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**Title**: How hedge woody species diversity and habitat change is a function of land use history and recent management in a European agricultural landscape.

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**Abstract**

European hedged agricultural landscapes provide a range of ecosystem services and are an important component of cultural and biodiversity heritage. This paper investigates the extent of hedges, their woody species diversity (including the influence of historical versus recent hedge origin) and dynamics of change. The rationale is to contribute to an ecological basis for hedge habitat management. Sample sites were allocated based on a multivariate classification of landscape attributes. All field boundaries present in each site were mapped and surveyed in 1998 and 2007. To assess diversity, a list of all woody species was recorded in one standard 30 m linear plot within each hedge. There was a net decrease in hedge habitat extent, mainly as a result of removal, and changes between hedges and other field boundary types due to the development and loss of shrub growth-form. Agricultural intensification, increased rural building, and variation in hedge management practices were the main drivers of change. Hedges surveyed at baseline, which were lost at resurvey, were more species rich than new hedges gained. Hedges coinciding with historical land unit boundaries of likely Early Medieval origin were found to be more species rich. The most frequent woody species in hedges were native, including a high proportion with *Fraxinus excelsior*, a species under threat from current and emerging plant pests and pathogens. Introduced species were present in circa 30% of hedges. We conclude that since hedge habitat distribution and woody species diversity is a function of ecology and anthropogenic factors, the management of hedges in enclosed agricultural landscapes requires an integrated approach.

*Keywords*: hedge; woody species; species diversity; introduced species; ecosystem services; landscape history.

**1. Introduction**

Hedges, usually defined as narrow woody linear features composed of woody species with shrubby growth forms, are one of the main types of field boundary in enclosed agricultural landscapes within Europe. Hedged agricultural landscapes, generally referred to as *bocage*, occur throughout Western Europe (Baudry et al., 2000), notably around the Atlantic fringe, in France and Galicia (north-west Spain). Hedges form a dense network throughout Ireland (Aalen et al., 1997), and are widespread in Britain (Rackham, 1997).

Hedges have originated mainly due to planting, but also by spontaneous natural colonisation of woody species along other field boundary and linear feature types, and occasionally as remnants, e.g. along an ownership boundary, left after the process of woodland assarting (clearance) for agricultural land (Forman and Baudry, 1984; Pollard et al., 1974; Rackham, 1997). While historically the main function of hedges was for agricultural land enclosure, they were usually managed as a source of wood for fuel and crafts, and for natural foodstuffs.

Enclosed agricultural landscapes can deliver multiple ecosystem services (e.g. Firbank et al., 2013) and are acknowledged as part of the European cultural and biodiversity heritage, (EEA, 2010); hedges, as characteristic components, are also recognised for their contribution to spatial connectivity and green infrastructure. Hedges have an ecological role and provide a range of ecosystem services to which their woody species diversity and associated linear features such as banks, ditches and verges, contribute (see Table S.1).

1.1. Plant species diversity in hedges

The flora of the hedge ground layer, and associated linear features, can contain a wide range of plant species (Critchley et al., 2013), although this can be largely affected by the adjacent land use and its management (Cherrill et al., 2001; Ernoult and Alard, 2011; French and Cummins, 2001), and can also be due to age (Deckers et al., 2005; Pollard et al., 1974). Due to their linear structure and limited width, hedges are typically characterised by a high edge to area ratio and thus consist mainly of edge habitat, and may act as habitat for woodland edge ground flora (Closset-Kopp et al., 2016; McCollin et al., 2000). Species-richness has been found to be greater in “green lanes”, i.e. two parallel hedges separated by an unmetalled (non-sealed) track (Walker et al., 2006); sunken types notably support woodland species (Deckers et al., 2005). Ditches associated with hedges may contain wetland species of habitats such as fen, swamp and reedbeds (Herzon and Helenius, 2008). Field margin strips associated with hedge verges which are managed specifically to provide benefits for wildlife, can contribute to biodiversity where arable crops are grown (Marshall and Moonen, 2002). Epiphyte communities (lichens, mosses, liverworts, algae), exploit the surfaces of bark, wood and leaves (Alexander et al., 2006).

The woody species composition of hedges is a major source of vascular plant biodiversity in agricultural landscapes, especially where other habitats such as woodland and scrub may be scarce. It has been proposed that hedges accumulate woody species over time (c. 1 per 100 year), assuming a baseline stock of one species in a standard thirty yard (27.4 m) length of hedge, Hooper’s Rule (Hooper, 1970; Pollard et al., 1974). Developed in parts of England, this relationship has been postulated as a method for dating hedges. Studies in Ireland (Condon and Jarvis, 1989; Doogue and Kelly, 2006; Synnott, 1973), and elsewhere in England (Cousins, 2004; Willmot, 1980), have critically assessed the application of the rule in other locations. Woody species richness may also depend on hedge origin, i.e. spontaneous, remnant or through planting with single or mixed species. When this is unknown, Hooper’s Rule may be used as a rough indicator of hedge antiquity (Barnes and Williamson, 2006; Edwards et al., 2006). One outcome of the rule is that a standard linear plot of length 30 m is now used as the basis for assessing hedge woody species diversity.

1.2. Threats to hedge habitat extent and woody species diversity

Field boundary removal as a result of agricultural intensification and increasing mechanization within Europe in the latter part of the 20thCentury, was the main threat to hedge habitat conservation and ecosystem services function, and to landscape structure, e.g. in Ireland (Cooper et al., 2002; Murray et al., 1992), Britain (Petit et al., 2003), and in France (Pointereau, 2001). More recently, compliance regulations specifying that farmers must follow statutory management requirements in order to qualify for full farm subsidy payments under the EU Common Agricultural Policy (CAP), and the introduction of agri-environment schemes (AES), has resulted in a decline in the rate of hedge loss (Carey et al., 2008; Norton et al., 2012), with the main threat being identified as lack of hedge maintenance.

