



The legacy of 20th Century landscape change on today's woodland carabid communities

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1 **The legacy of 20th Century landscape change on today's woodland**
2 **carabid communities**

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19 **(A) ABSTRACT**

20 **Aim**

21 For many species, the effects of landscape change can involve a time lag and result in an
22 extinction debt. The landscape matrix plays a vital role in supporting species populations.
23 However, the importance of the historical composition and configuration of landscape
24 mosaics has received little attention, with studies focusing on the effects of loss and
25 fragmentation of single (focal) habitat over time. We investigated the importance of historical
26 and contemporary landscape heterogeneity (composition and configuration) to identify how
27 landscape change has, and is continuing to have, an effect on current woodland carabid
28 communities.

29 **Location**

30 Lowland Britain.

31 **Methods**

32 Carabids were sampled from woodlands in 36 tetrads of 4 km². Ordination methods analysed
33 current community response to representations of contemporary and historical (1930's)
34 landscape heterogeneity. The effects of 80 years of landscape change on current carabid
35 assemblages were compared among tetrads.

36 **Results**

37 Results are consistent with an extinction debt; carabid communities correlated significantly
38 with the historical composition and configuration of the landscape, but not contemporary
39 landscape configuration. Community assemblages have been shaped, and many species
40 remain affiliated with landscape conditions that no longer exist, notably, large patches of

41 broadleaf woodland and semi-natural grassland. Recent introduction of conifer plantations
42 has had a negative effect on the abundance of many woodland species. For many common,
43 slow-dispersing species, contemporary and historical landscapes offered sub-optimum
44 woodland coverage indicating a lag effect that exceeds 80 years. Increased arable landcover
45 and loss of semi-natural grassland and heathland points towards an ongoing detrimental
46 impact on carabid populations.

47 **Main conclusions**

48 Compared with focal-habitat studies, the landscape mosaic approach provides a more
49 comprehensive understanding of the effects of widespread landscape change on species
50 communities. Conservation guidance includes new planting, maintenance and restoration of
51 semi-natural habitats, implemented across multiple spatial scales and where feasible,
52 considering both historical and contemporary landscape heterogeneity.

53

54 **(B) Keywords** Carabidae, community analysis, extinction debt, landscape change, landscape
55 heterogeneity, landscape mosaic.

56 **(A) INTRODUCTION**

57 Landscape change poses a serious threat to global biodiversity and there is concern regarding
58 the loss of species in wooded-agricultural environments (Hendrickx *et al.*, 2007; Fahrig *et al.*,
59 2011). Over the last 80 years, agricultural intensification has led to widespread landscape
60 modification across much of Europe, Australia and North America (Lunt & Spooner, 2005;
61 Schweiger *et al.*, 2005). The loss and fragmentation of semi-natural habitats, plus
62 transformation of land to intensive agriculture has fundamentally altered the compositional
63 heterogeneity (the number and proportions of different landcover types) and configurational
64 heterogeneity (the spatial arrangement of different landcover types) in the rural environment
65 (Fahrig *et al.*, 2011). Changes to landscape heterogeneity alter the ecological filters which
66 affect species-landscape processes such as dispersal, resource availability and colonisation
67 (Mayfield *et al.*, 2010), ultimately influencing the abundance and diversity of species able to
68 occupy habitats and exist in a landscape (Baessler & Klotz, 2006; Hendrickx *et al.*, 2007).

69 While some species respond almost immediately to landscape change, often there is a time
70 lag effect (relaxation time), whereby species persist in a habitat, but the conditions they
71 require for long-term survival are no longer being met fully; this is commonly referred to as
72 an ‘extinction debt’ (Diamond, 1972; Tilman *et al.*, 1994). The present occupancy of species
73 in a habitat patch may therefore, overestimate the carrying capacity of the current landscape
74 and consequently, underestimate the threat to biodiversity even if no further landscape
75 change occurs (Adriaens *et al.*, 2006; Piqueray *et al.*, 2011). Previous studies provide
76 convincing evidence of extinction debts and lag effects across a range of habitats, taxa and
77 spatial scales (see review by Kuussaari *et al.*, 2009). As such, a key issue in conservation
78 biogeography is to identify how species respond to current landscape heterogeneity, but also
79 to consider the temporal aspect. Ascertaining how species communities have been affected

80 and might continue to change in response to ongoing landscape change provides an indication
81 of how biodiversity might respond to future conservation and land management decisions.

