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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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25 **Abstract**

26 Hedgerows provide key habitat and refuges for wildlife in otherwise intensively-
27 managed landscapes, and may play a role in connecting increasingly fragmented
28 habitats. However, the processes governing changes to the floral biodiversity of hedges
29 are poorly understood. We analysed a unique, long-term data set of plant species
30 richness over a 70 year period at 357 hedgerow sites in southern England to quantify
31 changes in α , β and γ diversity, and identify the role of hedge management and other
32 possible drivers of change. Alpha diversity increased in hedgerows, while a reduction
33 in β diversity was indicated by taxonomic homogenisation, whereby previously distinct
34 communities of species become more similar to one another over time. Changes in the
35 regional species pool (γ diversity) differed with plant life-history; it increased for woody
36 species but decreased among herbaceous hedge species. Hedgerow communities shifted
37 towards species associated with higher soil fertility, a more competitive ecological
38 strategy and, in unmanaged hedgerows, greater shade tolerance. Probable drivers for
39 these changes include the move from traditional forms of management such as
40 coppicing and hedge-laying towards either no management or frequent cutting with a
41 mechanical flail, and eutrophication. The extent of changes in plant diversity over time
42 was determined by both historic and recent hedgerow management, but these
43 management effects varied with plant life-history attributes. However, changes in
44 hedge quality and floral diversity were not linked directly to a 60% increase in the
45 proportion of land use categories classified as ‘intensive’ adjacent to the sites over the
46 70 years. Recommendations are made for future hedgerow management based on
47 conservation objectives for specific groups of hedge plant species.

48

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

51 **1. Introduction**

52

53 Hedges are a key habitat in many areas of the world including Europe, North America,
54 Africa and China, and have been a large component of managed landscapes for over
55 two thousand years (Deckers et al. 2004; Hannon and Sisk 2009; Yu et al. 1999).

56 Hedges have the potential to play a significant role in habitat conservation, as they are a
57 widespread habitat for wildlife (Baudry et al. 2000; Gelling et al. 2007; Hannon and
58 Sisk 2009), and may provide important refuges for a variety of plants, invertebrates,
59 birds and mammals within otherwise intensively managed landscapes (French and
60 Cummins 2001; Merckx and Berwaerts 2010; Wehling and Diekmann 2009). Hedgerow
61 networks, and associated linear habitats, could also play a key future role in adaptation
62 to climate change by connecting habitat fragments and facilitating the movement of
63 species through the wider countryside (Davies and Pullin 2007; Lawton et al. 2010).

64

65 Changes in land use and management, climate and an increase in invasive species can
66 lead to a loss of biodiversity (Hooper et al. 2012). Declines may be manifest as losses
67 in α (declines in local species richness), β (e.g. biotic homogenisation) and γ (species
68 declines over a whole landscape) biodiversity (Ernoult and Alard 2011; Keith et al.
69 2009; Lambdon et al. 2008; Olden and Rooney 2006). Hedge floristic diversity is very
70 variable, and has been related to hedge age (Roy and de Blois 2008); a long history of
71 human intervention in terms of planting (Boutin et al. 2002) and management (Deckers
72 et al. 2004); adjacent land use (Ernoult and Alard 2011); and numerous landscape
73 parameters including connectedness of the hedge network (Davies and Pullin 2007).
74 These previous studies have addressed current hedge floral diversity rather than changes

75 in diversity over time. Changes to biodiversity, and analyses of their drivers, are best
76 examined using long-term data on community change at multiple sites in a landscape.
77 However, datasets amenable to this type of analysis are rare.