A range of current and emerging invasive non-native pests and diseases threaten native tree and shrub species composition in hedges. A recent example is ash (*Fraxinus excelsior*) dieback disease caused by the fungal pathogen *Chalara fraxinea* (anamorph) and *Hymenoscyphus pseudoalbidus* (teleomorph), while the emerald ash borer beetle *Agrilus planipennis*, a serious pest of ash species in North America, is also emerging as a severe threat to ash in Europe (Mitchell et al., 2014; Thomas, 2016). Native woody species in hedges may also face competition from alien introductions. While there has been a history of non-native plant species introduction to Ireland (Reynolds, 2002), there has been no systematic ecological study of the extent, distribution and frequency of introduced woody species in hedge habitats of the rural landscape.

1.3. Aims

This paper assesses the woody species diversity (richness and composition) of hedges in a European enclosed agricultural landscape. We investigate recent changes in the extent of hedge habitat, the dynamics of hedge loss and gain, and associated changes in woody species diversity. The diversity of hedges established by historical and recent territorial land organisation is also compared. The rationale is to contribute to an ecological basis for hedge habitat conservation and management within the context of rural land use.

**2. Methods**

2.1. Study area

The study area was Northern Ireland (NI), Fig. 1. NI has a mid-latitude western European location with an oceanic climate. The planar area, measured to the high water mark of medium tides in coastal locations, is 14,160 km2. Circa 68% (9676 km2) of the landscape is lowland, i.e. less than 150 m elevation. Gleyed soils are widely distributed (Cruickshank, 1997). The upland landscape, which is mostly below 300 m, includes extensive cover of blanket peat. Agriculture is largely grass-based (DARD, 2007) and is concentrated in the lowlands and marginal uplands. Agricultural grassland and crops total 8452 km2 and make up circa 62% of the land area.

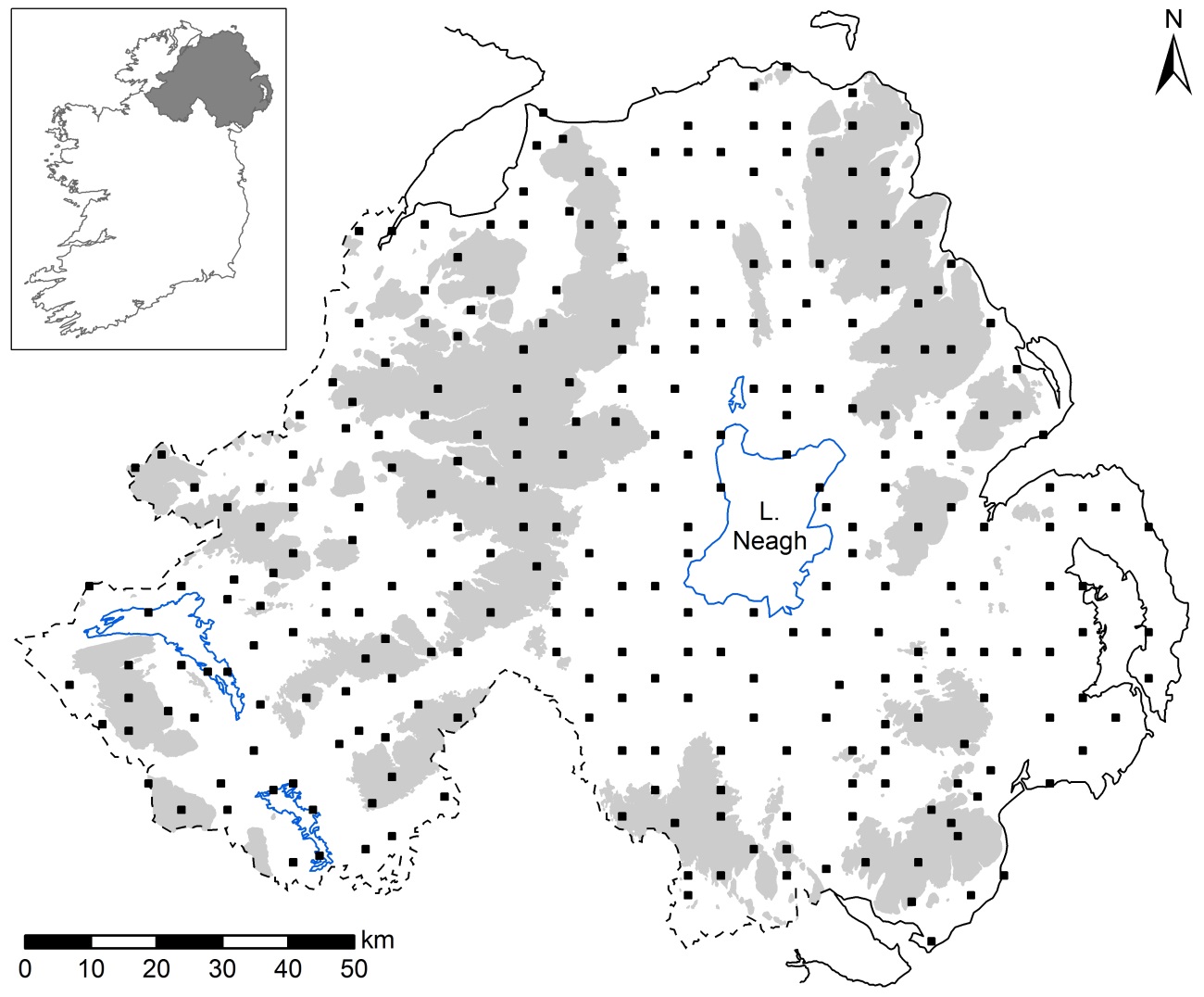


Figure 1. The study area (NI) and distribution of 1 km squares (■), each containing one quarter kilometre (500 m x 500 m) sample site. Shaded areas denote land above 150 m elevation.

