



# Hedgerows as habitat for woodland plants

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*For hedgerows to act as corridors for woodland plants they must provide habitat conditions to suit species' autecological requirements. This supposition was tested by examining differences in the habitat and autecological characteristics of woodland plants according to their relative frequency in hedgerows and woodlands using a novel Habitat Preference Index (HPI). Indicator values for habitat and autecological characteristics of plant species were derived from Ellenberg and other published sources. Analyses were done separately for three main types of landscape in which hedgerows are found in Britain: (1) Lowland Arable; (2) Lowland Pastoral; and (3) Marginal Upland. The relative frequency of plant species across all three landscape types was similar and significant differences between HPIs and environmental indicators were found for all three landscape types. Plants more frequently found in hedgerows had significantly higher indicator scores for soil fertility, temperature, continentality together with reduced soil acidity, in comparison to those species more frequent in woodlands. Analyses of autecological indicators failed to show similar consistent trends across landscape types except for the number of woodland types of the National Vegetation Classification (NVC) in which species occur. Plants more frequently found in hedgerows were associated with fewer woodland communities suggesting that hedgerows contain only a narrow range of recognised woodland NVC stand types. Also, a significantly higher proportion of ancient woodland indicators were found in the group of plants that were more frequent in woodlands. Overall, results suggested that the environments of hedgerows are more similar to woodland edges than interiors. Qualitative differences between the environmental characteristics of hedgerows and woodlands are such that certain woodland plant species are highly likely to be limited in their capacity to use hedgerow networks. Implications for conservation of biodiversity are considered.*

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## Introduction

Linear landscape features have attracted considerable interest amongst conservationists due to their potential to facilitate movements of individuals between spatially segregated populations (Forman and Baudry, 1984; Saunders and Hobbs, 1991; Opdam *et al.*, 1995; Bennett, 1999). Regional ecological networks are already being planned on the basis that linear features function as corridors (Smith and Hellmund, 1993; Jongman, 1995; Arts *et al.*, 1995; Nowicki *et al.*, 1996) although some reviewers have warned that such recommendations

may be premature; not only is evidence for the efficacy of movement corridors scant, but the significance of such movements in the context of maintaining the integrity of interconnected populations has yet to be determined (Hobbs, 1992; Simberloff *et al.*, 1992; Dawson, 1994; Mann and Plummer, 1995; Rosenberg *et al.*, 1997).

An essential prerequisite for investigating a corridor function for plants of hedgerows is the identification of woodland species that have the potential to colonise them. Woodland plant species occur in hedgerows due to one, or a combination, of several different processes: they are able to spread from woodlands into hedgerows by: (1) short distance seed dispersal or vegetative spread ('spatial diffusion') (Peterken

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and Game, 1981; Bossuyt *et al.*, 1999); or (2) occasional long-distance seed dispersal ('stepping-stone' movements): (3) for their presence in hedgerows may be explained by the survival of relic populations in 'ghost' woodland boundaries (Pollard, 1973; Peterken and Game, 1981); or (4) for species which are widespread in the surrounding countryside their presence in hedgerows may simply reflect the random colonisation of one of a number of suitable habitats. Here, we investigate the autecological and habitat characteristics of woodland plant species in relation to their relative frequencies in woodlands and hedgerows. We do this in order to establish what conditions are necessary for hedgerows to facilitate movements of woodland plants in fragmented landscapes. As such this represents a preliminary analysis. It addresses a necessary requirement for hedgerows to serve as corridors. However, we expect to be able to distinguish any environmental differences between hedgerows and woodlands and detect autecological differences between their constituent species.

## Methods

### *Primary data source and analytical approach*

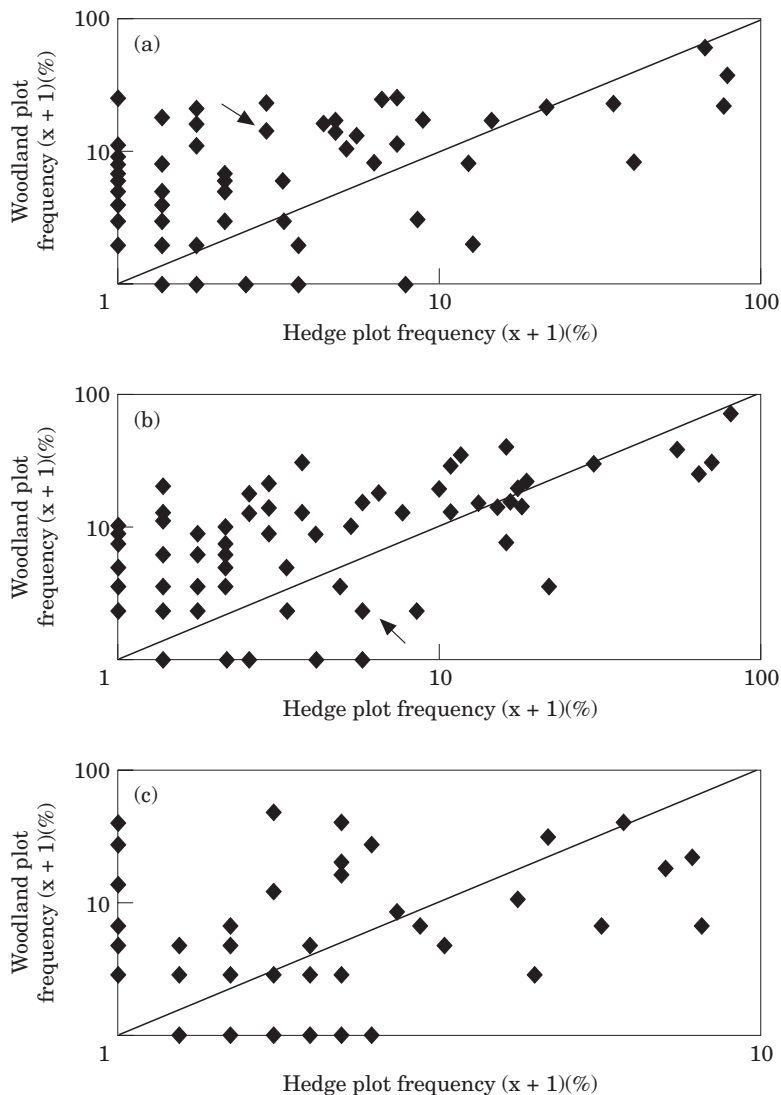
The database used for the analysis was from the Countryside Survey 1990 (CS1990) (Barr *et al.*, 1993). The data were collected in 1990 from 508 1-km squares distributed at random within the 32 environmental classes of the Institute of Terrestrial Ecology Merlewood Land Classification (Bunce *et al.*, 1996). The botanical data were collected from up to 27 locations in each 1-km square and for the present analysis the following data for vascular plants were extracted from two types of plots: (1) main plots of 200 m<sup>2</sup> within woodlands; and (2) hedgerow plots of 1 × 10 m laid out from the centre of two hedgerows, where present, selected at random within the 1-km square.

Plots were further aggregated into the four landscape types, Lowland Arable, Lowland Pastural, Marginal Upland and upland. Arable landscapes comprise 34% of GB and are concentrated on East Anglia, the East Midlands and the central valley and eastern

lowlands of Scotland. Land use is dominated by cereals and other arable crops and intensively managed grassland. Pastural landscapes comprise 20% of GB and are found widely in south-west England, west Wales, the west Midlands and north-west England. Land cover is dominated by managed grasslands. Marginal Upland covers 16% of GB and occurs on the fringes of the uplands in all areas of north and west Britain, especially in Wales. Land use comprises a diverse mix of low-intensity agriculture, forestry, seminatural vegetation and a limited area of crops (for distribution maps of these landscape types see Bunce *et al.*, 1996). Since no hedgerows were recorded in upland it was excluded from further analyses. The total number of plots were 94, 76 and 53 in woodland, and 268, 255 and 410 in hedgerow, in Arable, Pastural and Marginal Upland, respectively.

