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Changes in hedgerow floral diversity over 70 years in an English rural landscape, and the impacts of management

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Abstract

Hedgerows provide key habitat and refuges for wildlife in otherwise intensively-managed landscapes, and may play a role in connecting increasingly fragmented habitats. However, the processes governing changes to the floral biodiversity of hedges are poorly understood. We analysed a unique, long-term data set of plant species richness over a 70 year period at 357 hedgerow sites in southern England to quantify changes in α, β and γ diversity, and identify the role of hedge management and other possible drivers of change. Alpha diversity increased in hedgerows, while a reduction in β diversity was indicated by taxonomic homogenisation, whereby previously distinct communities of species become more similar to one another over time. Changes in the regional species pool (γ diversity) differed with plant life-history; it increased for woody species but decreased among herbaceous hedge species. Hedgerow communities shifted towards species associated with higher soil fertility, a more competitive ecological strategy and, in unmanaged hedgerows, greater shade tolerance. Probable drivers for these changes include the move from traditional forms of management such as coppicing and hedge-laying towards either no management or frequent cutting with a mechanical flail, and eutrophication. The extent of changes in plant diversity over time was determined by both historic and recent hedgerow management, but these management effects varied with plant life-history attributes. However, changes in hedge quality and floral diversity were not linked directly to a 60% increase in the proportion of land use categories classified as 'intensive' adjacent to the sites over the 70 years. Recommendations are made for future hedgerow management based on conservation objectives for specific groups of hedge plant species.

Keywords: diversity, species richness; regional species pool, plant traits, management, taxonomic homogenisation, eutrophication, land use change

1. Introduction

Hedges are a key habitat in many areas of the world including Europe, North America, Africa and China, and have been a large component of managed landscapes for over two thousand years (Deckers et al. 2004; Hannon and Sisk 2009; Yu et al. 1999). Hedges have the potential to play a significant role in habitat conservation, as they are a widespread habitat for wildlife (Baudry et al. 2000; Gelling et al. 2007; Hannon and Sisk 2009), and may provide important refuges for a variety of plants, invertebrates, birds and mammals within otherwise intensively managed landscapes (French and Cummins 2001; Merckx and Berwaerts 2010; Wehling and Diekmann 2009). Hedgerow networks, and associated linear habitats, could also play a key future role in adaptation to climate change by connecting habitat fragments and facilitating the movement of species through the wider countryside (Davies and Pullin 2007; Lawton et al. 2010).

Changes in land use and management, climate and an increase in invasive species can lead to a loss of biodiversity (Hooper et al. 2012). Declines may be manifest as losses in α (declines in local species richness), β (e.g. biotic homogenisation) and γ (species declines over a whole landscape) biodiversity (Ernoult and Alard 2011; Keith et al. 2009; Lambdon et al. 2008; Olden and Rooney 2006). Hedge floristic diversity is very variable, and has been related to hedge age (Roy and de Blois 2008); a long history of human intervention in terms of planting (Boutin et al. 2002) and management (Deckers et al. 2004); adjacent land use (Ernoult and Alard 2011); and numerous landscape parameters including connectedness of the hedge network (Davies and Pullin 2007). These previous studies have addressed current hedge floral diversity rather than changes in diversity over time. Changes to biodiversity, and analyses of their drivers, are best examined using long-term data on community change at multiple sites in a landscape. However, datasets amenable to this type of analysis are rare.

To investigate floral biodiversity changes in hedgerows, we used a unique botanical data set for 357 hedge sites across a study area of 2 600 km^2 (in Dorset, a southern English county), collected in the 1930s and again in 2001. This dataset allows quantification of changes in α, β and γ diversity, and investigation of drivers of these changes. Changes in the Dorset flora over a similar time scale have been examined previously for woodland (Keith et al. 2009) and grassland (Newton et al. 2012) sites. While γ diversity decreased, there was no change in α diversity over time for woodland sites, but taxonomic homogenisation had occurred (Keith et al. 2009). Taxonomic homogenisation is one component of biotic homogenisation, a loss of β diversity, which leads to spatially distinct communities becoming more similar to each other over time (Olden and Rooney 2006). Among the grassland sites α and γ diversity had increased over time, with no evidence of taxonomic homogenisation. For both habitats, analysis of plant species changes suggested eutrophication due to atmospheric deposition of nitrogen and agricultural fertilisers was the major driver of change (Keith et al. 2009; Newton et al. 2012). Species changes in the woodlands suggested reduced management and the resulting increased shading was an additional driver of biodiversity loss (Keith et al. 2009). However, neither study directly tested for the effects of management or agricultural intensification on changes to plant communities.

Hedges require management to prevent them encroaching on adjacent agricultural land, and developing into scrub or lines of trees (Barr et al. 2005; Baudry et al. 2000). Traditionally, this management would have included hedge-laying or coppicing, both of which are infrequent management techniques applied every 20 – 40 years, which rejuvenate hedges by encouraging them to produce new shoots from the base of woody species and maintains them as stock-proof barriers. Over 50% of the woody hedge biomass is removed during hedge-laying or coppicing, and between this infrequent rejuvenation management, hedges would have been trimmed every few years by hand to maintain their shape. Over the last 70 years frequent cutting with a mechanised flail has become the dominant form of management across Europe (Croxton et al. 2004). While the removal of hedgerows is prohibited in many European countries (Baudry et al. 2000), the total length of hedgerows is still diminishing due to a lack of any management or over-intensive management (e.g. severe flailing every year) (Carey et al. 2008). The impact of management methods on hedgerow flora is little studied, especially in the context of ameliorating biodiversity loss.