2.1.1. Sampling programme

A sampling programme was set up to estimate the extent of terrestrial habitats and field boundaries and to monitor change in NI on behalf of the Environment Agency (Cooper et al., 2002; Cooper et al., 2009; McCann et al., 2009). Sample sites (size 500 m x 500 m, *n* = 287), each of which was located within an Ordnance Survey Irish grid 1 km square (Fig. 1), were allocated by stratified random sampling based on a multivariate classification of map attributes such as elevation, slope, soils and geology (Cooper, 1986), to represent landscape structure. The sampling fraction was 0.5%, i.e. the total area of the sites as a percentage of the total landscape area (excluding a large waterbody area, mainly Lough Neagh, which was treated as a constant).

2.1.2. Hedge habitat survey

Field boundary survey was carried out in summer 1998 (baseline) and repeated in 2007 (resurvey), using the sample sites. Within each site, all field boundaries present were mapped and surveyed, except for those boundaries within curtilage (i.e. gardens and land associated with urban areas, farm or domestic buildings) and within woodland. The scale of resolution for field boundary mapping was a minimum mapping length of 20 m. Individual field boundary end-points were usually the intersections with other field boundaries (McCann et al., 2009), see Fig. S.1.

Hedges were defined as linear features (<5 m wide) composed of woody species with a shrubby growth form (either natural or induced by management), covering more than 25% of the boundary length (McCann et al., 2009). Woody species nomenclature followed Webb et al. (1996) and Stace (1997). Woody species not classed as hedge-forming, were the shrubs *Ulex europaeus* and *Cytisus scoparius*, climbers–scramblers such as *Hedera helix*, *Lonicera periclymenum*, *Rosa canina* and *Rubus fruticosus*, and dwarf shrubs such as *Vaccinium myrtilus*.

If more than one linear feature occurred along the same field boundary, a type classification hierarchy based on structure and ecology was employed. This is necessary in order to estimate the extent of field boundaries without double accounting, and for monitoring purposes. The hierarchy was Hedge > Wall > Bank > Fence > Half bank > Ditch > Line of trees; hence a field boundary with a hedge, bank and fence present, would be classed as a hedge.

The main species of shrubs and trees, management and structure attributes were recorded for each mapped field boundary. In the case of hedges only, a list of all woody species present in one standard 30 m length linear plot per individual boundary, was recorded to measure diversity; the plot was located by random sampling between the two end points of the hedge boundary. Species classed as climbers or scramblers, e.g. *R. fruticosus* were included as woody species, but dwarf shrubs, e.g. *V. myrtilus*, were not included. For practical purposes in the field, some taxa were recorded at genus level (e.g. *Picea* spp.). Note that for baseline hedges, only a count of woody species was recorded in each 30 m diversity plot.

Mapped field boundaries for baseline and resurvey were captured as digital polylines based on an Ordnance Survey Northern Ireland (OSNI) 1:2500 scale polyline template using ArcGIS version 10.0. Lengths (m) for all field boundary polylines were calculated and inserted into an associated ArcGIS field boundary database (McCann et al., 2012). Statistical analysis to estimate the total length for all field boundary types was based on the ratio estimate method for random sampling (Som, 1973). This is a simple method of estimation suitable for surveys in which the type of frequency distribution might vary between items; analyses can therefore be carried out without a prior need to examine each distribution in turn (Cochran, 1977). Analysis was carried out by database programming.

2.2. Woody species diversity in hedges

Hedge polylines were extracted from the field boundary ArcGIS dataset shapefile. A minimum length of 29.50 m was applied for a hedge to be included in the analysis. Analysis of species richness and species composition was carried out at the individual hedge level.

Individual hedges mapped and surveyed within each site can differ in e.g. historical versus recent origin, farm ownership, management and structure attributes and membership of an AES, and could be considered independent. However, while it is known that it is the number of sites which predominately affects statistical power, any potential *design effect*, i.e. as a result of hedge survey being clustered within sites compared with a completely random but impractical sample of hedges throughout the whole landscape, was taken into consideration. Statistical analyses based on cluster sampling (Cochran, 1977; Som, 1973) were therefore employed where applicable. In the case of subsets of the data, when there was on average circa 1 data record per site, clustering was not an issue and analytical methods based on random sampling were employed.

2.2.1. Woody species richness

The number of woody species listed for each hedge 30 m diversity plot was collated and the count data inserted into an attribute field in the database. Initially, the data was investigated by simple (random sampling) univariate descriptive statistics, e.g. the mean, standard deviation (SD), variance, skewness and kurtosis, using SPSS version 20.0 for Windows. Normality was assumed if values of skewness and kurtosis fell within the range −1.0 to +1.0 (McCune and Grace, 2002), and also if circa 68% of observations fell within ±1 SD from the mean (Fowler et al., 1998). Parametric analyses were used in statistical significance testing unless otherwise stated.

The mean and standard error for the number of woody species in hedge 30 m diversity plots were calculated using the ratio estimate for cluster sampling (Cochran, 1977; Som, 1973). Analysis was carried out by database programming but could also be run within a complex samples Descriptives module in SPSS.

2.2.2. Woody species composition

The frequency of each woody species in hedge 30 m diversity plots was calculated. In order to calculate frequencies in sites, the species present in all hedge 30 m diversity plots were collated into a single composite plot for each site. For interpretative purposes, species ecological attributes were taken mainly from Grime et al. (2007) and also Clapham et al. (1989). Native or introduced status was taken from Reynolds (2002) and Webb et al. (1996). For analytical purposes, *Salix* spp. has been allocated as mainly native, but does contain a very small number of long-leaved introduced willow species which were not coded separately at the time. A small number of native *Ulmus glabra* records, have been combined with the data for introduced elm species (e.g. *Ulmus procera*), due to identification issues of elms in hedges. *Pinus sylvestris*, formerly a native species in Ireland, was classed as a post-extinction re-introduction.

Whittaker’s beta diversity index (βW = γ / ᾱ – 1), (Whittaker, 1972), was calculated to indicate the non-directional variation in the identities of species among hedge 30 m diversity plots, i.e. without reference to any specific gradient (Anderson et al., 2011). This index gives the number of times by which the overall species richness (γ) in the data set as a total composite sample is greater than the average richness (ᾱ) in the sample units. The one is subtracted to make zero beta diversity correspond to zero variation in species presence, i.e. if βW = 0, then all the sample units have all the species.