82 In temporal landscape research, a frequently adopted approach is to quantify and assess the
83 interactions which exist between contemporary and past landscapes and current species
84 distributions (e.g. Lindborg & Eriksson, 2004; Piessens & Hermy, 2006; Kuussaari *et al.*,
85 2009; Cristofoli *et al.*, 2010; Piqueray *et al.*, 2011; Husáková & Münzbergová, 2014). This
86 approach reconstructs contemporary and past landscape configurations for a focal habitat of
87 interest e.g., semi-natural grasslands (Sang *et al.*, 2010) or old-growth forest (Berglund &
88 Jonsson, 2005). The presence of an extinction debt is inferred if the variation in current
89 species richness, or the response of a functional group of species, is better explained by
90 historical rather than contemporary landscape conditions. However, the binary classification
91 of landscapes as either ‘focal habitat’, where resources required for the study taxa are met, or
92 ‘hostile matrix’ (Fahrig *et al.*, 2011) means that conclusions regarding how species respond
93 are solely based on contemporary and past configurations of one habitat type. It is however,
94 known from studies that have analysed species response to current landscape conditions, that
95 wider landscape heterogeneity is an important determinant of biodiversity (Haslem &
96 Bennett, 2008; Duflot *et al.*, 2014; Neumann *et al.*, 2016). The ‘landscape mosaic’ approach,
97 recognises that species are not only affected by the amount and spatial configuration of their
98 focal habitat, but *also* by the composition of the heterogeneous matrix which can provide
99 resources, alternative useable habitat and influence species dispersal (Fahrig *et al.*, 2011). In
100 landscapes where focal habitat has been recently destroyed or fragmented, species might have
101 dispersed into new patches, found alternative habitats in the matrix or, remained as an
102 isolated population in the now compromised habitat patch. The past composition and
103 configuration of the matrix is therefore, likely to be of significant explanatory importance for
104 current species assemblages. Despite this, the effect of historical landscape composition has

105 received minimal attention (but see Lunt & Spooner, 2005; Baessler & Klotz, 2006; Aguirre-
106 Gutiérrez *et al.*, 2015; Cousins *et al.*, 2015).

107 Post WWII in Britain, large areas of broadleaf woodland were cleared for intensive
108 agriculture, fragmented by urban infrastructure, or converted to commercial coniferous
109 plantations (Fuller *et al.*, 2007). This had a detrimental effect on woodland biodiversity
110 (Hinsley *et al.*, 1995; Bellamy *et al.*, 1996; Mason, 2007). Landscape modification also
111 occurred across other semi-natural habitats including species-rich grasslands and lowland
112 heathland (Vickery *et al.*, 2001; Warren *et al.*, 2001). The alteration of landscape processes
113 throughout the wider environment could potentially have affected species community
114 assemblages in woodlands today.

115 This study investigated the response of woodland ground beetle communities (Coleoptera;
116 Carabidae) to the contemporary and historical landscape heterogeneity (composition and
117 configuration) of wooded-agricultural landscape mosaics in southern Britain (Fig. 1).
118 Carabids were chosen as biological indicators as they are functionally diverse and sensitive to
119 landscape change (Aviron *et al.*, 2005; Barbaro & van Halder, 2009). We analysed carabid
120 response at the community level to include both specialist and generalist species, without
121 restricting natural community variability or biasing carabid response by relying on specialists
122 (Adriaens *et al.*, 2006). We asked, 1) do current woodland carabid communities exhibit a
123 correlation with contemporary *and* historical landscapes when considering both the
124 composition and configuration of landscape mosaics? 2) Is there evidence that current carabid
125 distributions relate more strongly to representations of the historical landscape than the
126 contemporary landscape, indicating a potential extinction debt? 3) Comparing results from
127 contemporary and historical landscapes, is it possible to infer how landscape change might
128 have had, or be having, an effect on current woodland carabid communities?

129 **(A) METHODS**

130 **(B) Study region**

131 The study was conducted in rural southern Britain (Fig. 1). The region is low-lying and
132 temperate: average elevation 140 m a.s.l., mean annual temperature 10.2 °C, average annual
133 precipitation 850 mm. In the 1930's prior to the onset of intensive agriculture, semi-natural
134 habitats including species-rich meadows, grazing pastures, lowland heath and large patches
135 of broadleaf woodland dominated the landscape. Arable land existed as small-scale plots used
136 for non-intensive cropping, market gardens and orchards (Southall *et al.*, 2007). Today, the
137 landscape is dominated by intensive arable farming (largely wheat, winter oil seed rape and
138 barley) and improved grassland (for livestock, hay and silage production). Broadleaf
139 woodland cover has been reduced into smaller, fragmented patches. Where larger woods have
140 been retained, sizeable blocks have been converted to commercial coniferous plantations.
141 Small areas of chalk downland, heathland and rough grassland exist as relict, isolated
142 fragments (Fig. 1).

143 **(B) Study design**

144 The study set-up follows previous research conducted by the authors in 2011. We refer
145 readers to Neumann *et al.*, (2015) for a full detailed description of the methods. Thirty-six 2 x
146 2 km study tetrads were selected across the study region (Fig. 1); each was centred on a patch
147 of broadleaf woodland, hereafter referred to as the sample woodland. Thirty of the sample
148 woodlands were classified as Ancient Semi-Natural Woodland (Ancient Woodland Inventory
149 – Natural England, 2013). The remaining six were continuously wooded for at least 165 years
150 (County Series 1846-1969 maps – OS, 2013). Sample woodland size varied from 3 ha to 350
151 ha (median 51 ha). All were predominantly broadleaf although some larger woodlands
152 contained stands of commercial coniferous plantation (Forestry Commission, 2013). The

153 composition of the landscape matrix within each tetrad was typical of the contemporary rural
154 environment but tetrads differed in terms of their landscape configuration (i.e., amount, size,
155 shape and arrangement of habitats). Tetrads contained uniform soil types, avoided areas of
156 steep topography, large urban areas and coastal regions and did not overlap.