In this study we build on previous analyses of long-term vegetation change in Dorset by testing the following hypotheses: H1) community composition of hedges has shifted over time towards species associated with higher soil fertility and with more competitive life-history strategies in response to eutrophication; H2) this shift in composition has led to taxonomic homogenisation (loss of β diversity) in hedges between the 1930s and 2001; H3) hedges with evidence of historic rejuvenation management are more diverse and have undergone less taxonomic homogenisation than those with no sign of historic management; H4) community composition of hedges with recent evidence of flailing has shifted away from species associated with shady conditions, and the species richness of published indicators of hedgerow quality has decreased, due to this management allowing more light into the hedge base; H5) the extent of change of hedge floral communities correlates with the increase in the proportion of the adjacent land area under intensive use.

These hypotheses were tested separately on hedgerow woody species, which make up the majority of the physical structure of hedges, and herbaceous hedge species, a more diverse plant community found in the base of hedges. We predicted that these two groups of species would respond differently to changes in hedgerow management and surrounding land use, due to their differing life histories.

2. Methods

2.1 *Vegetation surveys*

2.1.1 *1930s survey of hedgerow plants*

Over 1000 hedgerow sites were surveyed by Professor Ronald Good in Dorset between 1931 and 1939, as part of a large-scale botanical survey covering a range of habitats (Good and Robinson 1948). Good (1937) chose sites to represent specific habitat types, to be "...reasonably distinct topographical and ecological entities..." and to be "...as evenly scattered as possible" across Dorset. The hedgerow sites varied in length from

57 to 1 040 metres and were surveyed by recording all vascular plant species encountered over approximately 1 hour. Each hedge was visited once, generating presence-absence data that are relatively robust to sampling error (Hirst and Jackson 2007). Hedgerow site locations were recorded on a series of large scale (1:10 560; six inches to the mile) Ordnance Survey maps which are stored at Centre for Ecology and Hydrology, and were digitised by Dorset Environmental Records Centre in 1999 (http://www.derc.org.uk/projects/good.htm). Good's data have been used in other analyses of long-term vegetation change in woodland (Keith et al. 2009; Keith et al. 2011), grassland (Newton et al. 2012) and cliff-top sites (Wichmann et al. 2008).

2.1.2 *2001 re-survey of hedgerow plants*

During the spring and summer of 2001, a random sample of 357 hedgerow sites was chosen from the original dataset and resurveyed once. The size and shape of the original plots was re-located using the annotations on the large scale survey maps. The presence of all plant species within each site was recorded using the Good (1937) method. In addition, the management status of each hedgerow site was recorded, in terms of evidence of 'histoic management' (categorised as either laid, coppiced or pollarded) and of 'recent management' within the preceding two years (categorised as flailed/trimmed, coppiced or laid). Coppicing can be detected in woody hedgerow species for decades after rejuvenation management, due to the characteristic growth of new shoots from a 'stool' (the main stem that is coppiced). Similarly, the presence of horizontal woody trunks is evidence of previous hedge-laying. The location of each hedgerow site was determined with a Geographical Positioning System, and a photograph taken of each site (Button 2003).

2.2 *Plant species classification and attributes*

Hedgerows containing ‘ancient woodland indicator species’ are considered to have a high conservation value due to the implication that they were once part of ancient woodlands. In the UK, the 1997 Hedgerow Regulations includes a list of 57 indicator species (electronic supplementary material Appendix A; http://www.legislation.gov.uk/uksi/1997/1160/schedule/1/made, last accessed 15 January 2013). Difference in the number of these indicator species at each hedge site between the 1930s and 2001 were analysed to measure change in habitat quality.

Plant species recorded in both surveys were classified according to the woodiness attribute in the PLANTATT data base (containing comprehensive information on status, size, life-history, geography and habitats for all British Plant species; Hill et al. 2004): (i) woody and semi-woody (referred to below as ‘woody’ species) vs. (ii) herbaceous plant species. This allowed us to determine whether the structural woody components of the hedgerows were responding differently over time compared with the herbaceous species growing in the base of the hedge.

We examined the potential processes behind observed botanical compositional changes by using values for PLANTATT attributes that indicate tolerance of specific environmental conditions. We examined whether average attributes (across species) per hedge site differed between the 1930s and 2001. Attributes that were analysed were height and Ellenberg values for N (nitrogen), L (light), R (soil acidity) and S (salt tolerance). The latter two attributes were included to test hypotheses that floral change was related to soil acidification (Stevens et al. 2010) or increased salinity caused by winter road gritting with rock salt introduced widely after the 1930s survey. The Comparative Plant Ecology database classifies vascular plant species by life-history strategy according to the 'CSR' model: competitiveness, stress tolerance and ruderality (Grime et al. 2007). We analysed average competitiveness and ruderality.

2.3 *Land use data from the 1930s and 2000*

Data on land use categories in Dorset were available from Hooftman and Bullock (2012), who digitised a land use map from the 1930s at a resolution of 10.8 × 10.8 m. The precision of the 1930s map was checked against contemporary ground vegetation surveys (Good and Robinson, 1948) and there was found to be close correspondence between the two. This map was combined with the National Soil Map of England and Wales to create 15 broad habitat types that correspond with those used in the Land Cover Map 2000. The Land Cover Map 2000 consists of 25m × 25m pixels derived from satellite spectral data, which are assigned to broad habitat types using maximum likelihood algorithms (Fuller et al. 2002).

The proportion of land within each broad habitat type was extracted using ArcMAP (ArcGIS v 9.3.1 ESRI) from the 1930s and 2000 map at three radii from the hedge centre line: 100m; 500m; and 1000m.

2.4 *Data analysis*

All data analyses were conducted in R version 2.14.0 (R Core Development Team 2011) and the vegan package (Oksanen et al. 2012). The relationship between the changes in species number within each hedge plot between the two surveys and the number of Julian days between the 1930s and 2001 survey dates was tested using Spearman's rank correlation test, to identify any possible bias caused by different sampling dates (Keith et al. 2009).