78

79 To investigate floral biodiversity changes in hedgerows, we used a unique botanical
80 data set for 357 hedge sites across a study area of 2 600 km² (in Dorset, a southern
81 English county), collected in the 1930s and again in 2001. This dataset allows
82 quantification of changes in α , β and γ diversity, and investigation of drivers of these
83 changes. Changes in the Dorset flora over a similar time scale have been examined
84 previously for woodland (Keith et al. 2009) and grassland (Newton et al. 2012) sites.
85 While γ diversity decreased, there was no change in α diversity over time for woodland
86 sites, but taxonomic homogenisation had occurred (Keith et al. 2009). Taxonomic
87 homogenisation is one component of biotic homogenisation, a loss of β diversity, which
88 leads to spatially distinct communities becoming more similar to each other over time
89 (Olden and Rooney 2006). Among the grassland sites α and γ diversity had increased
90 over time, with no evidence of taxonomic homogenisation. For both habitats, analysis
91 of plant species changes suggested eutrophication due to atmospheric deposition of
92 nitrogen and agricultural fertilisers was the major driver of change (Keith et al. 2009;
93 Newton et al. 2012). Species changes in the woodlands suggested reduced management
94 and the resulting increased shading was an additional driver of biodiversity loss (Keith
95 et al. 2009). However, neither study directly tested for the effects of management or
96 agricultural intensification on changes to plant communities.

97

98 Hedges require management to prevent them encroaching on adjacent agricultural land,
99 and developing into scrub or lines of trees (Barr et al. 2005; Baudry et al. 2000).
100 Traditionally, this management would have included hedge-laying or coppicing, both of
101 which are infrequent management techniques applied every 20 – 40 years, which
102 rejuvenate hedges by encouraging them to produce new shoots from the base of woody
103 species and maintains them as stock-proof barriers. Over 50% of the woody hedge
104 biomass is removed during hedge-laying or coppicing, and between this infrequent
105 rejuvenation management, hedges would have been trimmed every few years by hand to
106 maintain their shape. Over the last 70 years frequent cutting with a mechanised flail has
107 become the dominant form of management across Europe (Croxtton et al. 2004). While
108 the removal of hedgerows is prohibited in many European countries (Baudry et al.
109 2000), the total length of hedgerows is still diminishing due to a lack of any
110 management or over-intensive management (e.g. severe flailing every year) (Carey et al.
111 2008). The impact of management methods on hedgerow flora is little studied,
112 especially in the context of ameliorating biodiversity loss.

113

114 In this study we build on previous analyses of long-term vegetation change in Dorset by
115 testing the following hypotheses: H1) community composition of hedges has shifted
116 over time towards species associated with higher soil fertility and with more
117 competitive life-history strategies in response to eutrophication; H2) this shift in
118 composition has led to taxonomic homogenisation (loss of β diversity) in hedges
119 between the 1930s and 2001; H3) hedges with evidence of historic rejuvenation
120 management are more diverse and have undergone less taxonomic homogenisation than
121 those with no sign of historic management; H4) community composition of hedges

122 with recent evidence of flailing has shifted away from species associated with shady
123 conditions, and the species richness of published indicators of hedgerow quality has
124 decreased, due to this management allowing more light into the hedge base; H5) the
125 extent of change of hedge floral communities correlates with the increase in the
126 proportion of the adjacent land area under intensive use.

127

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

133

134

135 **2. Methods**

136

137 *2.1 Vegetation surveys*

138

139 *2.1.1 1930s survey of hedgerow plants*

140

141 Over 1000 hedgerow sites were surveyed by Professor Ronald Good in Dorset between
142 1931 and 1939, as part of a large-scale botanical survey covering a range of habitats
143 (Good and Robinson 1948). Good (1937) chose sites to represent specific habitat types,
144 to be “...reasonably distinct topographical and ecological entities...” and to be “...as
145 evenly scattered as possible” across Dorset. The hedgerow sites varied in length from

146 57 to 1 040 metres and were surveyed by recording all vascular plant species
147 encountered over approximately 1 hour. Each hedge was visited once, generating
148 presence-absence data that are relatively robust to sampling error (Hirst and Jackson
149 2007). Hedgerow site locations were recorded on a series of large scale (1:10 560; six
150 inches to the mile) Ordnance Survey maps which are stored at Centre for Ecology and
151 Hydrology, and were digitised by Dorset Environmental Records Centre in 1999
152 (<http://www.derc.org.uk/projects/good.htm>). Good's data have been used in other
153 analyses of long-term vegetation change in woodland (Keith et al. 2009; Keith et al.
154 2011), grassland (Newton et al. 2012) and cliff-top sites (Wichmann et al. 2008).