157 ***(B) Contemporary map data***

158 Landcover Map 2007 (LCM2007) (Morton *et al.*, 2011) and Ordnance Survey MasterMap
159 Topography data (OSMM) (OS, 2010) were used to quantify contemporary land-use.
160 LCM2007 is an up-to-date UK land-use map representing the UK Biodiversity Action Plan
161 Broad Habitats derived from 30 m resolution satellite imagery (NERC, 2011). The spatial and
162 thematic accuracy of LCM2007 when validated against ground reference data was 83% and
163 the minimum mappable area was 0.5 ha meaning small or complex-shaped features e.g.,
164 small water bodies, are not well represented (NERC, 2011). To overcome these inaccuracies
165 the LCM2007 data were combined with the OSMM Topography data. OSMM details
166 landscape features (e.g. buildings, roads, woodlands, water bodies) as individual polygons
167 with 2.5 – 6.0 m spatial accuracy in rural areas but does not specify definitive landcover
168 information (OS, 2010). For each tetrad, a comprehensive landcover dataset was created in
169 ArcMap 10.1 (ESRI, 2011) using information from both datasets.

170 ***(B) Historical map data***

171 The first systematic survey of land in Great Britain was carried out under the direction of
172 Professor Dudley Stamp in the early 1930's (Hooftman & Bullock, 2012). The Dudley Stamp
173 Maps (DSM) categorised land-use at the one-inch-to-the-mile (1:63,360) scale and were
174 printed between 1933 and 1949. Digitisation of the original paper maps was completed in
175 2011 (Clark, 2011). DSM maps seven Broad Habitats: (i) forest and woodland; (ii)

176 meadowland and permanent grasslands; (iii) arable land; (iv) water; (v) heath and moorland;
177 (vi) urban core; (vii) suburban (gardens etc.) (Southall *et al.*, 2007).

178 ***(B) Landscape heterogeneity spatial analysis***

179 ArcMap 10.1 was used to quantify the contemporary and historical landscape heterogeneity
180 (landscape composition and configuration) within each tetrad (Table 1). To facilitate
181 comparisons between current and past landscapes, the contemporary LCM2007 data were
182 classified to be comparable with the Broad Habitats represented in the DSM (see Table S1,
183 Supporting Information).

184 ***(C) Landscape composition***

185 Contemporary landscape composition in each tetrad was represented by the relative
186 proportion of the eight Broad Habitat variables. Six were used to characterize the historical
187 landscape composition; improved grassland and coniferous plantation were not present
188 historically (Table 1).

189 ***(C) Landscape configuration***

190 Landscape configuration metrics measured the number, amount, shape and spatial
191 configuration of the Broad Habitat variables in each tetrad (Table 1). Discrete habitat patches
192 had an edge-to-edge Euclidean distance of at least 20 m from another patch of the same type.
193 Functionally, 20 m exceeds the ‘interaction distance’ for many common carabid species
194 (Brouwers & Newton, 2009). The number of patches and mean patch area indicated the
195 degree of structural fragmentation of a Broad Habitat type (Cristofoli *et al.*, 2010).

196 ***(C) Additional constraining variables***

197 The detection of true landscape effects on communities can be hampered by constraining
198 variables (Table 1). For all analyses, the effects of carabid sampling date and spatial
199 autocorrelation (where tetrads in close proximity to each other can possess more similar
200 landscape or biotic conditions than those from a random set of observations) were accounted
201 for (see below) (Heikkinen *et al.*, 2004; Oliver *et al.*, 2010).

202 **(B) Sampling carabid communities**

203 Carabid communities in each sample woodland were surveyed using 10 pitfall traps set
204 between May and early August 2011. Two pitfall traps were placed at the centre of each
205 sample woodland. Further pairs were set along the most northerly, southerly, easterly and
206 westerly facing-woodland edge adjacent with the non-woodland habitat. Pitfall traps
207 (diameter 60 mm, depth 80 mm) were one third filled with ethylene glycol (50%) and water
208 (50%). In each tetrad, traps were set continuously for 14 days, randomly assigned between
209 May and August to avoid clusters of tetrads in close proximity trapping species over the same
210 time period. Individuals collected were pooled for each tetrad and identified to species using
211 Luff (2007).

212 **(B) Statistical analyses**

213 The effects of contemporary and historical landscape heterogeneity on current woodland
214 carabid communities were explored using partial canonical correspondence analyses (pCCA)
215 in Canoco 5 (ter Braak & Šmilauer, 2012). Analyses followed a two-step process: 1) global
216 permutation tests 2) interactive forward selection procedure. Partial methods were used in all
217 tests to account for, and remove any variation explained by ‘sampling date’. The effect of
218 spatial autocorrelation was addressed using principal coordinates of neighbour matrices
219 (PCNM) (see Borcard & Legendre, 2002).