The number of plots in which plant species were recorded were converted to percentage frequencies. Scatter graphs reveal the differing frequency patterns in the three landscape types (Figure 1). In each case the diagonal line shows the 1:1 ratio; species distributed about this line have approximately equal frequencies in woodlands and hedgerows whereas species above the line are more frequent in woodlands and species below the line are more frequent in hedgerows. For example, Dog's Mercury *Mercurialis perennis* in Lowland Arable landscape, had frequencies of 16.0% and 3.7% in woodland and hedgerow respectively (Figure 1(a)) while Hedge Garlic *Alliaria petiolata* in Lowland Pastural landscape had frequencies of 1.3% and 7.5% in woodland and hedgerow, respectively (Figure 1(b)).

The difference in frequency between the *x* and *y* co-ordinates for each species was used to formulate a novel Habitat Preference Index (HPI). The theoretical limits of this Index range from +100 to -100 for species which are present in all samples in one habitat but are absent from the other. Species which are more frequent in woodland have a positive value while species which are more common in hedgerows have a negative value. Therefore, *Mercurialis perennis* in Lowland Arable was assigned a value 12.3, whereas *Alliaria petiolata* in Lowland Pastural was assigned a value of -6.1. These HPI values



**Figure 1.** Comparisons of frequencies of plant species in woodland vs. hedgerows in: (a) Arable, (b) Pastural, and (c) Marginal Upland landscapes. These data are expressed on a log-scale to display the relationships clearly. The arrows indicates the positions of (a) *Mercurialis perennis*, and (b) *Alliaria petiolata*.

were used as the dependent variables in statistical analyses (see below).

### Choice of species

Woodland probably contains the richest flora of all habitats in Britain in part because they often encompass non-woodland habitats such as rides, ponds and launds (Peterken and Francis, 1999). Since our primary interest was investigating the potential of hedgerows to facilitate the movement of woodland plants we limited our analyses to 'woodland' species and take Peterken's (1974) definition as the

starting point to select species to enter into analyses. Peterken defined woodland plant species as: those species able to withstand the shade of a closed woodland canopy; those which create a canopy; and other species that in some way require woodland conditions, such as woodland edge species. We excluded species able to create a canopy (i.e. trees and shrubs) from our analyses, since their presence in woodlands is often influenced by historical management practices (Rackham, 1980; Peterken, 1981). In order to objectively select species able to withstand shade we used Ellenberg's Light (L) values, recalibrated for use in Britain (Ellenberg *et al.*,

1991; Hill *et al.*, 2000), to define a threshold for inclusion in analyses. Ellenberg's L is based on a scale of 1, plants of deep shade, through to 9, plants of full sun. We selected an Ellenberg's L-value of 6 as the maximum for inclusion in the analyses. We recognise the subjectivity involved in this choice of threshold value, and the possibility that some woodland species, for example certain edge species, may be excluded. However, on inspection of species included/excluded using this particular threshold value it meant that non-woodland species with a value of 7, such as Yarrow *Achillea millefolium*, Poppy *Papaver rhoeas*, Ribwort Plantain *Plantago lanceolata* and Greater Plantain *Plantago major* were excluded from analyses whilst typical woodland/woodland edge species with a value of 6, Cow Parsley *Anthriscus sylvestris*, Cleavers *Galium aparine*, Ground Ivy *Glechoma hederacea*, Bracken *Pteridium aquilinum* and Stinging Nettle *Urtica dioica* were included. The final filter applied to the list was to remove any species which were not recognised as members of woodland communities of the National Vegetation Classification (Rodwell, 1991), and which were not classified by Stace (1991) as woodland or hedgerow species. This removed a further seven species: *Alopecurus myosuroides*, *Bromus racemosus*, *Fumaria officinalis*, *Hypericum maculatum*, *Polygonum amphibium*, *Trichophorum caespitosum* and *Veronica persica*. Out of an initial 372, 349 and 211 species (excluding trees and shrubs) in Arable, Pastural and Marginal Upland, respectively, the number of woodland species was filtered down to 97, 88 and 63 in the three landscape types.

However, even after this procedure was applied it should be recognised that hedgerows may not be the only alternative non-woodland habitat for woodland plant species. Species such as *G. aparine* may be found in a wide range of habitats and even species that may be regarded as fairly strict woodland specialists, such as Wood Anemone *Anemone nemorosa*, are capable (under favourable management) of surviving in alternative habitats, such as grassland, long after the removal of original woodland cover (Boatman, 1971). The implications of this for our analyses was that we needed to control for the potential number of habitats in which species could occur. This is considered further, below.

## **Autecological and habitat indicators**

Ellenberg values (Ellenberg *et al.*, 1991) were used to assign indicator scores for habitat characteristics of individual plant species. Four Ellenberg values (Light, Moisture, Reaction and Nitrogen), recalibrated for use in Britain by Hill *et al.* (1999), were used along with two further original ones, Temperature and Continentality. However, Hill *et al.* (2000) suggested that the use of these last two indicators may be unreliable in Britain, thus these were used with care to avoid placing an over-reliance on their efficacy. Ellenberg assigned a value to each species according to the environmental characteristics of habitats where they occur on the following scales: Light (scale 1: plants of deep shade through to 9: plants of full sun); Moisture (scale 1: extreme dryness, to 9: wetland plants with categories 10–12 for submerged plants in aquatic habitats); Reaction (scale of soil acidity from 1: calcifuges, to 9: calcicoles); Nitrogen (scale from 1: extremely infertile soils, to 9: extremely fertile soils); Temperature (scale from 1: cold indicators found only in alpine zones, to 9: Mediterranean species); and Continentality (scale 1: extreme continental species, to 9: oceanic plants of western Europe which are rare in the east) (Table 1). Although originally developed in Central Europe, Ellenberg indicators have been validated for use with the British flora by Thompson *et al.* (1993), Hill and Carey (1997) and Hill *et al.* (2000).

Plant species were assigned qualitative scores for autecological attributes of using data extracted from Grime *et al.* (1988). Data for weight of dispersule (SEEDWGHT)(scale from 1: too small to be measured easily; through to 7: >10.00 mg), capacity for lateral spread (LATERAL)(scale from 1: therophytes (lateral spread exceedingly limited) to 5: perennials (diameter >1000 mm)), presence of a seed bank (SEEDBANK)(scale from 1: most seed germinating shortly after being shed, to 4: large persistent seed bank throughout the year), and C, S and R-radii were entered into analyses (Table 1). The latter represent positions of species' functional types according to underlying gradients of stress, competition and disturbance. Competitors are typically fast-growing, clonal perennials which do well in productive environments. Stress-tolerators are slow-growing