2.3. Woody species diversity in historical land unit boundary hedges

Historical land unit (HLU) boundary hedges were defined as those coinciding with boundaries resulting from a territorial land organisation system dating from at least 400 AD in the Early Medieval period. In Ireland, McErlean (1983) has shown that these land units resulted from the subdivision of a larger agriculturally independent unit, the ballybetagh (Gaelic estate) into 4 units (Quarters), and each Quarter into mainly 4 sub-units (the ballyboes or tates), commonly referred to as townlands. Other boundary hedges are likely to have originated mainly by planting during 18th and 19th century periods of land enclosure within townlands. While hedge age was not measured directly, HLU boundary hedges were assumed to be older.

HLU versus other boundary hedges were identified by spatial overlay of the hedge polyline dataset on a 1:2500 scale townland boundary shapefile provided by OSNI. The townland boundary line was also checked against OSNI 1st and 2nd edition six inch County Series historic maps available as digital copies (license DMOU203, 2011). A small number of hedges (c. 20) were split by townland and non-townland boundary sections, each greater than the minimum length of 29.50 m for inclusion in analyses. In this case woody species diversity data was allocated to both categories. A comparison of woody species diversity in HLU versus other boundary hedges was then carried out.

2.3.1. Woody species richness

The mean number of woody species in 30 m diversity plots for HLU and other boundary hedges was calculated. Comparison of means was carried out by an independent samples *t*-test using a General Linear Model (GLM) run within an SPSS complex samples module to take account of clustering.

2.3.2. Woody species composition

A chi-square (χ2) test of independence using a 2 x 2 contingency table was applied to compare the frequencies of woody species between HLU and other boundary hedges as sample size was large and only the row sums were fixed; calculations were carried out without *Yates’s correction for continuity* (Lydersen et al., 2009; Sokal and Rohlf, 1995). The null hypothesis *H*0 is that there is no difference in the observed and expected frequencies. Generally, for *p* = 0.05, if χ2 >3.84, then *H*0 is rejected; and the significance value only applied where all expected frequencies are ≥5.0. However, *p*-values were calculated using a Crosstabs module run within SPSS complex samples to take account of clustering.

The mean number of introduced woody species in 30 m diversity plots for HLU and other boundary hedges was calculated and a comparison of means (*t*-test) carried out. The frequency of hedges with at least one introduced woody species present was also calculated.

2.4. Change with time

2.4.1. Hedge habitat

A change in the field boundary type recorded at resurvey compared with baseline was defined as a transition. Field survey recorded up to three codes to describe the type transitions, mainly related to hedge planting, new fencing or wall construction, and hedge cutting or lack of management. Also included were codes for transitions related to field boundary loss or removal due to e.g. agricultural field enlargement, buildings construction and woodland planting (McCann et al., 2009). Drivers of change were extracted from the transition data.

Transition from a non-hedge field boundary type to a hedge was defined as a gain, while transition from a hedge to a non-hedge field boundary type was defined as a loss. Net change was determined by total gains minus total losses. Digital lengths for all field boundary transitions were calculated using overlay of resurvey and baseline polyline shapefiles in ArcGIS, and inserted into the transitions database. Statistical analysis to estimate the total lengths of change and transitions for hedges was based on the ratio estimate method for random sampling (Cochran, 1977; Som, 1973). Confidence intervals (*z* x *SE*) were based on a *z*-value of 1.97.

2.4.2. Woody species richness

The mean number of woody species in hedge 30 m diversity plots at baseline and resurvey was calculated and compared using the ratio estimate for cluster sampling (Cochran, 1977; Som, 1973).

The mean number of woody species in 30 m diversity plots for hedge transition losses was compared with that for hedge transition gains using an independent samples *t*-test for Equality of Means run within SPSS. In addition to data normality checks, Levene’s test was used to check for homogeneity of variances. When Levene’s test was significant, Welch’s *t*-test which does not assume equality of variances was employed (critical *t* values were *p* = 0.05).

**3. Results**

3.1. Hedge habitat

Hedges were the main field boundary type in the landscape with an estimated length of 113648 km (*SE* = 4394 km), accounting for 52.2% of all primary field boundary types (see Table S.2). Hedge density was circa 8.0 km/km2. In the field survey, hedges were present with variable numbers (X̅ = 26.6, *SD* = 16.3) in 234 of the 287 sample sites.

3.2. Woody species diversity in hedges

3.2.1. Woody species richness

Using simple (random sampling) descriptive statistics, the mean number of woody species in hedges was 4.73 (*n* = 6229, *SD* = 2.08). Count data values ranged from 1 to 13 (Table 1), and the modal number was 5.0. Tests for normality indicated that the data were suitable for input to parametric statistical analysis.

Table 1. Frequency distribution of the number of woody species in hedge 30 m diversity plots (n = 6229).

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | Number of woody species | | | | | | | | | | | | |
|  | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
| *n* | 289 | 604 | 938 | 1121 | 1198 | 909 | 582 | 298 | 169 | 81 | 23 | 16 | 1 |
| *f* (%) | 4.6 | 9.7 | 15.1 | 18.0 | 19.2 | 14.6 | 9.3 | 4.8 | 2.7 | 1.3 | 0.4 | 0.3 | <0.1 |

Statistical analysis based on cluster sampling gave a standard error (*SE* = 0.10) for the mean (X̅ = 4.73).

3.2.2. Woody species composition

In hedges and in sites, native species *Crataegus monogyna* and *R. fruticosus* were the most frequent (Table 2). Less frequent in hedges, but widespread in sites, were *F. excelsior* and *U. europaeus*. Introduced (non-native) woody species had much lower frequencies in hedges than native species, but some were widespread in sites. The introduced trees, *Acer pseudoplatanus* and *Fagus sylvatica* were the most frequent, with *Symphoricarpos albus* the most frequent shrub. Introduced species make up over half (*n* = 39) of the total (*n* = 72) listed in Table 2.