220 Four pCCA models were run; one each testing for an effect of landscape composition or
221 landscape configuration in both contemporary and historical landscapes on woodland carabid
222 communities. For each model, a constrained ordination containing all the explanatory
223 variables (Table 1) was run to check for significance of the joint effects; a global permutation
224 test was considered significant where $p < 0.05$ using 9999 Monte-Carlo permutations. The
225 Monte-Carlo test repeatedly shuffled the species data while keeping the explanatory
226 landscape variables (and ‘sampling date’ covariate) fixed to identify any biologically
227 plausible structure in the data. Following a significant result, partial interactive forward
228 selection (pIFS) was used to reduce the whole set of variables to a more parsimonious subset
229 that explained a good proportion of the constrained variation in the carabid community
230 composition. At each step, the landscape variable that added most to the explained
231 community composition variation was selected (in addition to the effects of explanatory
232 variables that had already been selected). The statistical significance of each variable was
233 determined using Monte-Carlo permutations. The results of pIFS were displayed as bi-plots
234 illustrating the 25 most important carabid species relationships with the selected landscape
235 variables. On the bi-plots, arrows representing landscape variables point in the direction of
236 the steepest increase in a variables value. Symbols representing beetle species can be
237 perpendicularly projected onto the landscape variable line using a calibration arrow in the
238 Canoco software to determine the optima of an individual species in respect to the value of
239 that landscape variable. This interpretation is underpinned by some assumptions (see
240 Legendre and Legendre, 1998), notably that species have a unimodal relationship of (log-
241 transformed) abundance with the landscape variable and that the landscape gradient is long
242 enough to allow a species to go from a sub-optimum low frequency and on to a level of past-
243 optimum lower frequency. Nonetheless, use of the calibration arrow provides a useful
244 indication of *approximated* species response, whereby ‘optimum’ represents the value of the

245 environmental variable in the study at which a species is predicted to have its highest (log)
246 abundance.

247 Multicollinearity between explanatory variables is common in study tetrads where landcover
248 composition sums to 1 (Heikkinen *et al.*, 2004). The landscape composition variables (Table
249 1) were $\log(x+1)$ transformed to maximise the linearity of their relation to each other and to
250 ensure that the ecological importance of all the landcover types for species was considered
251 (Cleveland, 1993; ter Braak & Šmilauer, 2012). In all cases, the correlation matrix and
252 variance inflation factors were consulted during the Global Permutation Test to check for
253 collinearity (ter Braak & Šmilauer, 2012). Correlation coefficients among the final
254 explanatory variables were all less than 0.6 (Table S2) (cf. Aviron *et al.*, 2005, Radford &
255 Bennett, 2007). The full matrix of carabid species were $\log(x+1)$ transformed to minimize
256 the impact of abundant species on the analyses (Vanbergen *et al.*, 2005).

257 (A) RESULTS

258 (B) *Land-use change*

259 Land-use changes are summarised in Table 2. Historically, study tetrads were dominated by
260 semi-natural grasslands and broadleaf woodland. Approximately 25% of the landscape was
261 used for arable production and 8% lowland heath and scrubland. Today, grasslands
262 represented 3.6% of tetrad landcover; a relative decline of 91%. Grassland patches almost
263 halved in number and decreased substantially in size. Lowland heath and scrub habitat
264 underwent a relative loss of 95%. The majority of grassland and heathland habitat was
265 converted to improved grassland and intensive arable land-use, together representing the
266 largest proportion of landcover in the contemporary landscape (combined average 241.6 ha or
267 60.4%).

268 Broadleaf woodland habitat declined by 10 ha on average; a loss of 2.4%. Despite a relatively
269 low level of loss, contemporary woodlands now exist as substantially smaller, more
270 numerous patches with increased woodland edge habitat. Coniferous plantations were not
271 present historically, but represented 14.2 ha (3.5%) of tetrad landcover today. Total woodland
272 habitat inclusive of coniferous plantations increased by 1.1%. Urban land-use and transport
273 infrastructure also increased over the 80 years.

274 Table S2 shows variable collinearity between different years. Variables of the same habitat
275 type showed moderate to strong positive correlations over time; broadleaf woodland ($r =$
276 0.63), urban ($r = 0.65$), inland water ($r = 0.67$) and road length ($r = 0.79$). Pairwise
277 comparisons indicated moderate positive correlation between historical semi-natural
278 grassland and contemporary improved grassland cover ($r = 0.56$) and historical heathland and
279 contemporary coniferous woodland cover ($r = 0.45$).

280 ***(B) Carabid community dynamics***

281 4677 carabid beetles comprising 76 species were recorded from the 36 tetrads. 80% were
282 from five widespread woodland and generalist habitat species: *Pterostichus madidus* (1809,
283 39% of the total), *Abax parallelepipedus* (1354, 29%), *Pterostichus melanarius* (303, 6%),
284 *Nebria brevicollis* (162, 3%) and *Calathus rotundicollis* (155, 3%). Other species recorded
285 frequently but in lower abundances included grassland, open habitat, agricultural and
286 heathland species (Table S3).

287 ***(B) Effect of spatial autocorrelation***

288 Principal coordinates of neighbouring matrices (PCNM) found no spatially conditioned
289 variation in the contemporary landscape composition or configuration variables ($p = 0.289$

290 and $p = 0.740$), nor the historical composition or configuration variables ($p = 0.326$ and $p =$
291 0.540) which could explain the carabid community composition.