Analyses were conducted separately on woody vs. herbaceous plant species (see explanation above). This allowed us to determine whether the structural woody components of the hedgerows were responding differently over time compared with the herbaceous species growing in the base of the hedge. It is unclear to what extent Good surveyed the habitat surrounding the hedgerows (e.g. road verges). To reduce any bias we restricted the herbaceous species for analysis to hedgerow species only (referred to below as 'hedge herbs'). These were herbaceous species categorised as growing along boundary and linear features or in woodland, following the broad habitat attributes list in PLANTATT (Hill et al. 2004). This reduced the 389 herbaceous species recorded by Good at the 357 sites to 190 'herbaceous hedge species'.

2.4.1 *Diversity changes over 70 years*

Paired t-tests were used to test whether average species richness per site (α diversity) had changed over time. Homogeneity of variance was verified prior to the paired t-tests using an F test. The effect of 1930s species richness on 2001 species richness was analysed using linear regression, to determine whether initial species richness affected the change in α diversity.

Following (Keith et al. 2009), Sorensen's similarity indices (*S*) were used to assess the homogenization of community composition across the sites over time, which is a measure of β diversity change (Koleff et al. 2003):

$$S = \frac{2a}{2a + b + c}$$

where *a* = the number of species present in both sites, *b* = the number of species present only in site 1, and *c* = the number of species present only in site 2. *S* was calculated for each hedgerow site in relation to each of the other 356 sites for the 1930s dataset, and an average value calculated per site (S_i^x). This was repeated for the 2001 dataset (S_j^x). The difference between (S_i^x) and (S_j^x) was tested using Wilcoxon paired ranks test: in the event of taxonomic homogenisation we expected $(S_j^x) > (S_i^x)$.

The change in total species richness across all sites or regional species pool (γ diversity) over time was tested using a bootstrap method (Sokal and Rohlf 1995). The data from both surveys was pooled, 357 sites were drawn at random from the pooled dataset and the total species richness calculated. This was repeated 10,000 times sampling with replacement, to create a distribution of expected γ diversity, from which a mean $(\tilde{\gamma}_{boot})$ and standard deviation $SD_{(\tilde{\gamma}_{boot})}$ were calculated. *Z* scores were calculated from observed total species richness at each survey time (γ_{obs}), to test whether total species richness at each survey time differed from the pooled species richness, where:

$$Z = \frac{\tilde{\gamma}_{boot} - \gamma_{obs}}{SD_{(\tilde{\gamma}_{boot})}}$$

2.4.2 *Changes in community composition over time*

The difference in community composition between the 1930s and 2001 was tested with a permutational multivariate analysis of variance using distance matrices (ADONIS) with 1000 permutations (Oksanen et al. 2012). Permutations were constrained within site, to take account of the spatial structure of the dataset (Oksanen et al. 2012). Changes in community structure were investigated further using detrended correspondence analysis (DCA; Leps and Smilauer 2003).

2.4.3 *Hedgerow management effects on changes in plant diversity*

The effects of each management timescale (old vs. recent) on the three measures of hedgerow community change (change in species richness, Sorensen similarity and hedgerow indicator species richness for each hedge site between 1930s and 2001) were tested using two-way ANOVAs, including the interaction between old and new management. There were three levels to the factor ‘old management’: none, coppiced vs. laid. ‘Recent management’ was simplified to two levels (none vs. recent management), as two of the recent management categories were present at too few hedgerow sites to provide robust results (only 4 of 357 hedgerow sites had been recently flailed and laid, and 8 sites recently laid). The vast majority of sites that had been recently managed were cut with a mechanised flail (253 sites). Prior to analysis, the hedgerow community change response variables were tested for normality using a Shapiro-Wilks test. ANOVA models were simplified by removing interactions and management factors that were not significant at $P < 0.05$. Following a significant ANOVA result for old management, posthoc Tukey HSD tests were used to determine which old management categories differed significantly.

2.4.4 *Change in community average attributes over 70 years*

Average values of the PLANTATT and CSR attributes (see above for details) across species were calculated for each site in the 1930s and 2001. The significance of changes in the average attributes between the 1930s and 2001 were analysed using paired t-tests if the response variables were normally distributed, or Wilcoxon paired ranks tests if not. In addition, hedge sites were divided according to whether they had received recent hedgerow management, and the significance of changes in average species attributes analysed separately for sites in each management category.

2.4.5 *Changes in land use adjacent to the hedge sites*

The broad habitat types extracted from the 1930s and 2001 land use maps were classified as ‘intensive land use’ (all arable habitat types, improved grassland, and all urban habitats) vs. ‘extensively managed’ (setaside (2001 only), neutral, calcareous and acid grasslands, woodland, heath, fens and marshes). The change in proportion of land use in these two categories was calculated between the 1930s and 2000 for each hedgerow site, to provide an index of land use intensification, within each of the three buffer areas around the hedge. The relationship between the land use intensification indices and changes in hedgerow plant communities in terms of species richness, Sorensen similarity index and the number of hedgerow indicator species were analysed using Spearman’s rank correlation tests.

3. Results

No relationship was found between the difference in species richness per hedgerow site from the 1930s to 2001, and the difference in Julian days between the two surveys (Spearman’s correlation test: woody species = -0.0185, $P>0.05$; herbaceous hedgerow species $\rho = 0.0953$, $P>0.05$), suggesting that differences in survey date did not bias the results.