155

156 *2.1.2 2001 re-survey of hedgerow plants*

157

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

169 hedgerow site was determined with a Geographical Positioning System, and a
170 photograph taken of each site (Button 2003).

171

172 *2.2 Plant species classification and attributes*

173

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

181

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

189

190 We examined the potential processes behind observed botanical compositional changes
191 by using values for PLANTATT attributes that indicate tolerance of specific
192 environmental conditions. We examined whether average attributes (across species) per

193 hedge site differed between the 1930s and 2001. Attributes that were analysed were
194 height and Ellenberg values for N (nitrogen), L (light), R (soil acidity) and S (salt
195 tolerance). The latter two attributes were included to test hypotheses that floral change
196 was related to soil acidification (Stevens et al. 2010) or increased salinity caused by
197 winter road gritting with rock salt introduced widely after the 1930s survey. The
198 Comparative Plant Ecology database classifies vascular plant species by life-history
199 strategy according to the ‘CSR’ model: competitiveness, stress tolerance and ruderality
200 (Grime et al. 2007). We analysed average competitiveness and ruderality.

201

202

203 *2.3 Land use data from the 1930s and 2000*

204

205 Data on land use categories in Dorset were available from Hooftman and Bullock
206 (2012), who digitised a land use map from the 1930s at a resolution of 10.8×10.8 m.
207 The precision of the 1930s map was checked against contemporary ground vegetation
208 surveys (Good and Robinson, 1948) and there was found to be close correspondence
209 between the two. This map was combined with the National Soil Map of England and
210 Wales to create 15 broad habitat types that correspond with those used in the Land
211 Cover Map 2000. The Land Cover Map 2000 consists of $25\text{m} \times 25\text{m}$ pixels derived
212 from satellite spectral data, which are assigned to broad habitat types using maximum
213 likelihood algorithms (Fuller et al. 2002).

214

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

218

219 *2.4 Data analysis*

220

221 All data analyses were conducted in R version 2.14.0 (R Core Development Team
222 2011) and the vegan package (Oksanen et al. 2012). The relationship between the
223 changes in species number within each hedge plot between the two surveys and the
224 number of Julian days between the 1930s and 2001 survey dates was tested using
225 Spearman's rank correlation test, to identify any possible bias caused by different
226 sampling dates (Keith et al. 2009).

227

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

238

239

240 2.4.1 *Diversity changes over 70 years*

241

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

247

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

251
$$S = \frac{2a}{2a + b + c}$$

252

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

259

260 The change in total species richness across all sites or regional species pool (γ diversity)
261 over time was tested using a bootstrap method (Sokal and Rohlf 1995). The data from

262 both surveys was pooled, 357 sites were drawn at random from the pooled dataset and
263 the total species richness calculated. This was repeated 10,000 times sampling with
264 replacement, to create a distribution of expected γ diversity, from which a mean ($\tilde{\gamma}_{boot}$)
265 and standard deviation $SD_{(\tilde{\gamma}_{boot})}$ were calculated. Z scores were calculated from
266 observed total species richness at each survey time (γ_{obs}), to test whether total species
267 richness at each survey time differed from the pooled species richness, where:

$$268 \quad Z = \frac{\tilde{\gamma}_{boot} - \gamma_{obs}}{SD_{(\tilde{\gamma}_{boot})}}$$

269

270 *2.4.2 Changes in community composition over time*

271

272 The difference in community composition between the 1930s and 2001 was tested with
273 a permutational multivariate analysis of variance using distance matrices (ADONIS)
274 with 1000 permutations (Oksanen et al. 2012). Permutations were constrained within
275 site, to take account of the spatial structure of the dataset (Oksanen et al. 2012).