**Table 1.** Explanation of ecological, habitat and dispersal variables used in analyses

Variable	Description	Categories
<i>Habitat indicators</i>		
Ellenberg's—L <sup>b</sup>	Light	Scale from 1: species of deep shade, to 9: plants of full sun
Ellenberg's—M <sup>b</sup>	Soil moisture	Scale from 1: arid-land plants, through to 9: (wetland plants) with categories 10–12 for water plants
Ellenberg's—R <sup>b</sup>	Soil reaction	A gradient of soil acidity and lime content from 1: calcifuges, to 9: calcicoles
Ellenberg's—N <sup>b</sup>	Soil nitrogen	Scale from 1: species with little requirement for soil nitrogen, to 9: species with high requirements for soil nitrogen
Ellenberg's—T <sup>a</sup>	Temperature	Scale from 1: cold indicators found only in alpine zones, to 9: Mediterranean species
Ellenberg's—K <sup>a</sup>	Continentality	Scale 1: extreme continental species, to 9: plants of western Europe which are rare in the east
<i>Autecological indicators</i>		
NHABTS <sup>c</sup>	(Between) habitat amplitude	Sum of habitats in which species is considered to be widespread (range 1–7)
WOODNVC <sup>d</sup>	(Within) habitat amplitude	Sum of NVC woodland communities in which species is found (range 0–22)
SEEDWGHT <sup>c</sup>	Dry weight of seed, achene or other	1: Too small to be measured easily 2: ≤0.20 mg 3: 0.21–0.50 mg 4: 0.51–1.00 mg 5: 1.01–2.00 mg 6: 2.01–10.00 mg 7: > 10.00 mg
SEEDBANK <sup>c</sup>	Size of seed bank	1: Most seed germinating shortly after being shed 2: Most seed persistent only until start of next growing season 3: A small amount of seed persists in the soil but concentrations only high after seed shed 4: Large persistent seed bank throughout the year
LATERAL <sup>c</sup>	Potential for lateral spread	1: Therophytes (lateral spread exceedingly limited) 2: Perennials with compact unbranched rhizomes or forming small tussocks (diameter < 100 mm) 3: Perennials with rhizomes or tussocks (100–250 mm) 4: Perennials (251–1000 mm) 5: Perennials (> 1000 mm)
C—radius <sup>c</sup> S—radius <sup>c</sup> R—radius <sup>c</sup>	Components of the CSR strategy representing the extent to which species are adapted to competition, stress or disturbance	Scale 1–5 with a value 5 representing the position most like the pure C, S or R strategy and a value 1 being most unlike the pure strategy

<sup>a</sup>Variables extracted from Ellenberg *et al.* (1991). See the text for further information.

<sup>b</sup>Variables extracted from Hill *et al.* (1999). See the text for further information.

<sup>c</sup>Variables extracted from Grime *et al.* (1988). See the text for further information.

perennials which often exhibit physiological adaptations to limitations posed by particular habitats. Ruderals are fast-growing and short-lived with a high reproductive output. These three primary strategies form the apices of a triangular ordination in

which secondary and tertiary strategies form zones within the overall matrix (Grime, 1974, 1979). Individual species were assigned a value according to their position within the matrix. Values range from 5, for plants which are C, S or R-strategists down to 1

at the opposite extreme (Thompson, 1994; Thompson *et al.*, 1995).

Two final ecological attributes entered into analyses were measures of ecological amplitude in habitats, NHABTS, and in woodland plant communities, WOODNVC. The latter was determined as the number of communities of the National Vegetation Classification (Rodwell, 1991) in which species occur (range of values 0–22). NHABTS describes the range of primary habitats in which the species are found (range 1–7) using information extracted from Grime *et al.* (1988). This value is the sum of the habitats in which species are considered to be widespread.

The approach we took was to enter HPI values into Spearman rank correlation tests with habitat and autecological indicator scores. In order to control for the range of habitats in which species could occur we repeated analyses using partial correlation coefficients, controlling for NHABTS. All statistical analyses were done using SPSS.

In order to test whether differences in dispersal mode could explain relative frequency of plants in woodlands and hedgerows we classified plant species by dispersal mode: anemochores (dispersal by means of wind)(specialised morphology being either minute, plumed or wrapped in woolly hairs, winged or strongly flattened, or small and shed from a capsule high above surrounding vegetation); endozoochore (dispersules with an ingested berry or nut); epizoochore (dispersules with an adhesive burr, awn or spiny calyx teeth); hydrochore (dispersal by water); myrmecochore (seeds with an elaiosome for dispersal by ants); and unspecified (plants without a specific dispersal mode, or mode of dispersal uncertain). G-tests were used to test for differences in frequencies in dispersal modes both within and between habitats.

## Results

### *Patterns of species' distribution*

The plant species used in the analyses, and their HPI values, are given in Table 2. The behaviour of plants across all three landscape types was consistent. Plants that were more frequent in woodland compared to hedgerows in one landscape were also

more frequent in woodland compared to hedgerows in the other two landscapes. This was shown by significant correlations in the HPIs for species in common between the three landscape types: Arable vs. Pastoral landscapes (Spearman's  $r_s=0.77$ ,  $P<0.001$ ,  $N=84$ ), Arable vs. Marginal Upland ( $r_s=0.61$ ,  $P<0.001$ ,  $N=62$ ), and Pastoral vs. Marginal Upland ( $r_s=0.49$ ,  $P<0.001$ ,  $N=57$ ). Examples of plants with high scores on the HPI (i.e. high frequency in woodland cf. hedgerows) included *Deschampsia flexuosa* (25.5, 19.3, 48.3 in Arable, Pastoral and Marginal Upland, respectively), *P. aquilinum* (18.9, 24.6, 26.5) and *Oxalis acetosella* (15.2, 15.5, 25.0). Species with high hedgerow scores included *Anthriscus sylvestris* (–31.0, –18.2, –1.5), *G. aparine* (–53.4, –38.7, 1.03), *Hedera helix* (–10.9, –16.5, –1.5) and *A. petiolata* (–10.5, –6.1, –0.73).

### *Habitat and autecological correlates of hedgerow and woodland species*

Significant correlations were found for several habitat indicators in all three types of landscape (Table 3). HPIs were significantly correlated with Ellenberg's R, N, T and K. Therefore, the plant species composition of hedgerows is consistent with a habitat that has a more continental and dryer climate with a higher soil nitrogen status and lower soil acidity, in comparison to woodland plots. There were few correlations with autecological indicators, except WOODNVC. Plants that were more frequent in hedgerows tended to be associated with fewer NVC woodland types compared to plants that were more frequent in woodlands. However, in contrast to these habitat indicators, when the effects of NHABTS were controlled for statistically these significant correlations were not sustained. HPIs were also significantly correlated with SEEDWGHT and S-radius for Arable landscape, and LATERAL in Marginal Upland. Only the last of these was maintained in partial correlation tests.

