type of timber-harvesting practice, whether clear-cutting, thinning or selective, had relatively little effect on understorey plant diversity in temperate North American forests (Duguid and Ashton 2013). However, in this case selective cutting did increase plant species diversity compared with unharvested controls, possibly because the frequency of interventions increased the opportunity for early successional ruderals to co-exist with late successional perennials, analogous to the situation in harvested traditional coppices in Europe.

High forests, if neglected or managed along continuous cover, selection, or close-to-nature forestry lines, are far less likely to sustain large populations of light-demanding, thermophilic species, unless disturbance is sufficiently frequent and on a scale large enough to trigger patches of young growth across the landscape. In a comparison of intensively managed shelterwoods in Germany with the more extensive felling practices in Romania, where a period of self-thinning was followed by clear-cutting, Schulze et al. (2014) suggested that shelterwoods were probably less effective in promoting a wider biodiversity. At a practical level, some forest owners might prefer the simplicity of a clear-cutting routine to more intricate, close-to-nature management designed to optimise stand structure, species composition, amounts of deadwood and habitat trees for conservation (Borrass, 2014).

The few studies directly comparing managed and unmanaged forests have tended to agree that veteran trees and deadwood should be retained in order to support a full biodiversity of species, because the disintegration phase in forest development generally provides the highest biodiversity (Winter and Brambach 2011). If a few trees are allowed grow to large diameters, e.g. for more than 150 years, they will increasingly provide the cavities, dendrothelms, bark cracks and fungal sporophores that are missing in younger stands. For beech-fir forests Larrieu et al. (2012) recommended conserving 10-20% of the forest area as veteran trees, retaining at least some individuals of >70cm diameter; similarly, for beech forests, Gossner et al. (2013) suggested retaining 'habitat' trees of >50cm diameter.

Since coppice rotations are far too short to allow trees to enter the disintegration phase, longer rotations incorporating significant amounts of young growth could be achieved in irregular and strip shelterwoods, wood pastures and standards within the coppice. Standards could potentially provide some microhabitats and deadwood, but are traditionally felled at relatively young biological ages, typically at 100 years or less (Matthews 1989; Harmer and Howe 2003), and would need to be retained for longer if their full biodiversity potential were to be realised. Larrieu et al. (2012; 2016) considered that intervals of 50 years without harvesting in coppice-with-standards was insufficient to reach tree-bearing microhabitat densities approaching those of old-growth forests; double this period was more likely to achieve it. Large diameters of deadwood, favoured by many saproxylic beetles, can coexist within relatively open and sunny conditions in coppices and wood-pastures (Seibold et al. 2015; Sebek et al. 2015). Rather longer standard tree rotations of 125 years have been recommended by others for conservation reasons, covering 20-25% of the area (Hopkins and Kirby 2007). A greater proportion of older trees within coppice is provided by the 'single tree orientated silviculture' method advocated by Manetti et al. (2016), in which low densities of target trees within the coppice are selected (e.g. 100 $ha^{-1}$) and thereafter favoured by frequent thinning of their immediate neighbours, until they become valuable timber trees. This system produces a varied horizontal and vertical canopy structure comprising isolated trees, thinned stools and unmanaged coppice, although the crop trees are destined to be harvested when biologically still young, at merchantable size. Another silvicultural technique is to manage groups of standards as mini-high forests, embedded within the coppice stand (Mairota et al. 2016).

Standing and lying deadwood accumulation is strongly linked to biodiversity; the larger pieces providing a stable and enduring environment for the larvae of large-bodied beetles (Gossner et al. 2013). In European forests, a deadwood threshold of the order of >20-50$m^3$ $ha^{-1}$ has been suggested as necessary to support a high diversity of saproxylic organisms (Müller and Bütler 2010; Lachat et al. 2013). However, a significant patch-scale threshold of >300 $m^3$ $ha^{-1}$ was found in old-growth, mixed-montane forests in the Czech Republic, more than twice the level recommended by Müller and Butler (2010) for this type of forest (Horák et al. 2014). In south-eastern Germany, both the quantity and the diversity of deadwood (in contrasting sunny and shady situations) were found to be important drivers of saproxylic beetle assemblages in a mixed montane broadleaved/coniferous forest (Seibold et al. 2016). An extensive review of biodiversity within European beech forests by Brunet et al. (2010) concluded that the general sensitivity of species groups to shelterwood management roughly followed the order:

herbaceous plants
< soil macrofungi
< ground dwelling arthropods
< land snails
< saproxylic fungi
< hole nesting birds and saproxylic insects
< epiphytic lichens and bryophytes
< epixylic bryophytes,

a further argument for retaining a proportion of veteran trees in order to fully represent the saproxylic and epiphytic species. Shortening rotation lengths, as in the increased exploitation of wood energy in aged coppices, could negatively impact saproxylic biodiversity if 'habitat trees' are not retained (Lassauce et al. 2013).