276 Changes in community structure were investigated further using detrended
277 correspondence analysis (DCA; Leps and Smilauer 2003).

278

279 *2.4.3 Hedgerow management effects on changes in plant diversity*

280

281 The effects of each management timescale (old vs. recent) on the three measures of
282 hedgerow community change (change in species richness, Sorensen similarity and
283 hedgerow indicator species richness for each hedge site between 1930s and 2001) were
284 tested using two-way ANOVAs, including the interaction between old and new

285 management. There were three levels to the factor ‘old management’: none, coppiced
286 vs. laid. ‘Recent management’ was simplified to two levels (none vs. recent
287 management), as two of the recent management categories were present at too few
288 hedgerow sites to provide robust results (only 4 of 357 hedgerow sites had been recently
289 flailed and laid, and 8 sites recently laid). The vast majority of sites that had been
290 recently managed were cut with a mechanised flail (253 sites). Prior to analysis, the
291 hedgerow community change response variables were tested for normality using a
292 Shapiro-Wilks test. ANOVA models were simplified by removing interactions and
293 management factors that were not significant at $P < 0.05$. Following a significant
294 ANOVA result for old management, posthoc Tukey HSD tests were used to determine
295 which old management categories differed significantly.

296

297 *2.4.4 Change in community average attributes over 70 years*

298

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

306

307 *2.4.5 Changes in land use adjacent to the hedge sites*

308

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

319

320

321 **3. Results**

322

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

328

329 *3.1 Changes in hedgerow diversity over 70 years*

330

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

333 ± 0.194 ; 2001: mean = 12.50 ± 0.163 ; $t_{356} = -16.41$, $P < 0.001$), and herbaceous hedge
334 species (1930s: mean = 23.3 , SE = 0.429 ; 2001: mean = 26.0 , SE = 0.462 ; $t_{356} = -6.58$,
335 $P < 0.001$). There was a positive relationship between mean species richness in the
336 1930s and 2001, but with a gradient < 1 for both woody species and herbaceous
337 hedgerow species (Figs. 1a and 1b respectively). Hedgerow sites with low species
338 richness in the 1930s therefore gained more species than average over the following 70
339 years, while hedgerows with high species richness gained fewer species than average or,
340 at the highest starting values, lost species.

341

342 Sorensen similarity indices were higher in 2001 than the 1930s, both for woody species
343 (1930s mean $S_i^x = 0.430 \pm 0.0049$; 2001 $S_j^x = 0.566 \pm 0.0037$; Wilcoxon paired ranks
344 test $V_{356} = 1077$, $P < 0.001$) and herbaceous hedge species (1930s $S_i^x = 0.342 \pm 0.0034$;
345 2001 $S_j^x = 0.432 \pm 0.0037$; $V_{356} = 1840$, $P < 0.001$). This demonstrates taxonomic
346 homogenisation among hedgerow sites and loss of β diversity over time, for both groups
347 of species.

348

349 Woody species showed increased γ diversity with time ($\gamma_{1930s} = 58$, $\gamma_{2001} = 71$), as the
350 number of species found in the 1930s was lower than expected for a random sample (Z
351 = 5.27 , $P < 0.001$). In contrast, γ diversity decreased over time for herbaceous hedge
352 species ($\gamma_{1930s} = 190$, $\gamma_{2001} = 168$, $Z = -1.95$, $P < 0.05$). There were 42 woody and 140
353 herbaceous hedge species common to both surveys. Sixteen woody species were lost
354 between the two surveys, and 29 woody species were gained. In contrast, 50
355 herbaceous hedge species were lost and only 28 species gained.

356

357 3.2 *Changes in hedgerow community composition*

358

359 Hedge community composition changed significantly between the 1930s and 2001 both
360 for woody (ADONIS statistic $R = 0.024$, $P < 0.001$) and herbaceous hedge species ($R =$
361 0.038 , $P < 0.001$). Although there was a shift in community composition of woody
362 species, there was still considerable overlap between the two communities of woody
363 species (DCA: Fig. 2a), and a reduction of the variation in community composition for
364 herbaceous hedge species (DCA: Fig. 2b).