There were significant differences in the frequencies of dispersal modes of plant species within woodland (Arable,  $G=25.7$ , 5 df,  $P<0.01$ ; Pastoral,  $G=40.7$ , 5 df,  $P<0.01$ ; Marginal Upland,  $G=11.2$ , 5 df,  $P<0.05$ ) but not within hedgerows (Arable,  $G=9.7$ , 5 df, ns; Pastoral  $G=7.2$ , 5 df, ns; Marginal Upland  $G=7.2$ , 5 df, ns). The three most commonly

Table 2. Plant species included in analyses

Arable	Pastural	Marginal Upland
<i>Deschampsia flexuosa</i>	25.53 * <i>Hyacinthoides non-scripta</i>	27.52 <i>Deschampsia flexuosa</i> 48.32
<i>Deschampsia cespitosa</i>	21.54 <i>Pteridium aquilinum</i>	24.57 * <i>Vaccinium myrtillus</i> 39.62
<i>Dryopteris filix-mas</i>	20.53 <i>Lonicera periclymenum</i>	23.62 <i>Galium saxatile</i> 38.40
<i>Agrostis capillaris</i>	19.19 <i>Deschampsia flexuosa</i>	19.34 <i>Agrostis capillaris</i> 34.50
<i>Pteridium aquilinum</i>	18.87 <i>Galium saxatile</i>	19.09 <i>Digitalis purpurea</i> 26.53
<i>Galium saxatile</i>	17.71 <i>Dryopteris filix-mas</i>	17.83 <i>Pteridium aquilinum</i> 26.53
<i>Digitalis purpurea</i>	15.21 * <i>Oxalis acetosella</i>	15.54 * <i>Blechnum spicant</i> 26.42
* <i>Oxalis acetosella</i>	15.21 <i>Deschampsia cespitosa</i>	11.62 * <i>Oxalis acetosella</i> 24.95
<i>Lonicera periclymenum</i>	13.29 <i>Ajuga reptans</i>	11.45 <i>Deschampsia cespitosa</i> 17.65
<i>Geum urbanum</i>	12.60 <i>Circaea lutetiana</i>	11.45 <i>Rubus fruticosus</i> 13.93
<i>Mercurialis perennis</i>	12.23 <i>Athyrium filix-femina</i>	11.20 <i>Dryopteris filix-mas</i> 13.87
* <i>Hyacinthoides non-scripta</i>	11.96 * <i>Veronica montana</i>	10.27 * <i>Luzula sylvatica</i> 13.21
<i>Circaea lutetiana</i>	10.64 * <i>Lysimachia nemorum</i>	10.13 * <i>Holcus mollis</i> 10.88
* <i>Vaccinium myrtillus</i>	10.64 <i>Geum urbanum</i>	9.77 <i>Athyrium filix-femina</i> 10.59
<i>Geranium robertianum</i>	10.10 <i>Mercurialis perennis</i>	9.40 <i>Ranunculus repens</i> 6.26
<i>Epilobium montanum</i>	9.89 * <i>Blechnum spicant</i>	9.21 * <i>Hyacinthoides non-scripta</i> 5.84
* <i>Holcus mollis</i>	9.19 <i>Epilobium montanum</i>	9.10 * <i>Anemone nemorosa</i> 5.66
* <i>Carex sylvatica</i>	8.51 <i>Primula vulgaris</i>	8.03 <i>Lathyrus montanus</i> 5.66
* <i>Luzula sylvatica</i>	8.51 * <i>Carex remota</i>	7.89 <i>Rubus idaeus</i> 5.66
<i>Brachypodium sylvaticum</i>	8.29 * <i>Lamiastrum galeobdolon</i>	7.11 <i>Teucrium scorodonia</i> 5.66
<i>Primula vulgaris</i>	7.40 * <i>Carex sylvatica</i>	6.58 * <i>Veronica montana</i> 5.17
<i>Ajuga reptans</i>	7.07 * <i>Vaccinium myrtillus</i>	6.58 * <i>Carex remota</i> 3.77
* <i>Moehringia trinervia</i>	6.38 * <i>Potentilla sterilis</i>	5.93 * <i>Poa nemoralis</i> 3.77
<i>Teucrium scorodonia</i>	6.38 * <i>Hypericum pulchrum</i>	5.40 <i>Veronica officinalis</i> 3.77
<i>Veronica chamaedrys</i>	5.47 <i>Teucrium scorodonia</i>	5.18 <i>Geranium robertianum</i> 3.71
* <i>Potentilla sterilis</i>	5.32 <i>Veronica chamaedrys</i>	4.90 <i>Rumex sanguineus</i> 3.53
* <i>Veronica montana</i>	5.32 * <i>Euphorbia amygdaloides</i>	4.87 * <i>Lysimachia nemorum</i> 3.29
* <i>Lamiastrum galeobdolon</i>	5.26 <i>Arum maculatum</i>	4.76 <i>Lonicera periclymenum</i> 2.80
<i>Silene dioica</i>	4.30 * <i>Conopodium majus</i>	4.48 <i>Ajuga reptans</i> 1.89
<i>Scrophularia nodosa</i>	4.26 * <i>Dryopteris affinis</i>	4.09 * <i>Dryopteris aemula</i> 1.89
<i>Rubus idaeus</i>	4.20 * <i>Anemone nemorosa</i>	3.95 <i>Dryopteris dilatata</i> 1.89
* <i>Blechnum spicant</i>	3.88 * <i>Luzula pilosa</i>	3.95 * <i>Hypericum pulchrum</i> 1.89
<i>Hypericum hirsutum</i>	3.88 * <i>Luzula sylvatica</i>	3.95 * <i>Luzula pilosa</i> 1.89
<i>Ranunculus repens</i>	3.59 * <i>Poa nemoralis</i>	3.95 <i>Primula vulgaris</i> 1.89
* <i>Euphorbia amygdaloides</i>	3.19 <i>Agrostis capillaris</i>	3.41 * <i>Chrysosplenium oppositifolium</i> 1.64
* <i>Luzula pilosa</i>	3.19 <i>Rubus idaeus</i>	2.77 * <i>Conopodium majus</i> 1.64
* <i>Lysimachia nemorum</i>	3.19 * <i>Carex pendula</i>	2.63 * <i>Lamiastrum galeobdolon</i> 1.64
* <i>Poa nemoralis</i>	3.19 * <i>Chrysosplenium oppositifolium</i>	2.63 <i>Stellaria holostea</i> 1.58
<i>Veronica officinalis</i>	3.19 * <i>Festuca gigantea</i>	2.63 <i>Veronica chamaedrys</i> 1.58
<i>Athyrium filix-femina</i>	3.14 * <i>Milium effusum</i>	2.63 <i>Brachypodium sylvaticum</i> 1.40
<i>Clematis vitalba</i>	3.08 <i>Ranunculus ficaria</i>	2.63 <i>Stachys sylvatica</i> 1.40
<i>Viola odorata</i>	2.82 <i>Stachys sylvatica</i>	2.32 <i>Viola riviniana</i> 1.40
<i>Rumex sanguineus</i>	2.22 * <i>Moehringia trinervia</i>	2.24 * <i>Potentilla sterilis</i> 1.16
<i>Cardamine flexuosa</i>	2.13 * <i>Polystichum aculeatum</i>	2.24 <i>Galium aparine</i> 1.03
<i>Epilobium tetragonum</i>	2.13 <i>Ribes rubrum</i>	2.24 <i>Silene dioica</i> 0.91
* <i>Festuca gigantea</i>	2.13 <i>Veronica officinalis</i>	2.24 <i>Epilobium montanum</i> 0.67
<i>Fragaria vesca</i>	2.13 <i>Brachypodium sylvaticum</i>	2.04 <i>Equisetum sylvaticum</i> 0.00
* <i>Hypericum pulchrum</i>	2.13 <i>Digitalis purpurea</i>	1.95 <i>Scrophularia nodosa</i> 0.00
<i>Listera ovata</i>	2.13 <i>Silene dioica</i>	1.95 <i>Bromus ramosus</i> -0.24
<i>Ribes rubrum</i>	2.13 <i>Clematis vitalba</i>	1.85 <i>Cardamine flexuosa</i> -0.24
<i>Trientalis europaea</i>	2.13 <i>Fragaria vesca</i>	1.85 <i>Circaea lutetiana</i> -0.24
<i>Valeriana officinalis</i>	2.13 <i>Rumex sanguineus</i>	1.59 <i>Epilobium obscurum</i> -0.24
* <i>Carex remota</i>	1.75 <i>Bromus ramosus</i>	1.46 <i>Epilobium tetragonum</i> -0.24
* <i>Adoxa moschatellina</i>	1.06 * <i>Allium ursinum</i>	1.32 * <i>Polypodium vulgare</i> -0.24
* <i>Anemone nemorosa</i>	1.06 <i>Convallaria majalis</i>	1.32 <i>Umbilicus rupestris</i> -0.24
<i>Atropa belladonna</i>	1.06 <i>Dryopteris dilatata</i>	1.32 <i>Lapsana communis</i> -0.49
* <i>Carex laevigata</i>	1.06 <i>Hypericum androsaemum</i>	1.32 <i>Alliaria petiolata</i> -0.73
* <i>Dryopteris affinis</i>	1.06 <i>Hypericum hirsutum</i>	1.32 <i>Geum urbanum</i> -0.73