3.1 *Changes in hedgerow diversity over 70 years*

Hedgerow plant α diversity was lower in the 1930s than in 2001. Mean species richness per hedge increased for both woody species (1930s: mean ± standard error (SE) = 9.44

± 0.194; 2001: mean = 12.50 ± 0.163; $t_{356} = -16.41$, $P < 0.001$), and herbaceous hedge species (1930s: mean = 23.3, SE = 0.429; 2001: mean = 26.0, SE = 0.462; $t_{356} = -6.58$, $P < 0.001$). There was a positive relationship between mean species richness in the 1930s and 2001, but with a gradient < 1 for both woody species and herbaceous hedgerow species (Figs. 1a and 1b respectively). Hedgerow sites with low species richness in the 1930s therefore gained more species than average over the following 70 years, while hedgerows with high species richness gained fewer species than average or, at the highest starting values, lost species.

Sorensen similarity indices were higher in 2001 than the 1930s, both for woody species (1930s mean $S_i^x = 0.430 \pm 0.0049$; 2001 $S_j^x = 0.566 \pm 0.0037$; Wilcoxon paired ranks test $V_{356} = 1077$, $P < 0.001$) and herbaceous hedge species (1930s $S_i^x = 0.342 \pm 0.0034$; 2001 $S_j^x = 0.432 \pm 0.0037$; $V_{356} = 1840$, $P < 0.001$). This demonstrates taxonomic homogenisation among hedgerow sites and loss of β diversity over time, for both groups of species.

Woody species showed increased γ diversity with time ($\gamma_{1930s} = 58$, $\gamma_{2001} = 71$), as the number of species found in the 1930s was lower than expected for a random sample ($Z = 5.27$, $P < 0.001$). In contrast, γ diversity decreased over time for herbaceous hedge species ($\gamma_{1930s} = 190$, $\gamma_{2001} = 168$, $Z = -1.95$, $P < 0.05$). There were 42 woody and 140 herbaceous hedge species common to both surveys. Sixteen woody species were lost between the two surveys, and 29 woody species were gained. In contrast, 50 herbaceous hedge species were lost and only 28 species gained.

3.2 *Changes in hedgerow community composition*

Hedge community composition changed significantly between the 1930s and 2001 both for woody (ADONIS statistic $R = 0.024$, $P < 0.001$) and herbaceous hedge species ($R = 0.038$, $P < 0.001$). Although there was a shift in community composition of woody species, there was still considerable overlap between the two communities of woody species (DCA: Fig. 2a), and a reduction of the variation in community composition for herbaceous hedge species (DCA: Fig. 2b).

3.3 *Effects of hedgerow management on plant communities*

3.3.1 *Changes in indicators of hedgerow quality*

Old and recent hedgerow management both caused a change in the number of indicator species of hedgerow quality, with no interaction between the two management types (Table 1a). On average, just over one indicator species was lost between the 1930s and 2001 when hedges had been coppiced historically. In contrast, a small gain in indicator species was seen where hedge-laying had taken place, with a very small average loss (0.33 species) in those hedgerow sites with no apparent old management. There was a greater decrease in the number of indicator species between the 1930s and 2001 for hedges with no recent management (1.3 species lost on average), compared with those that had recently been flailed (0.019 species lost; Table 1b).

3.3.2 *Changes in species richness (α diversity)*

The increase in the number of woody species (α diversity) between the 1930s and 2001 was unaffected by whether the hedgerow site was historically coppiced or laid, but a smaller increase in woody species richness over time was found in sites with no evidence of old management (Table 1a). In contrast, herbaceous hedge α diversity increased between the 1930s and 2001 at hedgerow sites that were coppiced or had no old management, but decreased in hedges that were laid (Table 1a). Recent management did not affect the change in woody or herbaceous hedge species richness (Table 1b), and there was no interaction between the two management time scales for either group of species.

3.3.3 *Taxonomic homogenisation (loss of β diversity)*

Taxonomic homogenisation, tested using Sorensen similarity indices, increased more among woody species if the hedgerow site had evidence of old hedge-laying or coppicing, compared with those with no old management (Table 1a). It was unaffected by recent management (Table 1b).

We found a significant effect of old management on taxonomic homogenisation for herbaceous hedge species (Table 1a), but also a significant interaction between old and recent management on this parameter ($F_{3,340} = 3.40$, $P < 0.05$). For hedges with recent management, the extent of taxonomic homogenisation among herbaceous hedgerow species was smaller if the hedge had been historically laid, compared with hedges with no historic management. In contrast, for hedges with no recent management, the type of old management had no effect on homogenisation (Tukey HSD tests, $P < 0.05$).

3.3.4 *Changes in species attributes*

Hedgerows had a higher proportion of woody species of shorter stature on average in the 1930s than 2001, and species with a lower average CSR competitive value (Table 2). Community average Ellenberg L values reduced (indicating species with a greater shade tolerance) between the 1930s and 2001 for woody species in those hedges which had not had recent management, but did not change in hedges with recent management. In contrast, hedges with recent management had increased Ellenberg N scores for woody species, but N scores did not change for woody species in hedgerows without recent management (Table 2).

Ellenberg N values also increased between the 1930s and 2001 for the herbaceous hedge communities and average competitive values decreased; these changes in attributes were unaffected by recent management (Table 2). Ellenberg L values increased among herbaceous communities in recently managed hedges, but decreased in hedges without recent management, though the average change was small in both cases. The average indicator of salt tolerance for the herbaceous communities increased between the 1930s and 2001 in recently managed hedgerows (Table 2).

3.5 *Changes in land use surrounding hedgerow sites*

The proportion of ‘intensive’ land use adjacent to the hedge increased by around 60% between the two surveys for all three radii from the hedge centre (100m radii: 58% increase in ‘intensive’ land use; 500m radii: 61%; 1000m radii: 62%). Surprisingly, there was no relationship between these large changes in the proportion of ‘intensive’ adjacent land uses, and changes in either the number of hedgerow indicator species, the species richness of the hedgerows or the β diversity of the hedgerow sites at any of the three radii (Spearman’s rank correlation tests, all $P > 0.05$).