365

366 3.3 *Effects of hedgerow management on plant communities*

367

368 3.3.1 *Changes in indicators of hedgerow quality*

369

370 Old and recent hedgerow management both caused a change in the number of indicator
371 species of hedgerow quality, with no interaction between the two management types
372 (Table 1a). On average, just over one indicator species was lost between the 1930s and
373 2001 when hedges had been coppiced historically. In contrast, a small gain in indicator
374 species was seen where hedge-laying had taken place, with a very small average loss
375 (0.33 species) in those hedgerow sites with no apparent old management. There was a
376 greater decrease in the number of indicator species between the 1930s and 2001 for
377 hedges with no recent management (1.3 species lost on average), compared with those
378 that had recently been flailed (0.019 species lost; Table 1b).

379

380 3.3.2 *Changes in species richness (α diversity)*

381

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

391

392 3.3.3 *Taxonomic homogenisation (loss of β diversity)*

393

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

398

399 We found a significant effect of old management on taxonomic homogenisation for
400 herbaceous hedge species (Table 1a), but also a significant interaction between old and
401 recent management on this parameter ($F_{3,340} = 3.40, P < 0.05$). For hedges with recent
402 management, the extent of taxonomic homogenisation among herbaceous hedgerow
403 species was smaller if the hedge had been historically laid, compared with hedges with

404 no historic management. In contrast, for hedges with no recent management, the type of
405 old management had no effect on homogenisation (Tukey HSD tests, $P < 0.05$).

406

407 *3.3.4 Changes in species attributes*

408

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

417

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

425

426 *3.5 Changes in land use surrounding hedgerow sites*

427

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

435

436

437 **4. Discussion**

438

439 *4.1 Changes in hedgerow community composition over 70 years*

440

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

451 In contrast to α and β diversity, the two groups of hedgerow species showed markedly
452 different responses in change in γ diversity (the overall species pool), which increased
453 over 70 years for woody species, but decreased for herbaceous species. The increase in
454 woody species is unlikely to be due to replanting, as only one site was recorded as
455 replanted in the 2001 survey. Within this Dorset landscape, re-surveys of Good's
456 woodland and calcareous grassland sites over a similar period showed intriguingly
457 different results. Woodland floras showed no change in α diversity, but decreased β and
458 γ diversities (Keith et al. 2009). In contrast, calcareous grasslands showed increased α
459 and γ diversities, but no change in β diversity (Newton et al. 2012). These very
460 contrasting results, and the differences between woody and herbaceous plant within the
461 same communities reported here, suggest that diversity patterns and their responses to
462 drivers can be idiosyncratic. Measures of diversity (α , β , γ) are not independent: these
463 indexes are related in terms of the level of difference between local populations (β -
464 diversity) and the slope of the local (α) vs. landscape (γ) species-area curves (Loreau
465 2000; Storch et al. 2012). For example, no changes in local diversity but with a
466 relatively steep species-area curve could be seen as positive, since it would indicate
467 more diversity among localities (β -diversity). In contrast, an increased local diversity
468 accompanied with a relatively flat or concave species species-area curve would indicate
469 homogenisation and could be interpreted more negatively. Among the different habitat
470 types and species groups these relations between α and β could be different, hence
471 leading to the different conclusions described above.