(Continued overleaf)

**Table 2.** (Continued)

Arable	Pastural	Marginal Upland
* <i>Dryopteris carthusiana</i>	1.06	<i>Rubia peregrina</i> 1.32
<i>Dryopteris dilatata</i>	1.06	<i>Scrophularia nodosa</i> 1.32
* <i>Epipactis helleborine</i>	1.06	* <i>Solidago virgaurea</i> 1.32
* <i>Galium odoratum</i>	1.06	<i>Impatiens glandulifera</i> 0.92
<i>Goodyera repens</i>	1.06	* <i>Melica uniflora</i> 0.92
<i>Impatiens parviflora</i>	1.06	<i>Viola odorata</i> 0.92
<i>Lilium martagon</i>	1.06	* <i>Polystichum setiferum</i> 0.53
* <i>Melica uniflora</i>	1.06	* <i>Viola reichenbachiana</i> 0.00
* <i>Milium effusum</i>	1.06	* <i>Holcus mollis</i> -0.07
<i>Pentaglottis sempervirens</i>	1.06	<i>Cruciata laevipes</i> -0.39
* <i>Polygonatum multiflorum</i>	1.06	<i>Humulus lupulus</i> -0.39
<i>Ranunculus ficaria</i>	1.06	* <i>Iris foetidissima</i> -0.39
* <i>Sanicula europaea</i>	1.06	<i>Melampyrum pratense</i> -0.39
* <i>Bromus ramosus</i>	1.01	<i>Ribes uva-crispa</i> -0.39
<i>Glechoma hederacea</i>	0.75	<i>Glechoma hederacea</i> -0.82
* <i>Geum rivale</i>	0.69	<i>Geranium robertianum</i> -0.96
<i>Ribes uva-crispa</i>	0.32	<i>Aegopodium podagraria</i> -1.04
<i>Arum maculatum</i>	-0.11	<i>Asplenium adiantum-nigrum</i> -1.18
<i>Cardamine impatiens</i>	-0.37	* <i>Polypodium vulgare</i> -1.29
<i>Chelidonium majus</i>	-0.37	<i>Lamium purpureum</i> -1.57
<i>Epilobium obscurum</i>	-0.37	<i>Umbilicus rupestris</i> -3.14
<i>Equisetum telemateia</i>	-0.37	<i>Lapsana communis</i> -3.39
<i>Polypodium vulgare</i>	-0.37	<i>Ranunculus repens</i> -3.70
* <i>Ruscus aculeatus</i>	-0.37	* <i>Vicia sepium</i> -4.71
<i>Symphoricarpos albus</i>	-0.37	<i>Alliaria petiolata</i> -6.14
<i>Humulus lupulus</i>	-0.75	<i>Stellaria holostea</i> -8.32
<i>Cruciata laevipes</i>	-1.49	<i>Rubus fruticosus</i> -10.01
<i>Lamium purpureum</i>	-1.55	<i>Hedera helix</i> -16.49
* <i>Vicia sepium</i>	-1.55	<i>Anthriscus sylvestris</i> -18.15
<i>Aegopodium podagraria</i>	-2.61	<i>Galium aparine</i> -38.67
<i>Stachys sylvatica</i>	-3.75	<i>Urtica dioica</i> -39.68
<i>Rubus fruticosus</i>	-4.29	
<i>Lapsana communis</i>	-5.34	
<i>Stellaria holostea</i>	-6.72	
<i>Alliaria petiolata</i>	-10.50	
<i>Hedera helix</i>	-10.87	
<i>Anthriscus sylvestris</i>	-30.99	
<i>Urtica dioica</i>	-39.26	
<i>Galium aparine</i>	-53.35	

For each species The Habitat Preference Index is shown. Nomenclature follows Stace (1991). AWIs are indicated by an asterisk. AWIs follows Rose (1999).

represented modes of dispersal were anemochores, unspecified (plants without a specific dispersal mode, or uncertain) and epizoochore (Figure 2). There were no significant differences in dispersal modes of plant species between woodland and hedgerow in any of the landscapes (Arable,  $G=3.0$ , 5 df, ns; Pastural  $G=7.8$ , 5 df, ns; Marginal Upland  $G=1.3$ , 5 df, ns).

## Discussion

The supposed corridor function of hedgerows assumes hedgerows are linear strips of

woodland which have the potential to facilitate the dispersal of woodland organisms between fragmented habitats. The results here indicate that the environments of woodlands and hedgerows differ in habitat quality for plants, particularly with respect to soil nutrient status and microclimate. In comparison to woodland plots, the plant species composition of hedgerows is consistent with an environment that is significantly more continental and dryer, and has a higher soil nutrient status and lower soil acidity, as shown by Ellenberg indicators.

These results are consistent with what is known about boundary layer microclimates