292 **(B) Carabid community response to contemporary and historical landscape heterogeneity**

293 *(C) Contemporary landscape composition*

294 Woodland carabid community composition was significantly related to contemporary
295 landscape composition (pCCA, $F = 1.3$, $p = 0.009$); the eight landscape composition variables
296 explained 29.7% of the total community variation (Table 3; Fig. 2). pIFS selected four Broad
297 Habitat variables that accounted for 18.0% of the total variation in carabid communities (Fig.
298 2). Species recorded less frequently during the study exhibited the strongest response; *C.*
299 *rotundicollis* (*C.rot*) was the only one of the five commonly trapped species to appear on the
300 bi-plot (Fig. 2). Most species associated negatively with contemporary expanses of arable
301 land and coniferous plantation which respectively explained 4.9% ($p = 0.015$) and 3.9% ($p =$
302 0.098) of the total variation (Table 3; Fig. 2). Species associated with mature broadleaf
303 woodlands including *Bembidion mannerheimii* (*B.man*), *Calodromius spilotus* (*C.spi*) and
304 *Acupalpus dubius* (*A.dub*) were among those to respond most negatively to these two
305 variables. Only heathland specialist *Nebria salina* (*N.sal*) and generalist woodland species *C.*
306 *rotundicollis* (*C.rot*) had their highest relative (log) abundances in landscapes containing 35 –
307 40% arable landcover and 3 – 6% coniferous plantation; values typical of the contemporary
308 landscape (Table 1; Fig. 2). *Notiophilus quadripunctatus* (*N.qua*), *Amara ovata* (*A.ova*) and
309 *Paranchus albipes* (*P.alp*) were most abundant in tetrads containing 3 – 4% semi-natural
310 grassland (mean cover 3.6%; Table 2, Fig. 2).

311 *(C) Historical landscape composition*

312 Woodland carabid community composition was significantly related to the historical
313 landscape composition (pCCA, $F = 1.3$, $p = 0.005$); the six variables explained 23.0% of the
314 total community variation (Table 3). Arable land ($p = 0.008$) and broadleaf woodland ($p =$
315 0.031) accounted for 10.2% of the total variation during pIFS (Table 3, Fig. 3). Thirteen of
316 the 25 species represented on the bi-plot responded to both the contemporary and historical
317 landscape composition (Figs. 2 and 3). However, with the exception of arable land, the two
318 models identified different explanatory landscape variables as key determinants of
319 community composition. Many species continued to display negative associations with
320 historical levels of arable land (Fig. 3). With the exception of *Calathus fuscipes* (C.fus) (an
321 inhabitant of arable fields) all other species represented on the bi-plot appeared at greater
322 abundance in tetrads with a proportion of arable land below that of the historical average
323 (23.5%). The approximate amount of broadleaf woodland cover that maximized the predicted
324 abundance of all species represented (other than agricultural species *Synuchus vivalis* (S.viv)
325 and *Bembidion quadrimaculatum* (B.qua)) was slightly greater than the historical average of
326 26.6% (Table 2, Fig. 3). *Pterostichus niger* (P.nig) (a large-bodied (18.5 mm), flightless
327 inhabitant of woodlands and damp grasslands) and *Carabus problematicus* (C.pro) (a very
328 large (24 mm), flightless inhabitant of woodland and heathland) were recorded in over two-
329 thirds of the study tetrads, but correlated only with historical landscape composition (Fig. 3).

330 (C) Contemporary landscape configuration

331 Woodland carabid communities exhibited a near-significant response to contemporary
332 landscape configuration when testing the joint effects (pCCA; $F = 1.3$, $p = 0.064$). The 9
333 configuration variables explained 32.1% of the total variation. Length of woodland edge and
334 mean woodland patch area explained the greatest proportion of the variation; 4.8% ($p =$
335 0.033) and 4.2% ($p = 0.084$) respectively (Table 3, Fig. 4). Grassland, heathland and open-
336 habitat species were most prevalent on the bi-plot. Those located in the positive bi-plot

337 quadrant (top-right) had highest predicted abundance where woodland edge exceeded 22 km
338 (contemporary mean 19.8 km). Woodland species including *Bembidion aeneum* (B.aen) and
339 specialist *Leistus fulvibarbis* (L.ful) were most abundant where landscapes contained large
340 woodland patches (~12 ha).

341 (C) Historical landscape configuration

342 Variation in current woodland carabid communities was better explained by historical
343 landscape configuration than contemporary landscape configuration when testing the joint
344 effects (pCCA: $F = 1.4$, $p = 0.006$, 34.7%) (Table 3). Four historical configuration variables
345 explained 17.7% of the total variation (Table 3, Fig. 5). Historically larger patches of
346 broadleaf woodland ($p = 0.062$) and semi-natural grassland ($p = 0.064$) explained the greatest
347 amount of carabid community variation (Table 3, Fig. 5). These two Broad Habitat types also
348 contributed to the largest proportions of total historical landcover (Table 2). *C. rotundicollis*
349 (*C.rot*), *A. parallelepipedus* (*A.par*) and *P. melanarius* (*P.mel*), three of the five most
350 frequently trapped species, were optimally associated with landscapes containing 0.2 – 0.6
351 km of transport routes (historical average of 1.8 km) (Table 2). In addition to *C.*
352 *problematicus* (*C.pro*) these common and widespread woodland species were found in greater
353 abundance in tetrads with 10 – 11.5 km of woodland edge habitat (historical average 11.3
354 km) and woodland patches sized 16 – 26 ha (historical average 16.3 ha). Woodland species *B.*
355 *mannerheimii* (*B.man*), *C. spilotus* (*C.spi*) and *A. dubius* (*A.dub*) positively associated with
356 historically large patches (> 28 ha) of broadleaf woodland (Fig. 5). *N. quadripunctatus*
357 (*N.qua*), *A. ovata* (*A.ova*) and *P. albipes* (*P.alb*) correlated strongly with landscapes that
358 historically contained grassland patches larger than 60 ha (historical average 36.7 ha) (Table
359 2, Fig. 5).