472

473

474 There was a shift in the community composition of woody hedgerow species over time,
475 though there was still considerable overlap between the two compositions. The sixteen
476 woody species that disappeared from these sites between the 1930s and 2001 include
477 three species of heather (*Erica tetralix*, *Erica cinerea* and *Calluna vulgaris*), two gorse
478 species (*Ulex gallii* and *Ulex minor*), alder buckthorn (*Frangula alnus*) and creeping
479 willow (*Salix repens*), which are associated with heathlands and acidic soils (Hill et al.
480 2004). The area of heathland in Dorset has reduced dramatically and become more
481 fragmented since the 1930s, as land has been converted to more intensive agriculture
482 and woodland (Hooftman and Bullock 2012). Loss of heathland communities may also
483 have been exacerbated by nitrogen deposition (Maskell et al. 2010). Woody species
484 gained between the 1930s and 2001 include a higher proportion of non-native species
485 (66%) than species that were retained (12%) or lost (13%) between the two surveys.
486 These included common, widespread neophyte species such as rhododendron
487 (*Rhododendron ponticum*), buddleja (*Buddleja davidii*), cherry laurel (*Prunus*
488 *laurocerasus*) and garden privet (*Ligustrum ovalifolium*).

489

490 Variation among the herbaceous plant communities decreased over time such that the
491 2001 community form a subset of the 1930s communities. In contrast to the woody
492 species, this indicates a loss of particular herbaceous communities. Hedgerow forbs that
493 have been lost also include species with a heathland association such as heath groundsel
494 (*Senecio sylvaticus*). These changes in community composition and evidence of
495 taxonomic homogenisation between the 1930s and 2001 for both woody and herbaceous
496 hedge species support our first two hypotheses.

497

498 4.2 *Effects of management on hedgerow composition*

499

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

510

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

521

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

529

530 *4.3 Drivers of change in the hedgerow flora*

531

532 Ellenberg N values increased with time for herbaceous hedge species, and for woody
533 species in hedges under recent management, supporting our first hypothesis, that
534 eutrophication is an important driver of changes to hedgerow plant communities. This
535 is similar to the increase in N values found in Dorset woodland (Keith et al. 2009) and
536 grassland (Newton et al. 2012) floras; both studies concluded that eutrophication was a
537 major factor in changes to Dorset plant community composition over the last 70 years.
538 Similarly, Bennie et al. (2006) suggested eutrophication was a driving force in changes
539 to chalk grassland floras across Britain over fifty years. However, we found no
540 correlation between the increase in the proportion of intensively managed adjacent land
541 and changes in hedgerow floras, leading us to reject our fifth hypothesis relating to land
542 use change. This may indicate that local land use change is a poor indicator of
543 eutrophication. Indeed, much eutrophication may be due to atmospheric nitrogen
544 deposition (Maskell et al. 2010) which is manifest at large spatial scales (Henry et al.
545 2011).

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

552

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

561

562 *4.4 Management recommendations and conclusion*

563

564 Generic recommendations for hedgerow management to counter biodiversity losses and
565 compositional changes are complicated by the differing responses of woody species,
566 hedgerow herbs, and indicator species of hedgerow quality. Nevertheless, some general
567 management guidance can be provided that is applicable to the conservation of
568 hedgerows in other regions. While some aspects of these changes have been shown
569 previously in other habitats in Dorset (Keith et al. 2009; Newton et al. 2012), this study

570 is unique in assessing the responses of different groups of flora separately, and in
571 analysing the effects of management to identify potential ways to reduce or slow down
572 biodiversity loss.

573

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

594

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604 **Table legends**

605

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

612

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

616

Table 1a

Diversity measure 2001 value - 1930s value	Old hedgerow management categories						ANOVA		
	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 2001 value - 1930s value	Recent management?				ANOVA
	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