**Table 3.** Tests of association between Habitat Preference Index and environmental indicators

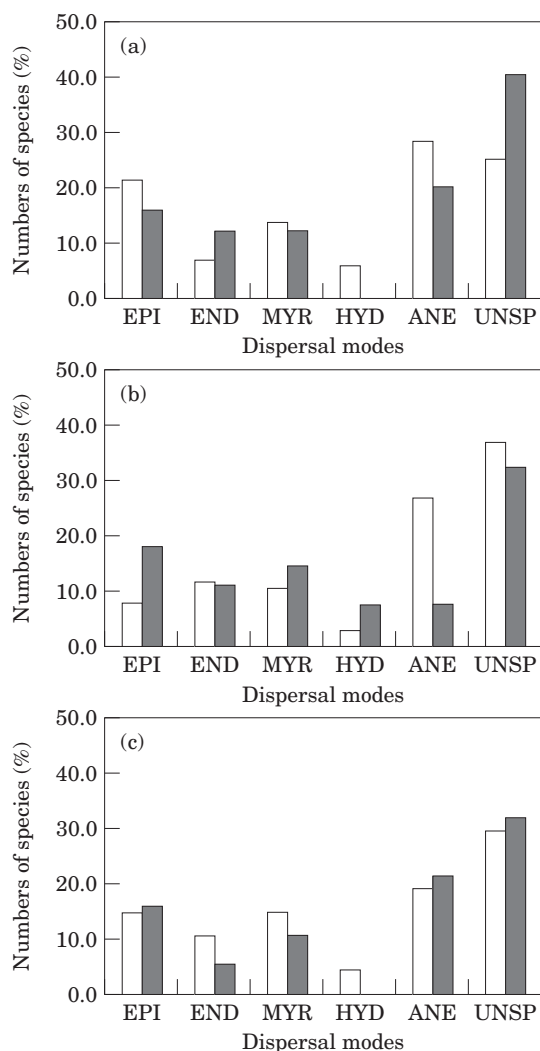
Variable	Lowland Arable		Lowland Pastural		Marginal Upland	
	$r_s$	Partial	$r_s$	Partial	$r_s$	Partial
<i>Habitat indicators</i>						
Ellenberg's—L	−0.09 (97)	−0.06 (71)	−0.27* (88)	−0.09 (70)	0.06 (63)	0.18 (57)
Ellenberg's—M	0.08 (97)	0.00 (71)	0.19 (88)	0.07 (70)	−0.03 (63)	−0.04 (57)
Ellenberg's—R	−0.43*** (97)	−0.49*** (71)	−0.40*** (88)	−0.48*** (70)	−0.69*** (63)	−0.74*** (57)
Ellenberg's—N	−0.42*** (97)	−0.52*** (71)	−0.37*** (88)	−0.49*** (70)	−0.58*** (63)	−0.58*** (57)
Ellenberg's—T	−0.48*** (97)	−0.52*** (71)	−0.49*** (88)	−0.48*** (70)	−0.51*** (63)	−0.53*** (57)
Ellenberg's—K	−0.26* (97)	−0.15 (71)	−0.26** (88)	−0.16 (70)	−0.15 (63)	0.02 (57)
<i>Autecological indicators</i>						
NHABTS	0.02 (79)	NA	−0.12 (77)	NA	−0.02 (60)	NA
WOODNVC	0.46*** (97)	0.13 (71)	0.33** (88)	0.04 (70)	0.38** (63)	0.33* (57)
SEEDWGHT	−0.27** (97)	−0.32 (71)	−0.14 (88)	−0.09 (70)	−0.19 (63)	−0.25 (57)
SEEDBANK	0.065 (90)	0.14 (71)	−0.19 (84)	−0.19 (70)	0.10 (62)	0.03 (57)
LATERAL	0.19 (97)	0.15 (71)	−0.09 (88)	−0.13 (70)	0.26* (63)	0.27* (57)
C—radius	−0.059 (97)	−0.23 (71)	−0.15 (88)	−0.01 (70)	−0.04 (63)	−0.01 (57)
S—radius	−0.29** (97)	0.39 (71)	0.18 (88)	−0.06 (70)	0.22 (63)	0.20 (57)
R—radius	−0.12 (97)	−0.08 (71)	0.01 (88)	0.17 (70)	−0.11 (63)	−0.20 (57)

For each landscape type, the Spearman rank correlation coefficient,  $r_s$ , and the partial correlation coefficient (controlling for NHABTS) are presented. The number of cases are given in parentheses and the level of significance is not significant unless indicated: \*\*\* $P < 0.001$ , \*\* $P < 0.01$ , \* $P < 0.05$ .

around hedgerows. Differences in relative exposure mean that microclimates near to the ground in hedgerows are more similar to those found at the woodland edges compared to the woodland interior (Forman, 1995). It is now firmly established that woodland edges differ from woodland interiors in microclimate and species composition (Murcia, 1995; McCollin, 1998), therefore, we would expect that the plant assemblages of hedgerows would be correspondingly more similar to those found in the woodland edge rather than the interior. For all three landscape types there was a very close match in HPIs. A similar response of plant species in all three landscape types suggest that the environmental gradient from woodland interior to hedgerow are similar, irrespective of differences in geography, climate and soils.

However, the majority of plant species were distributed about the 1:1 diagonals in

Figure 1, meaning that they had similar frequencies in both woodlands and hedgerows. This suggests that hedgerows provided a suitable habitat for the majority of woodland plant species in this sample. Also, since no significant differences in either the representation of different dispersal modes of plants in woodlands and hedgerows, and few consistent autecological differences were found, the implication was that differences in autecology could not explain differences in woodland and hedgerow floras. The strong significant positive correlations between HPIs and WOODNVC for each landscape suggest that only a limited number of NVC woodland communities were present in hedgerows. This could either reflect the reduced environmental variation in hedgerows, although it should be recognised that species' associations in hedgerows may not necessarily reflect NVC types. Nonetheless limited habitat variation



**Figure 2.** Dispersal categories of woodland hedgerow plants in (a) Lowland Arable; (b) Lowland Pastural; (c) Marginal Upland. Woodland species, □; hedgerow species, ■ EPI, Epizoochores; END, Endozoochores; MYR, Myrmecochores; HYD, Hydrochores; ANE, Anemochores; UNSP, Unspecified or uncertain.

could be a factor that would restrict colonisation of hedgerows by certain woodland plant species.

The reasons why certain woodland plant species either do not occur, or occur with a limited frequency, in hedgerows are probably the same as the reasons put forward to explain why ancient woodland indicators (AWIs) are seldom found in secondary woodlands (see Hermy *et al.*, 1999 for recent review). First, some hedgerows probably owe their origin to the clearance of original woodland, and since the dominant plant species of temperate woodlands are long-lived

perennials which are effectively confined to sites which have had a long continuity of tree cover (Bierzuchudek, 1982; Rackham, 1980; Peterken and Game, 1984; Inghe and Tamm, 1985; Dzwonko and Loster, 1989; Dzwonko, 1993), remnant populations of woodland plant species could conceivably have survived in such hedgerows. Second, because of the dependence upon vegetative spread or myrmecochory they are inherently poor colonizers (Dzwonko and Loster, 1992), or else climatic change since plants first colonised now prevents them from setting good seed (Rackham, 1976; Pigott and Huntley, 1981). Third, they may be inhibited from colonising new sites by the higher nutrient status of the soils, especially phosphate levels, which makes hedgerows unsuitable, or encourages the growth of highly competitive plants which could also effectively exclude AWIs (Peterken and Game, 1984; Honnay *et al.*, 1998; Hermy *et al.*, 1999).

The results presented here are consistent with environmental differences between woodlands and hedgerows since the HPIs were significantly correlated with Ellenberg indicators for microclimate, soil nitrogen and pH. We tentatively rule out the second explanation since no significant differences were found in the dispersal modes between plant species in woodland and hedgerow in any of the three landscapes. However, we are unable to rule out the possibility that the presence of plants in hedgerows is due to the survival of remnant populations although the presence of woodland 'ghost' hedgerows in samples cannot account for the habitat differences highlighted in the analyses. However these results could arise if there was a significant difference in the proportions of AWIs in woodlands compared to hedgerows which there was ( $G=7.0$ ,  $P<0.05$ , 2 df).

Since the data used here were put to purposes for which they were not originally intended, it is possible that the sampling regime was not ideal. For instance, we are not sure what effects differences in plot size between samples in hedgerows and woodlands would have had on the results. Woodland plots were 20 times larger than hedgerow plots. Taking into account the total numbers of plots in each landscape, the overall area sampled in woodlands was larger than hedgerows by a factor of *c.* 7.0, 6.0 and 2.5 times for Arable, Pastural and Marginal

Upland, respectively. The differences in plot size and total area sampled could bias the results by picking up more rare woodland species in woodland plots as compared to hedgerows. However, since we rely solely on frequency data the effects of these differences should not be too apparent. It could also be argued that the total sampling area should be weighted according to the relative surface area of woodland and hedgerows in each landscape. Assuming a median width of 2 m and an estimated total of 464 000 km of hedgerow in Britain (Barr and Gillespie, 2000; Hinsley and Bellamy, 2000) the surface area covered by hedgerows is equivalent to c. 4% of the total woodland area. Therefore, the apparent bias in sample area in favour of woodland in this study is reasonable given the disparity between the surface area of woodlands and hedgerows overall. One final corollary: the work presented here does not attempt to substitute for carefully designed and executed field study.