The mean number of introduced woody species in hedges was 0.38 (*SE* = 0.02). The frequency of hedges with at least one introduced woody species was circa 30% (1797), and in sites circa 90% (210). Whittaker’s beta diversity (βW) was estimated to be 14.2.

Table 2. Percentage frequency of woody species in hedge 30 m diversity plots and in composites for sites. Status: I = introduced, N = native.

|  |  |  |  |
| --- | --- | --- | --- |
|  | Hedges | | Sites |
|  |  | *n* = 5995 | *n* = 234 |
| Species | Status | *f* (%) | *f* (%) |
| *Crataegus monogyna* | N | 90.5 | 99.6 |
| *Rubus fruticosus* | N | 74.9 | 95.7 |
| *Hedera helix* | N | 48.6 | 84.6 |
| *Fraxinus excelsior* | N | 46.9 | 90.6 |
| *Rosa canina/*spp. | N | 29.6 | 74.4 |
| *Prunus spinosa* | N | 29.5 | 76.1 |
| *Ilex aquifolium* | N | 21.3 | 65.8 |
| *Ulex europaeus* | N | 19.1 | 77.8 |
| *Lonicera periclymenum* | N | 16.9 | 64.1 |
| *Acer pseudoplatanus* | I | 13.8 | 74.8 |
| *Sambucus nigra* | N | 8.7 | 60.3 |
| *Alnus glutinosa* | N | 7.7 | 58.1 |
| *Corylus avellana* | N | 7.7 | 44.9 |
| *Salix* spp. | N | 7.3 | 50.4 |
| *Fagus sylvatica* | I | 5.1 | 49.6 |
| *Ligustrum vulgare* | N | 4.6 | 39.7 |
| *Symphoricarpos albus* | I | 4.3 | 38.5 |
| *Salix cinerea* | N | 4.3 | 26.1 |
| *Sorbus aucuparia* | N | 4.3 | 40.2 |
| *Prunus avium* | N | 1.9 | 19.2 |
| *Cupressaceae* | I | 1.9 | 31.2 |
| *Prunus* spp.*/domestica* | I | 1.8 | 18.8 |
| *Prunus domestica (institia)* | I | 1.7 | 21.8 |
| *Rubus idaeus* | N | 1.7 | 19.2 |
| *Ligustrum ovalifolium* | I | 1.3 | 17.5 |
| *Quercus petraea/*spp. | N | 1.2 | 13.7 |
| *Viburnum opulus* | N | 1.1 | 13.7 |
| *Salix aurita* | N | 1.1 | 14.1 |
| *Ulmus* spp. | I | 1.0 | 12.0 |
| *Betula pubescens* | N | 0.8 | 13.2 |
| *Fuchsia magellanica* | I | 0.8 | 8.1 |
| *Betula pendula/*spp. | N | 0.7 | 12.8 |
| *Cystisus scoparius* | N | 0.7 | 10.3 |
| *Quercus robur* | N | 0.7 | 9.0 |
| *Malus domestica* | I | 0.6 | 9.8 |
| *Salix caprea* | N | 0.6 | 9.0 |
| *Malus sylvestris* | N | 0.5 | 9.8 |
| *Prunus padus* | N | 0.5 | 8.5 |
| *Prunus laurocerasus* | I | 0.5 | 7.3 |
| *Buxus sempervirens* | I | 0.4 | 9.0 |
| *Ribes sanguineum* | I | 0.4 | 6.4 |
| *Aesculus hippocastanum* | I | 0.3 | 7.7 |
| *Ribes uva-crispa* | I | 0.3 | 7.3 |
| *Picea* spp. | I | 0.3 | 4.7 |
| *Rhododendron ponticum* | I | 0.3 | 5.1 |
| *Tilia* spp. | I | 0.3 | 5.1 |
| *Pinus sylvestris* | I | 0.2 | 5.6 |
| *Solanum dulcamara* | N | 0.2 | 4.7 |
| *Escallonia* spp. | I | 0.2 | 4.3 |
| *Rubus spectabilis* | I | 0.2 | 3.8 |
| *Populus tremula* | N | 0.2 | 4.3 |
| *Laburnum* spp. | I | 0.2 | 3.4 |
| *Abies* spp. | I | 0.2 | 3.8 |
| *Berberis* spp. | I | 0.2 | 3.8 |
| *Larix* spp. | I | 0.2 | 3.8 |
| *Cotoneaster* spp. | I | 0.2 | 3.4 |
| *Syringa vulgaris* | I | 0.1 | 3.0 |
| *Taxus baccata* | N | 0.1 | 2.6 |
| *Euonymus europaeus* | N | 0.1 | 2.6 |
| *Ribes nigrum* | I | 0.1 | 1.7 |
| *Populus* spp. | I | 0.1 | 1.7 |
| *Griselinia littoralis* | I | 0.1 | 0.9 |
| *Carpinus betula* | I | 0.1 | 0.9 |
| *Spiraea* spp. | I | 0.1 | 1.7 |
| *Castanea sativa* | I | 0.1 | 1.3 |
| *Sorbus hibernica/aria* | N | 0.1 | 1.3 |
| *Acer campestre* | I | <0.1 | 0.4 |
| *Buddleja davidii* | I | <0.1 | 0.4 |
| *Cornus* spp. | I | <0.1 | 0.4 |
| *Eucalyptus* spp. | I | <0.1 | 0.4 |
| *Juglans* spp. | I | <0.1 | 0.4 |
| *Pinus* spp. | I | <0.1 | 0.4 |

3.3. Woody species diversity in historical land unit boundary hedges

3.3.1. Woody species richness

Based on cluster sampling, a GLM independent samples *t*-test, (*t*(233) = 2.798, *p* = 0.006), indicated that the mean number of woody species in HLU boundary hedges (*n* = 480, X̅ = 5.10, *SE* = 0.09), was significantly greater than that for other hedges (*n* = 5773, X̅ = 4.71, *SE* = 0.10).