To optimise conservation objectives, it is frequently suggested that older trees and old-growth features should be deliberately interspersed amongst conventional forest cycles - an ideal situation would be a mosaic of different forest structures and ages at a landscape or regional scale. Several authors cited conservation measures using variable retention harvests, in which patches of unharvested 'tree islands', or *'îlots de sénescence'*, are connected by a network of 'deadwood corridors', set within a productive, multi-aged forest matrix (Vandekerkove et al. 2013; Mason and Zapponi 2015; Larrieu et al. 2106). High density patches of mature trees would theoretially provide a more humid microclimate for fungi, bryophytes and lichens than would the spatially separated trees in a conventional coppice-with-standards arrangement. The best places for retaining veteran trees are likely to be within forest patches possessing a long history of continuity (Brin et al. 2016). Deadwood could also be retained in situ as part of regular harvesting, where the particular tree species may also be important. Gossner et al. (2016) suggested that leaving some larger-sized logs of subordinate trees such as *Carpinus betulus* behind on the forest floor could help to conserve saproxylic beetle diversity more effectively than would leaving larger amounts of dominant species, such as beech.

A study by Winter and Brambach (2011) showed that uniformly managed forests were less diverse in the number of different forest growth stages that they represented than their equivalent in matched forest reserves. A landscape mosaic consisting of different forest types and ages might be expected to provide habitats for far more species than one type more uniformly managed (Schulte et al. 2006). Interacting patchworks, networks, and gradients within the landscape will ultimately determine forest conservation and biodiversity (Forman 1995; Lindenmayer and Franklin 2002). If, on the other hand, a whole landscape were given over to the small-scale dynamics of close-to-nature silviculture, this would tend to reduce overall beta-diversity and homogeneity in forest structure (Decocq et al. 2005). Building in increased structural diversity, using a variety of systems - clear-felling, shelterwood cutting, group selection, single tree selection, etc. - would offer greater complexity from a silvicultural point of view (Schall and Ammer 2013).

# Conclusions

The Natura 2000 network uses criteria of species rarity and endemicity to represent Europe's threatened biodiversity. This is also true at international, national and regional levels, where priority species and some habitats are given special conservation and protection status. With the emphasis on the protection of rare and threatened species, this appears to be more of a bottom-up exercise than one based on the habitat type (Maiorano et al. 2015). The former is a fine filter, whereas the latter, though a coarse filter, could nevertheless be regarded as a surrogate for the presence of notable and rare species. However, the Natura 2000 system can be said to provide a positive 'umbrella' for many groups of non-Annex species, with some exceptions such as amphibians and reptiles (European Commission 2016; van der Slius et al. 2016).

An intimate knowledge of habitat requirements is needed to manage and maintain healthy populations and to balance the claims of several competing species. However, the Natura 2000 exercise will always be incomplete: many taxonomic groups have yet to be assessed or updated, as can be seen from the continuous revision of the European Red Lists and priority species lists used by different countries. In particular, invertebrates (such as arachnids and molluscs), soil fauna, bats and small mammals have poor representation. Taking one example, only 17 saproxylic beetles are listed on HDII whereas 407 appear on the EU27 Red List, 57 (14%) of which are in the threatened categories. Many are still 'data deficient', with more waiting to be assessed, some of which will likely be found to be threatened (Nieto and Alexander 2010) (Table 2).

Although the HDII list is in serious need of revision and regular updating (Hochkirch et al. 2013), this is likely to remain a long-term project. A recent EU Working Document on the two Natura 2000 Directives found that they were indeed 'fit for purpose' in achieving the broader framework of EU Biodiversity policy. While it could be argued that more improvements in species coverage and alignment with international agreements would be desirable, these could generate uncertainty, leading to delays in the full implementation of the Directives while increasing costs and decreasing legal certainty (Milieu et al. 2016).

Comparatively few Natura 2000 species are 'coppice' specialists, but these and more generalist species have an important role to play. Götmark (2013) suggested that, depending on forest size and objectives, four types of conservation management strategies should be combined:

1) minimal intervention, which could eventually apply to coppices that are no longer managed;

2) traditional management, based on historical research, such as coppicing and pollarding;

3) non-traditional management, for example to promote old-growth characteristics, though this is not applicable to most coppices, or a particular composition of tree species; and

4) management specifically to promote threatened, indicator and other species.

A silvicultural portfolio embracing the extremes of all successional stages, from coppicing of young trees through to old growth, best promises to enhance diversity at a landscape level. Forestry certification schemes currently set standards for tree retention and deadwood, but some also acknowledge the contribution to biodiversity of traditional forest management, such as coppicing and pollarding. A review of the impacts of forestry practices in Britain and

Ireland found that most improvements to forest biodiversity resulted from the temporary open space after harvesting, or through permanent open space, often associated with the road and ride network (Bellamy and Charman 2012). Given the potentially huge array of species comprising forest biodiversity, young growth alone cannot provide niches for all of them, whereas, in coppicing it can be used to promote iconic species as well as cosmopolitan ones. Other species, including many of those listed in the Annexes of Natura 2000, depend on high forest structures and old growth by combining different forest development stages. Overall biodiversity will only increase if both the protected and 'typical' species of forest habitats are given equal scrutiny.

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