### Implications for conservation

The implications of these habitat differences between hedgerows and woodlands are that hedgerows are, at best, likely to act as selective filters for woodland plant species. Movements of distances of several hundred kilometres have been achieved for plant species along non-wooded linear features over periods of several decades. For example, Oxford Ragwort *Senecio squalidus* radiated out along railway ballast from Oxford, England, where it was introduced to the Botanic Garden in 1794 AD (Kent, 1958, 1960). Further indirect evidence for spatial diffusion comes from the recent invasion of salted road verges by plants such as *Lactuca serriola*, *Puccinella* spp., *Spergularia marina*, *Cochlearia officinalis* and *C. danica*, and of water courses by Himalayan Balsam *Impatiens glandulifera* (Mathews and Davison, 1976; Kitchener, 1983; Scott, 1985, Carter and Prince, 1988; Stace, 1991).

Diffusion from woodlands into hedgerows tends to be much slower and tends to be by much more inconspicuous species. Rates of migration of woodland plants in northern temperate forests vary from 0–5.5 m year<sup>-1</sup> (Matlack, 1994; Cain *et al.*, 1998; Honnay *et al.*, 1998; Bossuyt *et al.*, 1999; Hermy

*et al.*, 1999) with rates often much less than 1.0 m year<sup>-1</sup> (Grasshof-Bokdam, 1997; Brunet and von Oheimb, 1998; Honnay *et al.*, 1999) thus movement is likely to be more successful where ancient woodland directly abut hedgerows (Pollard, 1973; Peterken and Game, 1981; Corbit *et al.*, 1999). Hedgerow networks cover distances of thousands of kilometres in the British countryside, therefore the time needed for plants to potentially colonise this network could take hundreds of years. Indeed, for species that have such a limited capacity for dispersal it may take several centuries for even a single hedge to be successfully colonised. For example, the distribution of Dogs Mercury *Mercurialis perennis* in hedgerows is largely confined to the close proximity of ancient woodlands (Peterken and Game, 1981; Pollard *et al.*, 1974) consistent with its limited capacity for vegetative spread, estimated to be c. 1.0 m yr<sup>-1</sup> (Rackham, 1975).

Habitat suitability for the long-term maintenance of plant populations is an important aspect of potential corridor function (Corbit *et al.*, 1999). The recent decline in traditional management of hedgerows and its replacement by mechanical hedge trimming has led to changes in hedgerow structure that further potentially mitigates against the survival of plant species in hedge bottoms (Bannister and Watt, 1994; Barr and Gillespie, 2000). In addition, agricultural intensification could have potentially damaging effects on plants in hedgerows due to eutrophication, especially in arable landscapes (McCollin *et al.*, 2000). Therefore, we suggest that whilst hedgerows may act as selective filters for the movement of certain woodland plant species, and thus contribute to the survival of isolated populations, it is more likely that qualitative differences in the environment of hedgerows and woodlands are such that the dispersal of the most restricted woodland plant species is unlikely to be enabled by hedgerows. For woodland species which are able to colonise hedgerows the timescale over which this is likely to occur leads us to doubt the sustainability of appropriate management regimes. We conclude that the continued survival and conservation of extant ancient woodlands and ancient hedgerows is imperative in order to conserve woodland plant populations.

Our work supports the assertion of Corbit *et al.* (1999), that further research is

required to investigate the corridor function of hedgerows. Field and historical studies are needed to evaluate alternative modes of colonisation (not just spatial diffusion), and to investigate the effects of differing forms of management on hedge bottom floras and on colonisation success.

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## References

- Arts, G. H. P., van Buuren, M., Jongman, R. H. G., Nowicki, P., Wascher, D. and Hoek, I. H. S. (eds) (1995). *Landschap. Ecological Networks* (special issue) **12**(3) Wageningen, The Netherlands: WLO.
- Bannister, N. R. and Watt, T. A. (1994). Hedgerow management: past and present. In *Hedgerow Management and Nature Conservation* (T. A. Watt and G. P. Buckley, eds), pp. 7–15. Wye, Ashford: Wye College Press.
- Barr, C. J. and Gillespie, M. K. (2000). Estimating hedgerow length and pattern characteristics in Great Britain Using Countryside Survey data. *Journal of Environmental Management* **60**, 23–32.
- Barr, C. J., Bunce, R. G. H., Clarke, R. T., Fuller, R. M., Furse, M. T., Gillespie, M. K., Groom, G. B., Hallam, C. J., Hornung, M. et al. (1993). *Countryside Survey 1990: Main Report*. London: HMSO.
- Bennett, A. F. (1999). *Linkages in the Landscape: The Role of Corridors and Connectivity in Wildlife Conservation*. Gland, Switzerland and Cambridge: IUCN.
- Bierzuchudek, P. (1982). Life histories and demography of shade-tolerant temperate forest herbs. *New Phytologist* **90**, 757–776.
- Boatman, D. J. (1971). Burton Bushes: an ecological view. *Hull Natural History Society Bulletin* **3**, 8–14.
- Bossuyt, B., Hermy, M. and Deckers, J. (1999). Migration of herbaceous plant species across ancient-recent forest ecotones in central Belgium. *Journal of Ecology* **87**, 628–638.
- Brunet, J. and von Oheimb, G. (1998). Migration of vascular plants to secondary woodlands in southern Sweden. *Journal of Ecology* **86**, 429–438.
- Bunce, R. G. H., Barr, C. J., Clarke, R. T., Howard, D. C. and Lane, A. M. J. (1996). Land classification for strategic ecological survey. *Journal of Environmental Management* **47**, 37–60.
- Cain, M. L., Damman, H. and Muir, A. (1998). Seed dispersal and the Holocene migration of woodland herbs. *Ecological Monographs* **68**, 325–347.
- Carter, R. N. and Prince, S. D. (1988). Distribution limits from a demographic viewpoint. In *Plant Population Ecology* (A. J. Davy, M. J. Hutchings and A. R. Watkinson, eds), pp. 165–184. Oxford: Blackwell.
- Corbit, M., Marks, P. L. and Gardescu, S. (1999). Hedgerows as habitat corridors for forest herbs in central New York, USA. *Journal of Ecology* **87**, 220–232.
- Dawson, D. (1994). *Are Habitat Corridors Conduits for Animals and Plants in a Fragmented Landscape? A Review of the Scientific Evidence*. Peterborough: English Nature.
- Dzwonko, Z. (1993). Relations between the floristic composition of isolated young woods and their proximity to ancient woodland. *Journal of Vegetation Science* **4**, 693–698.
- Dzwonko, Z. and Loster, S. (1989). Distribution of vascular plant species in small woodlands in the Western-Carpathian foothills. *Oikos* **56**, 77–86.
- Dzwonko, Z. and Loster, S. (1992). Species richness and seed dispersal to secondary woods in southern Poland. *Journal of Biogeography* **19**, 195–204.
- Ellenberg, H., Weber, H. E., Düll, R., Wirth, V., Werner, W. and Paulissen, D. (1991). Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica* **18**, 1–248.
- Forman, R. T. T. (1995). *Land Mosaics*. Cambridge: Cambridge University Press.
- Forman, R. T. T. and Baudry, J. (1984). Hedgerows and hedgerow networks in landscape ecology. *Environmental Management* **8**, 495–510.
- Grasshof-Bokdam, C. (1997). Forest species in an agricultural landscape in the Netherlands: effects of habitat fragmentation. *Journal of Vegetation Science* **8**, 21–28.
- Grime, J. P. (1974). Vegetation classification by reference to strategies. *Nature* **250**, 26–31.
- Grime, J. P. (1979). *Plant Strategies and Vegetation Processes*. London: Wiley.
- Grime, J. P., Hodgson, J. G. and Hunt, R. (1988). *The Comparative Plant Ecology*. Chapman and Hall, London.
- Hermy, M., Honnay, O., Firbank, L., Grasshof-Bokdam, C. and Lawesson, J. (1999). An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. *Biological Conservation* **91**, 9–22.
- Hill, M. O. and Carey, P. D. (1997). Prediction of yield in the Rothamsted Park Grass Experiment