4. Discussion

4.1 *Changes in hedgerow community composition over 70 years*

As hypothesised, there were large changes in hedgerow plant community diversity between the 1930s and 2001. These changes differed depending on both the scale of measurement and the group of species under consideration. Alpha diversity (species richness per site) increased for both woody and herbaceous hedge species, with hedgerows that had lower species richness in the 1930s gaining more species than average, and sites with higher initial species richness gaining fewer species or losing species over 70 years. Beta diversity reduced over time for woody and herbaceous hedge species, suggesting sites became taxonomically more similar. Similar patterns have been shown for several other habitats (e.g. Olden and Rooney 2006), which demonstrates the importance of considering diversity at more than one spatial scale.

In contrast to α and β diversity, the two groups of hedgerow species showed markedly different responses in change in γ diversity (the overall species pool), which increased over 70 years for woody species, but decreased for herbaceous species. The increase in woody species is unlikely to be due to replanting, as only one site was recorded as replanted in the 2001 survey. Within this Dorset landscape, re-surveys of Good's woodland and calcareous grassland sites over a similar period showed intriguingly different results. Woodland floras showed no change in α diversity, but decreased β and γ diversities (Keith et al. 2009). In contrast, calcareous grasslands showed increased α and γ diversities, but no change in β diversity (Newton et al. 2012). These very contrasting results, and the differences between woody and herbaceous plant within the same communities reported here, suggest that diversity patterns and their responses to drivers can be idiosyncratic. Measures of diversity (α, β, γ) are not independent: these indexes are related in terms of the level of difference between local populations (β-diversity) and the slope of the local (α) vs. landscape (γ) species-area curves (Loreau 2000; Storch et al. 2012). For example, no changes in local diversity but with a relatively steep species-area curve could be seen as positive, since it would indicate more diversity among localities (β-diversity). In contrast, an increased local diversity accompanied with a relatively flat or concave species species-area curve would indicate homogenisation and could be interpreted more negatively. Among the different habitat types and species groups these relations between α and β could be different, hence leading to the different conclusions described above.

There was a shift in the community composition of woody hedgerow species over time, though there was still considerable overlap between the two compositions. The sixteen woody species that disappeared from these sites between the 1930s and 2001 include three species of heather (*Erica tetralix*, *Erica cinerea* and *Calluna vulgaris*), two gorse species (*Ulex gallii* and *Ulex minor*), alder buckthorn (*Frangula alnus*) and creeping willow (*Salix repens*), which are associated with heathlands and acidic soils (Hill et al. 2004). The area of heathland in Dorset has reduced dramatically and become more fragmented since the 1930s, as land has been converted to more intensive agriculture and woodland (Hooftman and Bullock 2012). Loss of heathland communities may also have been exacerbated by nitrogen deposition (Maskell et al. 2010). Woody species gained between the 1930s and 2001 include a higher proportion of non-native species (66%) than species that were retained (12%) or lost (13%) between the two surveys. These included common, widespread neophyte species such as rhododendron (*Rhododendron ponticum*), buddleja (*Buddleja davidii*), cherry laurel (*Prunus laurocerasus*) and garden privet (*Ligustrum ovalifolium*).

Variation among the herbaceous plant communities decreased over time such that the 2001 community form a subset of the 1930s communities. In contrast to the woody species, this indicates a loss of particular herbaceous communities. Hedgerow forbs that have been lost also include species with a heathland association such as heath groundsel (*Senecio sylvaticus*). These changes in community composition and evidence of taxonomic homogenisation between the 1930s and 2001 for both woody and herbaceous hedge species support our first two hypotheses.

4.2 *Effects of management on hedgerow composition*

This study has provided valuable insights into the effects of management on hedgerow plant communities. Richness of woody species appeared to benefit from past reduction in woody biomass through hedge coppicing or laying. This practice is likely to reduce competition for resources and allow the persistence of slower growing species. Similar beneficial effects on α diversity have been found in coppiced and pollarded hedges in Belgium (Deckers et al. 2004). Our third hypothesis, that historic rejuvenation management retains hedgerow floral diversity, is thus supported for woody species. However, the response of both herbaceous indicators of hedge quality and more generalist herbaceous species was more complex as they depended on the type of historic management that was applied.

Historic coppicing resulted in the richness of published indicators of hedgerow quality declining. Coppicing requires the complete removal of the woody canopy to encourage re-growth from the base. This will result in increased light levels and disturbance which are unlikely to favour such sensitive, shade-tolerant woodland species. In contrast, the average α diversity of hedge herbaceous species increased between the 1930s and 2001 under coppicing or no management. Generalist herbaceous hedge species are likely to benefit from the open, light habitats created by coppicing, and by the gradual opening up of the hedge base and increasing gappiness under no management. Richness of these species decreased under historic hedge laying as this practice aims to retain a dense, homogenous and stock-proof hedge structure at the base.

The increase in taxonomic homogenisation among the herbaceous hedge communities was greater in hedgerows with no historic management. This may indicate a move towards a more uniform basal flora associated with higher soil nitrogen content, slightly greater shade tolerance and species with a more competitive strategy, as found by Keith et al. (2009) for Dorset woodlands. In contrast, the disturbance and heterogeneous hedge structure of coppicing may result in more taxonomic diversity between hedgerows.

4.3 *Drivers of change in the hedgerow flora*

Ellenberg N values increased with time for herbaceous hedge species, and for woody species in hedges under recent management, supporting our first hypothesis, that eutrophication is an important driver of changes to hedgerow plant communities. This is similar to the increase in N values found in Dorset woodland (Keith et al. 2009) and grassland (Newton et al. 2012) floras; both studies concluded that eutrophication was a major factor in changes to Dorset plant community composition over the last 70 years. Similarly, Bennie et al. (2006) suggested eutrophication was a driving force in changes to chalk grassland floras across Britain over fifty years. However, we found no correlation between the increase in the proportion of intensively managed adjacent land and changes in hedgerow floras, leading us to reject our fifth hypothesis relating to land use change. This may indicate that local land use change is a poor indicator of eutrophication. Indeed, much eutrophication may be due to atmospheric nitrogen deposition (Maskell et al. 2010) which is manifest at large spatial scales (Henrys et al. 2011).