3.3.2. Woody species composition

Species significantly more frequent in HLU boundary hedges were the native, *Alnus glutinosa*, *Corylus avellana*, *Prunus spinosa*, and *Salix* spp. (Table 3). *C. monogyna* was more frequent in other boundary hedges.

Table 3. Woody species showing different frequencies in historical land unit (*n* = 459) versus other (*n* = 5560) boundary hedge 30 m diversity plots, tested using chi-square. Status: I = introduced, N = native.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  |  | Hedge boundary | |  |  |  |
|  |  | HLU | Other |  |  |  |
| Species | Status | *f* (%) | *f*(%) | χ2 | *p* | φ |
| *Crataegus monogyna* | N | 87.6 | 90.8 | 5.04 | 0.065 | −0.029 |
| *Prunus spinosa* | N | 35.7 | 29.0 | 9.25 | 0.019 | 0.039 |
| *Ilex aquifolium* | N | 24.6 | 21.1 | 3.13 | 0.209 | 0.023 |
| *Alnus glutinosa* | N | 17.0 | 7.0 | 59.21 | <0.001 | 0.099 |
| *Corylus avellana* | N | 15.9 | 7.0 | 47.47 | <0.001 | 0.089 |
| *Salix* spp. | N | 14.8 | 6.7 | 41.30 | <0.001 | 0.083 |
| *Cupressaceae* | I | 0.4 | 2.0 | 5.45 | 0.022 | −0.030 |

Introduced species had similar frequencies in HLU and other boundary hedges, with the exception of species of the *Cupressaceae* family, which were significantly more frequent in other hedges (Table 3).

The mean number of introduced woody species was similar in HLU (X̅ = 0.38, *SE* = 0.03), and other (X̅ = 0.38, *SE* = 0.02) boundary hedges. Based on cluster sampling, a GLM independent samples *t*-test, (*t*(233) = −0.017, *p* = 0.987), confirmed the similarity. The frequency of hedges with at least one introduced woody species present was also similar, circa 31% in HLU boundary hedges and circa 30% in other boundary hedges.

3.4. Change with time

3.4.1. Hedge habitat

There was a statistically significant net decrease in hedge length of −4.6% (−5472 km, *SE* = 1186 km) from 119120 km at baseline to 113648 km at resurvey, (*t*(286) = −4.614, *p*<0.001), (also see Table S.2).

Hedge transition losses totalled −12505 km, −10.5% of baseline, (Table 4). These were mostly to no field boundary present (−7514 km), mainly by removal due to field enlargement or building construction, and by hedges subsumed within woodland planting or scrub habitat development. There were also hedge losses to earth banks (−1976 km), mainly by shrub growth form development to tree growth form, and to fences (−2406 km).

Hedge transition gains totalled 7033 km, 5.9% of baseline, (Table 4). These were mostly from earth banks (2548 km) and fences (2448 km), mainly as a result of shrub growth form regeneration by cutting or planting. There was also a gain of 1271 km from no field boundary present, mainly by new planting.

Table 4. Estimated transitions (km) between hedges and other field boundary types from baseline to resurvey. Percentage losses and gains were calculated from an estimated baseline hedge length of 119120 km. An asterisk indicates statistical significance (*p* ≤ 0.05).

|  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Hedge losses | | | | | Field boundary | | Hedge gains | | | | |
| km | SE | % loss |  | | classification type | | km | SE | % gain |  | |
| 96.2 | 41.3 | 0.08 | \* | | Mortared wall | | 41.9 | 18.2 | 0.04 | \* | |
| 133.3 | 73.3 | 0.11 |  | | Dry stone wall (DSW) | | 436.5 | 179.0 | 0.37 | \* | |
| 49.5 | 21.1 | 0.04 | \* | | Ruined DSW / Stone bank | | 179.9 | 63.6 | 0.15 | \* | |
| 1975.6 | 260.8 | 1.66 | \* | | Earth bank | | 2547.8 | 327.1 | 2.14 | \* | |
| 2405.7 | 254.7 | 2.02 | \* | | Fence | | 2447.8 | 320.3 | 2.05 | \* | |
| 110.5 | 42.4 | 0.09 | \* | | Half-bank | | 78.1 | 42.9 | 0.07 |  | |
| 169.8 | 59.3 | 0.14 | \* | | Ditch | | 29.9 | 30.0 | 0.03 |  | |
| 50.2 | 22.8 | 0.04 | \* | | Line of Trees | | 0.0 | 0.0 | 0.00 |  | |
| 7514.1 | 856.0 | 6.31 | \* | | No Field Boundary | | 1271.3 | 197.6 | 1.07 | \* | |
| 12504.8 | 1002.2 | 10.50 | \* | | Total | | 7033.3 | 630.2 | 5.90 | \* | |

3.4.2. Woody species richness

While the mean number of woody species in hedges at resurvey (*n* = 6229, X̅ = 4.73, *SE* = 0.10) was fewer than that for baseline hedges (*n* = 6610, X̅ = 4.82, *SE* = 0.09), the net decrease was not found to be statistically significant.

Comparison of the woody species richness of hedges surveyed at baseline, which were lost at resurvey, with that of new hedges gained, using an independent samples *t*-test for Equality of Means, indicated that the mean for total losses (4.91) was significantly greater than that for total gains (3.84), (Table 5). Included in the totals were losses and gains between hedges and fences, and between hedges and no field boundary present; both of these transitions resulted in significant decreases in mean woody species richness. A decrease in mean woody species richness for transitions between hedges and earth banks was not found to be statistically significant (Table 5).