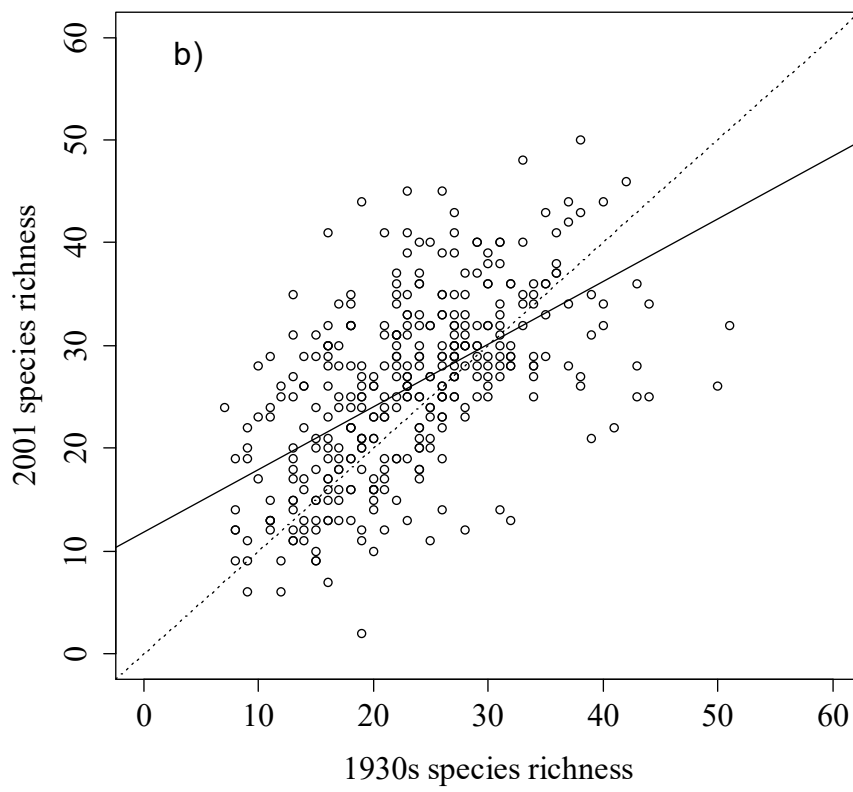
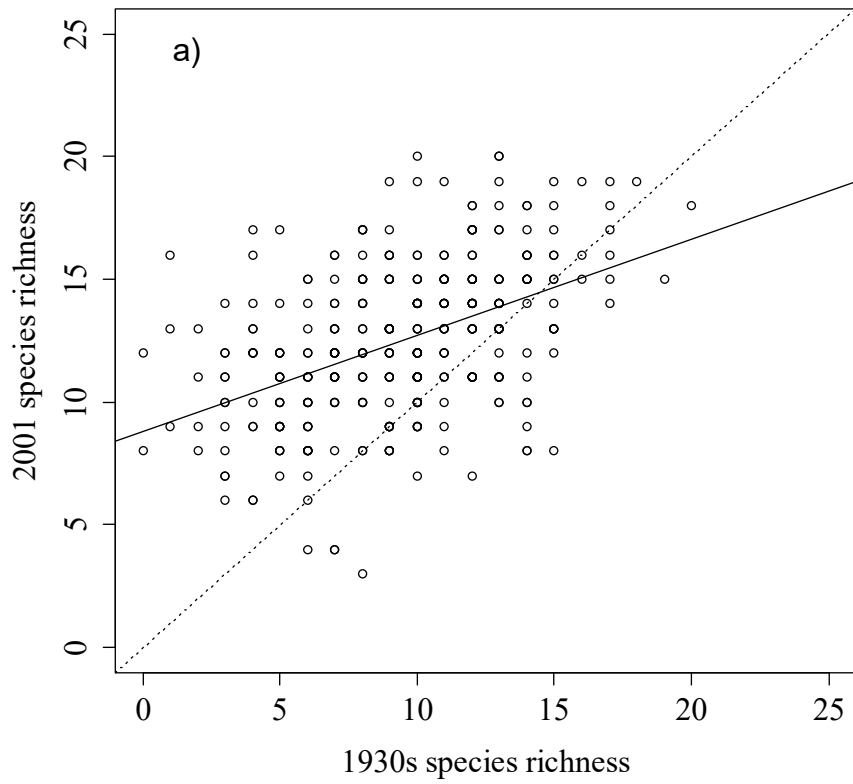
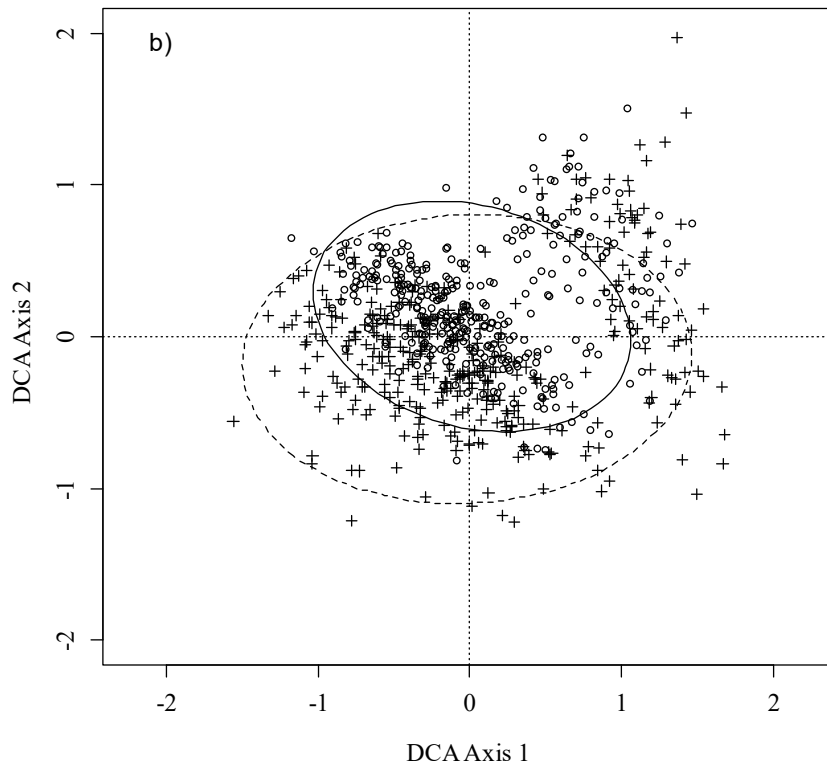