360 (A) DISCUSSION

361 Recently, it has become more widely accepted that species perceive landscapes in a complex
362 manner and utilise resources from different landcover types beyond their focal habitat
363 (Haslem & Bennett, 2008; Oliver *et al.*, 2010; Fahrig *et al.*, 2011). It has also been
364 demonstrated that the response of many species to landscape change is typically not instant,
365 but involves a time lag (Diamond, 1972). It was therefore, anticipated that populations would
366 exhibit a response to a variety of habitats present in the contemporary landscape, but also
367 those representative of the historical landscape (Kuussaari *et al.*, 2009; Watts *et al.*, 2010).

368 ***(B) Evidence of extinction debt for carabid communities in wooded-agricultural***
369 ***landscapes***

370 Carabid communities correlated significantly with both contemporary and historical
371 landscape composition, although more of the variation was explained by the contemporary
372 landscape. However, the significant effect of historical landscape composition is indicative
373 that some species may be experiencing a lag effect i.e., persisting as a result of landscape
374 conditions which no longer exist placing them at heightened risk of future extinction
375 (Lindborg & Eriksson, 2004). By contrast, the significant response of current carabid
376 communities to historical but not contemporary landscape configuration is consistent with an
377 extinction debt (Lindborg & Eriksson, 2004; Berglund & Jonsson, 2005; Sang *et al.*, 2010).

378 In the landscape composition models, 13 of the same species represented on the bi-plots
379 responded to both contemporary and historical conditions yet, apart from arable land,
380 different explanatory variables were identified. This is strong evidence that past habitat
381 availability is a key factor explaining current community assemblages (Sang *et al.*, 2010), and
382 also indicates that many of the same species are continuing to react to different, altered
383 conditions in the contemporary landscape. The negative association of many species to
384 historical amounts of arable land and positive relationship with historical availability of

385 broadleaf woodland is not unexpected as species will often respond most strongly to the
386 extent of preferred or avoided elements in a landscape (Judas *et al.*, 2002; Heikkinen *et al.*,
387 2004; Aviron *et al.*, 2005). Indeed, the approach adopted in other temporal landscape studies
388 assumes that species will correlate significantly with representations of their focal habitat.
389 However, in this study, the same species did not yield a response to contemporary broadleaf
390 woodland cover, despite only declining by 2.4% over the 80 years and with a moderately
391 strong correlation between years (i.e., tetrads with greater woodland cover historically
392 retained greater amounts of woodland today (Table S2)). What was observed was a continued
393 negative association to the vast increase in arable land cover, and also to coniferous
394 plantations which were not present historically. In lowland Britain, most conifer plantations
395 are sited on heathland (Spencer & Haworth, 2005) (which showed moderate correlation
396 between years), and within large patches of broadleaf, often ancient semi-natural woodland
397 (Rackham, 2003; Natural England, 2013). The strong negative association with conifers was
398 most evident for species typical or specialist of mature woodland including *B. mannerheimii*,
399 *C. spilotus* and *A. dubius*; these species also optimally associated with large patches of
400 broadleaf woodland in the historical model. The ongoing impacts of woodland conversion are
401 likely to continue to be detrimental as abundance and richness measures within introduced
402 coniferous plantations have consistently been found to be lower than those associated with
403 mature broadleaf woodland (Wiezik *et al.*, 2007; Oxborough *et al.*, 2010). Contrarily, there is
404 evidence that heathland soil structure and fertility is less altered by plantations, helping to
405 support heathland specialists such as *N. salina* and offering potential areas for conservation
406 restoration focus (Spencer & Haworth, 2005).

407 In the landscape configuration models, carabid communities were most strongly associated
408 with historically large patches of broadleaf woodland and semi-natural grasslands. These two
409 habitats contributed to the largest proportion of historical landcover, again indicating a legacy

410 whereby current woodland carabid assemblages have been shaped, and remain affiliated to
411 features which were dominant 80 years ago. The continued prevalence of *N. quadripunctatus*,
412 *A. ovata* and *P. albipes* (open/grassland habitat species) in landscapes that retain just 3 – 4%
413 grassland cover today, suggests that some species may only persist if landscape conditions
414 were exceptionally favourable previously, i.e., the highest abundance of these species was in
415 tetrads that historically included grassland patches larger than 60 ha (average historical patch
416 size 36.7 ha). Further studies adopting the temporal landscape mosaic approach but sampling
417 within grassland habitats would help confirm this assumption.