Table 5. Comparison of the mean number of woody species in hedge 30 m diversity plots for the main transitions between hedges and other field boundary types from baseline to resurvey. An independent samples t-test for Equality of Means was appropriate in all cases.

|  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Hedge losses | | | Field boundary | Hedge gains | | | Difference | | *t*-test |  |  |
| no. woody species | | | classification | no. woody species | | |  |  |  |  |  |
| *n* | X̅ | *SD* | type | *n* | X̅ | *SD* | X̅ | *SE* | *t* | df | *p* |
| 839 | 4.91 | 2.05 | Total | 409 | 3.84 | 2.02 | −1.07 | 0.12 | 8.733 | 1246 | <0.001 |
| 129 | 4.94 | 1.83 | Earth bank | 153 | 4.52 | 2.07 | −0.42 | 0.23 | 1.796 | 280 | 0.074 |
| 165 | 4.56 | 2.03 | Fence | 134 | 3.24 | 1.79 | −1.32 | 0.22 | 5.928 | 297 | <0.001 |
| 509 | 5.09 | 2.12 | No Field Boundary | 76 | 3.46 | 2.04 | −1.63 | 0.26 | 6.255 | 583 | <0.001 |

Note that the mean number of woody species in hedges which had no transition (i.e. remained unchanged) was similar between baseline (*n* = 5771, X̅ = 4.81, *SE* = 0.10) and resurvey (*n* = 5820, X̅ = 4.80, *SE* = 0.10).

**4. Discussion**

4.1. Hedge Habitat

The high hedge density recorded for NI (c. 8.0 km/km2) which accounted for 52% of all field boundaries, is similar to that found in other Irish cultural landscapes (Foulkes, 2010), where agriculture is predominantly grass-based (CSO, 2012; DARD, 2007), and is associated with smaller average field and farm sizes than found elsewhere. In Britain, for comparison, hedges (c. 477000 km, c. 2.0 km/km2) make up circa 30% of the total estimated length of field boundaries (Carey et al., 2008); field boundaries classed as hedges in Brittany (France), have a density of 6.7 km/km2 (Thenail et al., 2014). The hedge densities found in some European enclosed agricultural landscapes highlight the contribution of the hedge network to biodiversity and ecosystem service provision. In locations with high annual rainfall, e.g. in Ireland, the hydrological regulation effect of the hedge network is particularly important for flood-risk reduction.

4.2. Woody species diversity in hedges

4.2.1. Woody species richness

The mean number of woody species in hedges for NI (4.73), is greater than that of Britain, i.e. c. 3.70 (Carey et al., 2008), in a study where only native species were recorded (Maskell et al., 2008). The mean number of introduced woody species (0.38) in NI hedges cannot account for this difference; therefore it can be concluded that the native woody species richness of hedges in NI is greater than that in Britain, despite having a smaller available species pool due to its more isolated biogeography.

4.2.2. Woody species composition

The most frequently occurring and widely distributed woody species are mainly native, and are those commonly found in Irish semi-natural broadleaf deciduous woodland and scrub. They have a wider ecological range, and have efficient dispersal mechanisms either by fruits or berries which are bird dispersed, or by wind dispersed winged seeds, while some can also reproduce vegetatively. The structural components of hedges also support species classed as climbers/scramblers. Most of the woody species present are insect pollinated, or occasionally wind pollinated, while some such as *R. fruticosus* can also be apomictic. This highlights the importance of hedges to pollinators given their recent decline and parallel declines in the plants that rely upon them (Potts et al., 2010).

Hedged agricultural landscapes are anthropogenic; therefore species planting can be a major dispersal factor in addition to natural means. Frequent woody species are *C. monogyna*, *P. spinosa*, and *Ilex aquifolium*, commonly planted due to their stockproof thorny attributes, while they also tolerate cutting. Other species could be planted as a source of wood e.g. *F. excelsior*, while *U. europaeus* was planted alongside field boundaries for a variety of agricultural purposes (Lucas, 1958). *Sambucus nigra* is a synanthrope associated with rural and farm buildings, and disturbance.

*F. excelsior*, found in 47% of hedges in this study, is also frequent (30%) in hedges within Britain (Maskell et al., 2013) and is widely distributed throughout Europe (Thomas, 2016). The high frequency of *F. excelsior* in hedges therefore makes the structural integrity of hedge habitat and woody species diversity particularly susceptible to disturbance caused by the effects of ash dieback disease, which has already been recorded throughout Europe, and also potentially by the emerging plant pest – emerald ash borer beetle. There will also be associated effects on hedge ecosystem service provision (Mitchell et al., 2014).

While most non-native introduced species have low frequencies in hedges, *A. pseudoplatanus* and *F. sylvatica*, both of which regenerate freely and are considered to have become naturalised in Ireland (Reynolds, 2002), are frequent and widespread. Valued for their wood, they were planted around buildings and in hedges, mainly during the 18thand 19thcenturies (MacEvoy, 1802). Other more frequent introduced species are ornamentals, e.g. the formerly more fashionable *S. albus*, *Ligustrum ovalifolium* and *Fuchsia magellanica*, and species with edible fruits, e.g. *Prunus domestica*. They are widely distributed, usually also associated with buildings fronting agricultural land and often persisting in nearby hedges even after the buildings may have become derelict or removed. A small number of introduced species, recognised as invasive in seminatural habitats such as woodland, scrub and heath, are frequent (>5%) in hedges in the landscape, for example, *Prunus laurocerasus* and *Rhododendron ponticum*. In recent decades, cypress species (*Cupressaceae*) have been widely planted around rural buildings.

Buildings are classed as a type of *introduced* patch in the patch–corridor–matrix model of landscape structure (Forman and Godron, 1986) originating as a result of disturbance due to settlement pattern and agricultural activity in the landscape and can persist over long time periods. They are also recognised as a source of introduced (non-native) plant species which can extend into adjacent hedges (line corridors). During the current study, the area of buildings increased by 17251 ha (30.35%) to 74098 ha, between baseline and resurvey (Cooper et al., 2009), while the number, area and edge density of building patches also increased (McKenzie et al., 2011); building was predominantly on agricultural grassland. This represents a potential major contemporary source of non-native woody species.

The value for Whittaker’s beta diversity (14.2) indicates the variation in the identities of species among the hedge 30 m diversity plots, representing that on average, individual hedges have only about one-fifteenth of the woody species richness of the whole data set. Introduced woody species, found in circa 30% of hedges and in circa 90% of sites in the landscape, are likely to contribute to the high value for beta diversity.