Whilst unmanaged hedges shifted towards more shade tolerant (higher Ellenberg L) herbaceous communities, recent management was associated with changes in the opposite direction.   This partially supports our fourth hypothesis, which predicted hedge trimming would lead to a reduction in plants associated with shady conditions. However, we also predicted that woodland indicator species richness would decline more in hedges that were flailed, but the reverse pattern was found.

Woody and herbaceous hedge communities showed increases in more competitive species over time, regardless of whether hedges were recently managed. Species with a more competitive strategy are likely to be able to capture resources in productive, relatively undisturbed environments, and often have high potential growth rates (Grime et al. 2007). This change in average strategies may link to the change in eutrophication driver and hedgerow management discussed above. Woody species also had a lower PLANTATT height attribute in the 1930s than 2001, which probably reflects the loss in short woody species associated with heathland discussed above (section 4.1).

4.4 *Management recommendations and conclusion*

Generic recommendations for hedgerow management to counter biodiversity losses and compositional changes are complicated by the differing responses of woody species, hedgerow herbs, and indicator species of hedgerow quality. Nevertheless, some general management guidance can be provided that is applicable to the conservation of hedgerows in other regions. While some aspects of these changes have been shown previously in other habitats in Dorset (Keith et al. 2009; Newton et al. 2012), this study is unique in assessing the responses of different groups of flora separately, and in analysing the effects of management to identify potential ways to reduce or slow down biodiversity loss.

The strong trend in taxonomic homogenisation over the 70 years to 2001, despite an average increase in species richness at individual sites, probably represents the key threat to hedgerow conservation in this and many lowland landscapes. This has mostly likely been driven by a decline in traditional hedge management practices (e.g. coppicing and laying) that were undertaken by hand and tended to be spatially and temporally more variable than the modern practice of cutting the majority of hedges with mechanical flails. A further driver of homogenisation is likely to be increased eutrophication, leading to more uniform plant communities dominated by competitive species associated with higher soil fertility, and in unmanaged hedges by more shade-tolerant herbaceous species. The most practical means of countering hedge floral homogenisation within modern farmed landscapes could to re-instate traditional forms of management to rejuvenate hedges and possibly to develop more time-efficient, low-cost alternatives approaches, such as the use of mechanical shaping saws, (Natural England 2007). Some of these management practices are grant aided under some European Agri-Environment Schemes, such as the English Entry Level and Higher Level Environmental Stewardship Schemes (Natural England 2013a,b). Finally, the selection of the most appropriate hedge management techniques are highly dependent on the composition of the hedgerow flora at each site, so improved training of practitioners and the provision of advice based on research and monitoring is also an important requirement if conservation policy is to be effective.

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Table legends

Table 1 Change (mean ± SE) in hedgerow α (site species richness) and β (taxonomic homogenisation indicated by Sorensen similarity) diversity measures for a) old and b) recent (in the two years preceding 2001) management categories, together with results of ANOVAs (** = $P < 0.01$, * = $P < 0.05$) and the number of hedgerow sites in each category. Old hedgerow management categories that differ significantly from each other are denoted with different letters (Tukey HSD tests P < 0.05).

Table 2 PLANTATT and CSR attributes (mean and SE) for hedgerow species present at each site in the 1930s and 2001 surveys, and results of paired t-tests and Wilcoxon paired ranks significance tests (*** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$).

Table 1a

Diversity measure		Old hedgerow management categories		ANOVA
2001 value - 1930s value	Coppiced	Laid	None	F
Number of indicator species	-1.25 ± 0.63 a	1.46 ± 0.93 b	-0.33 ± 0.15 a	3.13 *
Number of woody species	4.16 ± 0.71 a	4.31 ± 1.38 ab	2.87 ± 0.19 b	5.17 **
Number of herbaceous hedge species	2.88 ± 1.04 ab	-3.62 ± 2.06 a	2.95 ± 0.46 b	3.07 *
Sorensen similarity for woody species	1.17 ± 0.02 a	0.17 ± 0.04 ab	0.13 ± 0.005 b	3.62 *
Sorensen similarity for herbaceous species	0.06 ± 0.01 ab	0.05 ± 0.02 a	0.09 ± 0.003 b	3.92 **
Number of sites in each category	32	13	300	

Table 1b

Diversity measure	Recent management?		ANOVA
2001 value - 1930s value	Yes	No	F
Number of indicator species	-0.02 ± 0.15	-1.32 ± 0.34	15.49 ***
Number of woody species	3.43 ± 0.36	2.98 ± 0.22	1.10
Number of herbaceous hedge species	2.56 ± 0.78	2.72 ± 0.49	0.03
Sorensen similarity for woody species	0.13 ± 0.01	0.13 ± 0.006	0.11
Sorensen similarity for herbaceous species	0.08 ± 0.007	0.09 ± 0.004	0.44
Number of sites in each category	265	77	