418 The degree of habitat fragmentation within a landscape has been found to be of significant
419 importance when it comes to identifying extinction debts (e.g. Cousins, 2009; Cristofoli *et*
420 *al.*, 2010; Piqueray *et al.*, 2011; Rybicki & Hanski, 2013). Here, the break-up of woodland
421 into smaller, more numerous patches, leading to an increase in edge habitat but with little loss
422 in total woodland cover is indicative of fragmentation. Evidence from the contemporary
423 configuration model however, suggested that the effect on species was not uniform: larger
424 patches may be key for specialists like *L. fulvibarbis*, while greater amounts of woodland
425 edge appeared to benefit other grassland, heathland and open-habitat species; possibly by
426 acting as a buffer, providing alternative useable or refuge habitat following substantial semi-
427 natural habitat loss (Schweiger *et al.*, 2005; Hendrickx *et al.*, 2007; Neumann *et al.*, 2015).

428 This highlights the need for a landscape mosaic approach that ensures the values of other
429 landcover types are not ignored. Likewise, although a negative effect of fragmentation was
430 not conclusive, it must be noted that focal habitat studies focussing on the response of
431 specialists are more likely to observe a significant effect as species will express higher
432 sensitivity to changes in their specific habitat, particularly in the absence of other landcover
433 information (Sang *et al.*, 2010). Nonetheless, there is increasing recognition that landscape
434 change impacts on the process of community assembly (Mayfield *et al.*, 2010) and that the

435 response of generalists are equally important to fully understand the ongoing impacts on
436 community structure (Cousins & Vanhoenacker, 2011; Piqueray *et al.*, 2011).

437 ***(B) How might landscape change be having an effect on carabid communities?***

438 This, and previous studies (e.g. Barbaro & Van Halder, 2009; Sang *et al.*, 2010; Dufлот *et al.*,
439 2014; Neumann *et al.*, 2015) indicate that specialists and carabids with lower dispersal ability
440 may be at greater risk following landcover change. In this study, large-bodied and flightless
441 carabids including *P. niger*, *C. problematicus*, *A. parallelepipedus* and *P. melanarius*
442 responded only to historical landscape conditions. All however, are considered common and
443 widespread (Luff, 2007) and were identified from more than two-thirds of the woodlands
444 sampled. The dispersal of large-bodied, flightless, carabids takes several generations and
445 successful colonisation of new patches may take hundreds of years (Jopp & Reuter, 2005).
446 Their frequency today should not be assumed to represent a stable and healthy population,
447 but may be better viewed as *persisting* (Oliver *et al.*, 2010) and in need of appropriate
448 targeted land management actions. Indeed, the relative abundance of these species was
449 greatest where the extent, shape and size of broadleaf woodland habitat was found to be
450 greater than, or at the threshold of that provided in the landscape 80 years ago. Although a
451 pertinent issue currently, the loss of woodland habitat in Britain can be dated back to the
452 Neolithic (Rackham, 1986) suggesting that, for many species, the extinction debt currently
453 being paid may relate to landscape conditions present well beyond the time period considered
454 here.

455 ***(B) Value of the landscape mosaic approach***

456 The landscape mosaic approach allows simultaneous consideration of landscape composition
457 and configuration as complementary components. Until now, temporal landscape studies
458 have only considered changes in the configuration of focal habitat (e.g. Lindborg & Eriksson,

459 2004; Cristofoli *et al.*, 2010; Sang *et al.*, 2010; Husáková & Münzbergová, 2014), which may
460 overemphasise the effects of landscape change on biodiversity. In this study, the landscape
461 mosaic approach stressed the importance of historical landscape conditions, but also
462 highlighted which habitats in the modified environment served to bolster populations and
463 those which were detrimental, providing a better understanding of how community
464 assemblages have been, and may continue to be shaped.

465 **(B) Conservation implications**

466 The detection of an extinction debt provides an unknown deadline for future biodiversity loss,
467 however, while species persist, there remains time for conservation measures to be applied.
468 Lowland Britain will remain dominated by intensive agriculture for the foreseeable, thus a
469 combination of management approaches are needed. For species with low dispersal power,
470 maintaining or increasing the size of woodland patches is advocated, while facilitating
471 species movement through the introduction and maintenance of linear features is a recognised
472 option where intensive agriculture dominates the landscape (Lawton *et al.*, 2010; Watts *et al.*,
473 2010). There is good evidence that species-rich hedgerows also offer comparable conditions
474 to woodland edges (Taboada *et al.*, 2004), which if providing refuge habitat for species of
475 open-habitats will ensure that linear features provide co-benefits throughout the matrix.
476 Active conversion of plantation woodland back to native tree species or heathland is
477 recognised (Spencer & Haworth, 2005) and guidance might consider restoration or new
478 woodland planting to be conducted at a level equivalent to the amount of habitat lost to
479 plantation. Restoration of heathland and species-rich grassland must be encouraged where
480 feasible (Piessens & Hermy, 2006) especially smaller patches implemented under farm-level
481 stewardship that connect larger restoration efforts. Finally, conservation actions should
482 consider the composition and configuration of both the historical and contemporary
483 landscape to ensure that efforts are applied where they are most suitable, encouraging

484 maximum biodiversity gain. For example, semi-natural grassland restoration might be best
485 undertaken on nutrient-depleted ex-arable land that retains a history of being on (or near to)
486 previous grassland sites to assist the development of species-rich swards (Walker *et al.*,
487 2004). While such strategic conservation planning ideally requires access to historical spatial
488 data, local knowledge will be invaluable where spatial datasets are unavailable.