As disturbance is known to increase the invasibility of communities to introduced species (Hobbs and Huenneke, 1992), and given that there is potential for further disturbance due to building in the landscape and the effects of plant pests and pathogen, the expansion of introduced woody species in hedges could continue. The ecological consequences and the associated effect on ecosystem services delivery may not yet be fully manifested.

4.3. Woody species diversity in historical land unit boundary hedges

4.3.1. Woody species richness

The greater mean number of woody species in HLU (townland) boundary hedges compared with other boundary hedges is possibly related to their origin e.g. in likely Early Medieval landscape spatial organisation (McErlean, 1983) and mixed species planting historically (Kelly, 1997), remnants in cases of woodland assarting, or accumulation of species over time. In more recent times, instances of hedges formed as remnants resulting from the clearance of ancient woodland are likely to be rare (e.g. McCourt and Kelly, 2007). Other boundary hedges originating mainly during 18thand 19thcentury periods of land enclosure could be planted as single or mixed species. Some land leases included clauses which compelled tenants to incorporate specific trees and shrubs into newly planted hedges (MacEvoy, 1802).

4.3.2. Woody species composition

Woody species mostly have similar frequencies in HLU and other boundary hedges. However, HLU boundary hedges have higher frequencies of *P. spinosa*, *I. aquifolium*, *A. glutinosa*, *C. avellana* and *Salix* spp., all common species of Irish woodland and scrub. Together with *F. excelsior*, these species are listed in the Old Irish Law texts of about 700 AD as being of high economic value (Kelly, 1976, 1997). The law texts also give descriptions of the main field boundary types, including the earth bank and ditch, substantial forms of which would have been used to delimit land divisions. Trees and shrubs were likely to have been planted in the bank to strengthen it, and those growing in this situation were more highly valued than others growing in woods (Kelly, 1997). A proportion of HLU boundaries coincide with natural watercourses or ditches, conditions also favouring the establishment of *A. glutinosa* and *Salix* spp. The higher frequency of *C. monogyna* in other boundary hedges relates to its continued economic value and use as the main species planted during the 18thand 19thcentury land enclosures. In recent decades the main function of hedges for stock control has been superceded by post and wire fences.

4.4 Change with time

4.4.1. Hedge habitat

The net decrease in estimated total length of hedges between baseline and resurvey signifies a continuing decrease (Cooper et al., 2002) in hedge habitat and a change in structure of the agricultural landscape.

Hedge transition losses to other field boundary types, mainly earth banks and fences, were mostly the same as the respective gains, with only the gains from earth banks being slightly larger. These were a result of variation in hedge management causing changes between shrub and tree growth form. Changes from shrub growth form to tree growth forms can occur fairly quickly in a mild, wet climate, if hedge management is reduced, while the high frequency of faster-growing tree species e.g. *F. excelsior* can be a contributing factor; hedges may eventually develop into lines of trees.

Hedge transition losses to no field boundary, however, were much larger than the respective gains. Therefore net hedge loss was mainly a result of removal due to building construction and field enlargement, and hedges subsumed within woodland planting or scrub habitat development. These processes were much greater than new hedge establishment from agri-environment schemes and other types of planting. This represents a major continuing loss of biodiversity and cultural heritage from the rural countryside. The processes involved, suggest that an ecosystem approach to managing the field boundary network is required at a landscape scale.

4.4.2. Woody species richness

A decrease in the mean number of woody species in hedges is linked to transitions between hedges and other field boundary types, mainly earth banks and fences, while in terms of effect size, the largest difference in means was found for hedge losses to no field boundary. In general, hedges involved in transition losses were on average more species rich than the hedge population overall, and notably richer than hedge transition gains. Therefore the loss of older more diverse hedges has not been compensated for by the more recent gain of hedges through planting or regeneration. Active management of existing field boundaries is therefore essential to maintain diversity.

4.5. Hedge management implications

Disturbance, usually through the partial or total destruction of biomass, is known to affect diversity (Connell, 1978). A more general definition of disturbance is any event that impacts on the niche relationships of the species (Shea et al., 2004). The principle can be employed in hedge management to maintain habitat extent and woody species diversity, and to deliver ecosystem service gains through managing the type and timing of cutting (e.g., to allow flowering and berrying or fruiting), planting, and invasive species control. Managing woody species growth form transitions that lead to the loss of hedge habitat extent and woody species richness is important. For example, lack of management can lead to hedge growth form transition to a line of trees, and uncontrolled grazing can create hedges with gaps. Active management should include inter-planting of native woody species in existing hedges. As part of spatial planning and building control, hedge planting around new or existing rural buildings should be of mixed native species.

As part of strategy for the management of field boundaries in enclosed European agricultural landscapes, hedges which coincide with historical land unit boundaries, or those of known antiquity, should be included in agri-environment schemes, where, for example, they could qualify as Ecological Focus Areas.

4.6. Conclusion

The extensive spatially and ecologically connected network of boundaries enclosing the 61,000 historical land units (townlands) in Ireland provides hedge habitat of particular cultural historic landscape and biodiversity value. This is likely to be the case for boundaries associated with other historical forms of landscape spatial organisation, similar to the ballybetagh–townland system, that occur in Britain (Rackham, 1997) and throughout Europe (MacCotter, 2008).

We conclude that the structure and distribution pattern of the hedge network is an outcome of changed historical and recent decadal land use, with current grass-based agricultural intensification, hedge loss, reduced hedge management practices and increased rural building development being the main pressures driving change. The woody species diversity of hedges is a function of history, ecology, synanthropy and disturbance, related to the anthropogenic nature of agricultural landscapes. Disturbance (biological and physical) caused by plant pests and pathogens, notably of *F. excelsior*, has the potential to be a serious threat to hedge habitat and species diversity, and delivery of ecosystem services.

Strategy for the management of hedges and other field boundaries in enclosed European agricultural landscapes should take into account history, ecology, conservation, land use, building control, spatial planning and ecosystem service provision; this is likely to require a multi-agency integrated approach.

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