Table 2

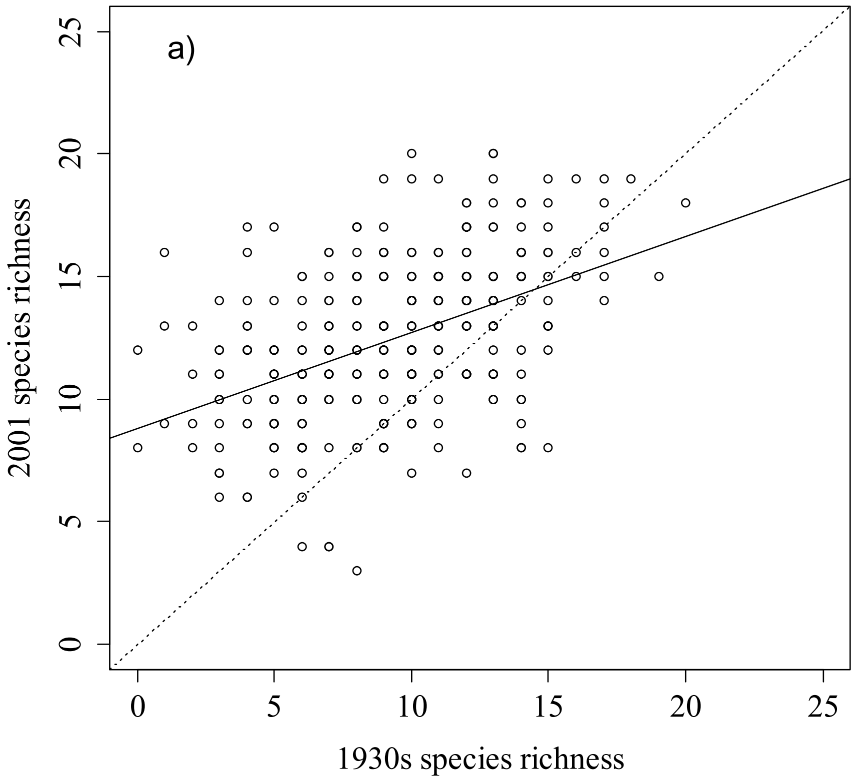
Species	PLANTATT / CSR attribute	Recent management?	1930s		2001		Paired t-test	Wilcoxon paired ranks test
			mean	± SE	mean	± SE		
Woody species	Height	Yes	1139	± 17.2	1192	± 13.7	-2.82**	
		No	1169	± 33.3	1323	± 27.5	-5.35***	
	L (light)	Yes	5.60	± 0.02	5.57	± 0.01	1.14	
		No	5.68	± 0.04	5.50	± 0.03	4.38***	
	R (pH)	Yes	6.53	± 0.02	6.57	± 0.02		13325
		No	6.41	± 0.06	6.46	± 0.04		1630
	N (nitrogen)	Yes	5.69	± 0.02	5.77	± 0.01	-5.16***	
		No	5.64	± 0.05	5.71	± 0.03	-1.76	
	S (salt tolerance)	Yes	0.07	± 0.004	0.08	± 0.002		11522
		No	0.07	± 0.008	0.06	± 0.004		1458
	Competitor	Yes	0.59	± 0.004	0.62	± 0.003	-5.78***	
		No	0.59	± 0.007	0.63	± 0.005	-4.45***	
	Ruderals	Yes	0.004	± 0.001	0.005	± 0.001		1685
		No	0.009	± 0.002	0.003	± 0.001		458**
Herbaceous hedge species	Height	Yes	97.7	± 1.28	95.7	± 0.80	2.19*	
		No	96.0	± 2.17	96.4	± 1.41	-0.23	
	L (light)	Yes	5.98	± 0.03	6.04	± 0.03	-3.18**	
		No	6.03	± 0.05	5.94	± 0.05	2.58*	
	R (pH)	Yes	6.52	± 0.02	6.54	± 0.02		16769
		No	6.43	± 0.04	6.46	± 0.03		1666
	N (nitrogen)	Yes	6.30	± 0.02	6.47	± 0.02	-9.61***	
		No	6.20	± 0.05	6.40	± 0.04	-4.84***	
	S (salt tolerance)	Yes	0.07	± 0.004	0.12	± 0.005		6353***
		No	0.07	± 0.007	0.08	± 0.008		1413
	Competitor	Yes	0.38	± 0.004	0.41	± 0.004	-7.62***	
		No	0.38	± 0.008	0.40	± 0.007	-3.07**	
	Ruderals	Yes	0.39	± 0.005	0.39	± 0.004	1.40	
		No	0.40	± 0.009	0.38	± 0.007	3.05**	

Figure legends

Fig. 1 a) Woody and b) herbaceous hedge species richness in Dorset hedgerow sites in the 1930s and 2001. In both cases the slope of the fitted regression (solid line) diverges from a gradient of 1 (dashed line). Woody species regression: $y = 0.391x + 8.81$, $R^2 = 0.214$, $P < 0.001$. Herbaceous hedge species regression: $y = 0.610x + 11.8$, $R^2 = 0.319$, $P < 0.001$.

Fig. 2 DCA biplot for communities of a) woody and b) herbaceous hedge species, + = 1930s communities, ○ = 2001 communities. The plot depicts bivariate standard deviational ellipses for axes 1 and 2 at a confidence limit of 90% for each survey time, with a dashed line for the 1930s ellipse and a solid line for the 2001 ellipse.