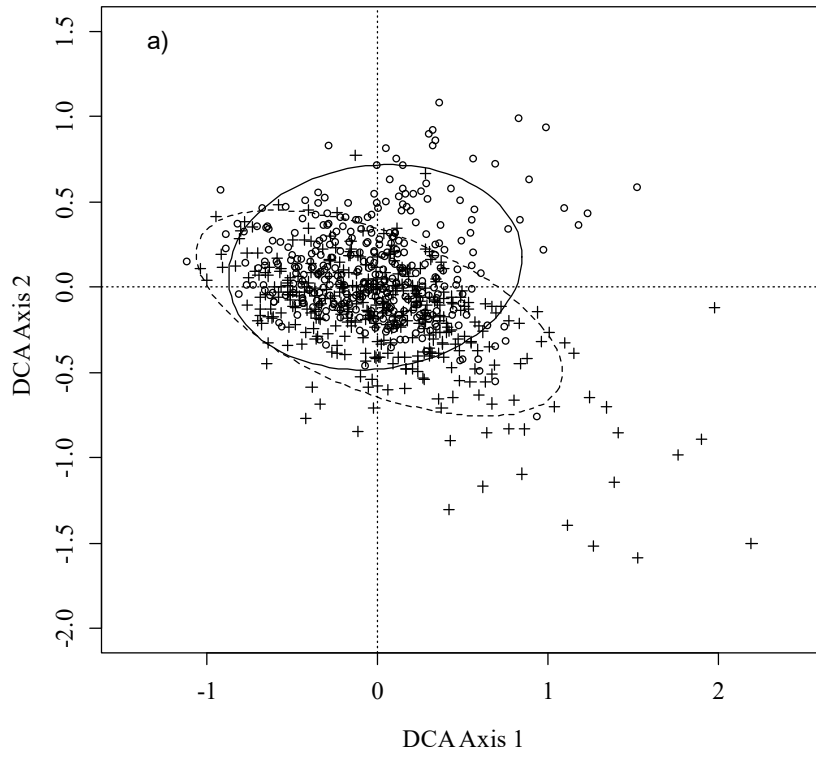


Figure 2



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