- by Ellenberg indicator values. *Journal of Vegetation Science* **8**, 579–586.
- Hill, M. O., Mountford, J. O., Roy, D. B. and Bunce, R. G. H. (1999). Ellenberg's indicator values for British plants. In *Ecofact Volume 2 Technical Annex*. London: Department of Environment, Transport and the Regions.
- Hill, M. O., Roy, D. B., Mountford, J. O. and Bunce, R. G. H. (2000). Extending Ellenberg's indicator values to a new area: an algorithmic approach. *Journal of Applied Ecology* **37**, 3–15.
- Hinsley, S. A. and Bellamy, P. E. (2000). The influence of hedge structure, management and landscape context on the value of hedgerows to birds: a review. *Journal of Environmental Management* **60**, 33–49.
- Hobbs, R. J. (1992). The role of corridors in conservation: solution or bandwagon? *Trends in Ecology and Evolution* **7**, 389–392.
- Honnay, O., Degroote, B. and Hermy, M. (1998). Ancient-forest plant species in western Belgium: a species list and possible ecological mechanisms. *Belgian Journal of Botany* **130**, 139–154.
- Honnay, O., Hermy, M. and Coppin, P. (1999). Impact of habitat quality on forest plant species colonization. *Forest Ecology and Management* **115**, 157–170.
- Inghe, O. and Tamm, C. O. (1985). Survival and flowering of perennial herbs. 4. The behavior of *Hepatica nobilis* and *Sanicula europaea* on permanent plots during 1943–1981. *Oikos* **45**, 400–420.
- Jongman, R. (1995). Nature conservation planning in Europe: developing ecological networks. *Landscape and Urban Planning* **32**, 169–183.
- Kent, D. H. (1958). *Senecio squalidus* L. in the British Isles-1. Early records (to 1877). *Proceedings of the Botanical Society of the British Isles* **2**, 115–118.
- Kent, D. H. (1960). *Senecio squalidus* L. in the British Isles-2, the spread from Oxford (1879–1939). *Proceedings of the Botanical Society of the British Isles* **3**, 375–379.
- Kitchener, G. (1983). Maritime plants on inland roads of West Kent. *Transactions of the Kent Field Club* **9**, 87–94.
- Mann, C. C. and Plummer, M. L. (1995). Are wildlife corridors the right path? *Science* **270**, 1428–1430.
- Mathews, P. and Davison, A. W. (1976). Maritime species on roadside verges. *Watsonia* **11**, 164.
- Matlack, G. R. (1994). Plant species migration in a mixed-history forest landscape in eastern North America. *Ecology* **75**, 1491–1502.
- McCollin, D. (1998). Forest edges and habitat selection in birds: a functional approach. *Ecography* **21**, 247–260.
- McCollin, D., Moore, L. and Sparks, T. (2000). The flora of a cultural landscape: environmental determinants of change revealed using archival sources. *Biological Conservation* **92**, 249–263.
- Murcia, C. (1995). Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution* **10**, 58–62.
- Nowicki, P., Bennett, G., Middleton, D., Rientjes, S. and Wolters, R. (eds) (1996). *Perspectives on Ecological Networks*. The Netherlands: European Centre for Nature Conservation.
- Opdam, P., Foppen, R., Reijnen, R. and Schotman, A. (1995). The landscape ecological approach in bird conservation: integrating the meta-population concept into spatial planning. *Ibis* **137**, 139–146.
- Peterken, G. F. (1974). A method for assessing woodland flora for conservation using indicator species. *Biological Conservation* **6**, 239–245.
- Peterken, G. F. (1981). *Woodland Conservation and Management*. London: Chapman and Hall.
- Peterken, G. F. and Francis, J. L. (1999). Open spaces as habitats for vascular ground flora species in the woods of central Lincolnshire, UK. *Biological Conservation* **91**, 55–72.
- Peterken, G. F. and Game, M. (1981). Historical factors affecting the distribution of *Mercurialis perennis* in Central Lincolnshire. *Journal of Ecology* **69**, 781–796.
- Peterken, G. F. and Game, M. (1984). Historical factors affecting the number and distribution of vascular plant species in central Lincolnshire. *Journal of Ecology* **72**, 155–182.
- Pigott, C. D. and Huntley, J. P. (1981). Factors controlling the distribution of *Tilia cordata* at the northern limits of its geographical range. III. Nature and causes of seed sterility. *New Phytologist* **87**, 817–839.
- Pollard, E. (1973). Hedges. VIII. Woodland relic hedges in Huntingdon and Peterborough. *Journal of Ecology* **61**, 343–352.
- Pollard, E., Hooper, M. D. and Moore, N. W. (1974). *Hedges*. London: Collins.
- Rackham, O. (1975). *Hayley Wood*. Cambridge: The Cambridge and Isle of Ely Naturalists' Trust.
- Rackham, O. (1976). *Trees and Woodlands in the British Landscape*. London: Dent.
- Rackham, O. (1980). *Ancient Woodland*. London: Arnold.
- Rodwell, J. S. (1991). *British Plant Communities Volume 1. Woodlands and Scrub*. Cambridge: Cambridge University Press.
- Rose, F. (1999). Indicators of ancient woodland. The use of vascular plants in evaluating ancient woods for nature conservation. *British Wildlife* **10**, 241–251.
- Rosenberg, D. K., Noon, B. R. and Meslow, E. C. (1997). Biological corridors: form, function and efficacy. *BioScience* **47**, 677–687.
- Saunders, D. A. and Hobbs, R. J. (eds) (1991). *Nature Conservation 2: The Role of Corridors*. London: Surrey Beatty and Sons.
- Scott, N. E. (1985). The updated distribution of maritime species on British roadsides. *Watsonia* **15**, 381–386.
- Simberloff, D., Farr, J. A., Cox, J. and Mehlman, D. W. (1992). Movement corridors: conservation bargains or poor investments? *Conservation Biology* **6**, 493–504.
- Smith, D. S. and Hellmund, P. C. (1993). *Ecology of Greenways*. Minnesota: University of Minnesota Press.
- Stace, C. (1991). *The New Flora of the British Isles*. Cambridge: Cambridge University Press.

- Thompson, K. (1994). Predicting the fate of temperate species in response to human disturbance and global change. In *NATO Advanced Research Workshop on Biodiversity. Temperate Ecosystems and Global Change* (T. J. B. Boyle and C. E. B. Boyle, eds), pp. 61–76. Berlin: Springer-Verlag.
- Thompson, K., Hodgson, J. G., Grime, J. P., Rorison, I. H., Band, S. R. and Spencer, R. E. (1993). Ellenberg numbers revisited. *Phytocoenologia* **23**, 277–289.
- Thompson, K., Hodgson, J. G. and Rich, T. C. G. (1995). Native or alien invasive plants: much of the same? *Ecography* **18**, 390–402.