Figure 1


a)
2001 species richness
1930s species richness
0
5
10
15
20
25
0
5
10
15
20
25

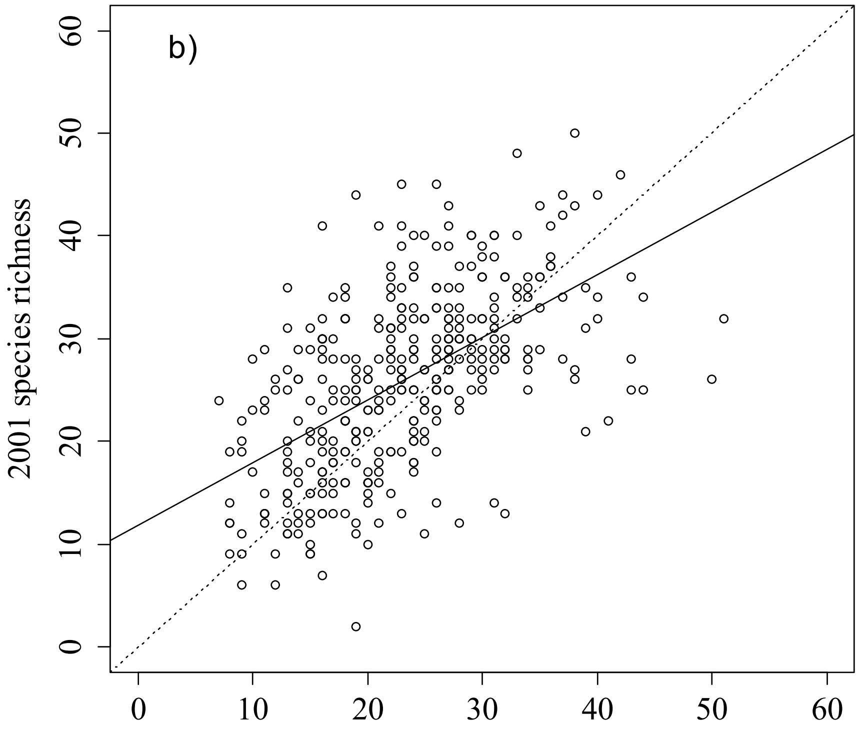
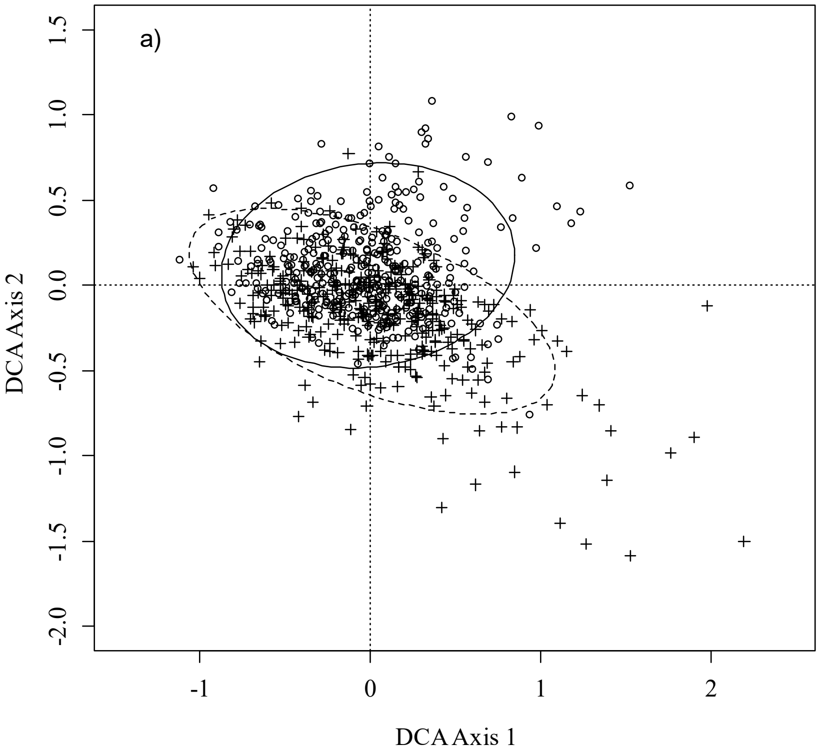
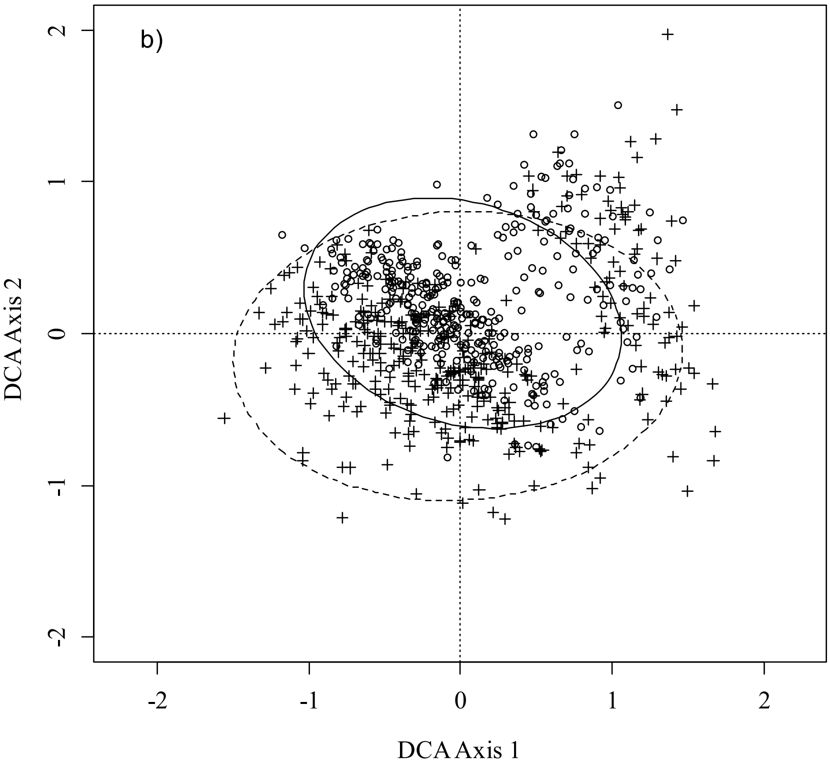

b)
2001 species richness
1930s species richness
0
10
20
30
40
50
60
0
10
20
30
40
50
60

Figure 2


a)
DCA Axis 2
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
-1
0
1
2
DCA Axis 1


b)
DCA Axis 2
2
1
0
-1
-2
-2
-1
0
1
2
DCA Axis 1

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