489

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493

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665

666 **(A) DATA ACCESSIBILITY STATEMENT**

667 Requests for access to data used and analysed in this study can be made by emailing the
668 corresponding author.

669

670 **(A) BIOSKETCH**

671 The research team comprises individuals from UK academic and conservation research
672 institutions with a broad range of expertise in landscape ecology and practical conservation
673 across multiple taxonomic groups (<http://www.reading.ac.uk/cwac/>).

674 JLN and GHG conceptualised the study. JLN collected and analysed the data, GJH and AH
675 assisted with carabid identification. JLN led the manuscript writing with input and editing
676 provided by all authors.

677 **Table 1:** Summary of landscape composition and landscape configuration variables used to represent the
 678 contemporary and historical landscape heterogeneity in 36 study tetrads. Table also details additional
 679 constraining variables considered in the analyses.

Main set	Sub set	Broad Habitat variables
Landscape composition	Woodland land-use	Amount (ha) of broadleaf woodland (“Woodland”)
		Amount (ha) of coniferous plantation (“Coniferous”)
	Agricultural land-use	Amount (ha) of arable land (“Arable”)
		Amount (ha) of improved grassland (“Improved grassland”)
		Amount (ha) of semi-natural grasslands (“Grasslands”)
	Semi-natural land-use	Amount (ha) of inland water (“Water”)
		Amount (ha) of heathland and scrub (“Heath and scrub”)
Urban land-use		Amount (ha) of suburban and urban (“Urban”)
Landscape configuration	Woodland metrics	Total number of woodland patches (“WP”)
		Mean area (ha) of woodland patches (“MPA”)
		Total length (km) of woodland edge (“WE”)
		Perimeter: Area ratio of the sample woodland (“PAR”)
	Semi-natural habitat metrics	Total number of semi-natural grassland patches (“NPG”)
		Mean area (ha) of semi-natural grassland patches (“MPG”)
		Total number of heathland and scrub patches (“NPH”)
		Mean area (ha) of heathland and scrub patches (“MPH”)
		Total length (km) of main roads and railways (“RD”)
Constraining variables	Sampling date	Date of first carabid collection after 7 days (fortnight midpoint)
	Spatial location	British National Grid coordinate (XY) at tetrad midpoint

680 Abbreviations in brackets represent variable identification code on analysis bi-plots

681 **Table 2:** Average change in the composition and configuration of Broad Habitats (BH) comparing between
 682 2007 (contemporary landscape) and the 1930's (historical landscape).

Landscape composition (BH)	Contemporary		Historical	
	Mean area	% cover of	Mean area	% cover of
	(ha)	tetrad	(ha)	tetrad
Arable land	155.7 ha	38.9%	94.0 ha	23.5%
Improved grassland	85.9 ha	21.5%	0 ha	0%
Broadleaf woodland	96.6 ha	24.2%	106.5 ha	26.6%
Coniferous plantation	14.2 ha	3.5%	0 ha	0%
Heath and scrub	1.7 ha	0.4%	32.8 ha	8.2%
Grasslands	14.4 ha	3.6%	155.2 ha	38.8%
Inland water	1.0 ha	0.2%	3.43 ha	0.9%
Suburban and urban	25.4 ha	6.3%	17.4 ha	4.3%

Landscape configuration (BH)	Contemporary	Historical
	Mean values	Mean values
Number woodland patches	19 patches	11 patches
Area woodland patches	6.2 ha	16.3 ha
Length woodland edge	19.8 km	11.3 km
Number grassland patches	5 patches	9 patches
Area grassland patches	3.0 ha	36.7 ha
Number heath /scrub patches	9 patches	2 patches
Area heath/scrub patches	0.2 ha	15.3 ha
Length of roads and railways	2.2 km	1.8 km

683

684 **Table 3:** Response of woodland carabid communities to contemporary and historical landscape composition and
 685 landscape configuration across 36 tetrads. Results show the key explanatory variables identified by interactive
 686 forward selection for each model, following a significant ($p < 0.05$) global permutation test.

Landscape composition	Global significance test			Interactive selection		
	F	P	Var	Key variables	Var	p-value
Contemporary	1.3	0.009	29.7%	Heath & scrub	5.0%	0.073
				Arable	4.9%	0.015
				Grassland	4.2%	0.045
				Coniferous	3.9%	0.098
Historical	1.3	0.005	23.0%	Arable	5.9%	0.008
				Woodland	4.3%	0.031
Landscape configuration	Global significance test			Interactive selection		
	F	P	Var	Key variables	Var	p-value
Contemporary	1.3	0.064	32.1%	WE	4.8%	0.033
				MPA	4.2%	0.084
Historical	1.4	0.006	34.7%	MPG	4.8%	0.064
				MPA	4.8%	0.062
				WE	4.3%	0.045
				RD	3.8%	0.085

687 Var = total variation in carabid community composition explained by all the landscape variables (global
 688 significance test) and the total amount of variation explained by each individual variable (identified during
 689 forward interactive selection). Refer to Table 1 for landscape variable abbreviations. Significance levels
 690 determined by Monte-Carlo global permutation tests.

691 **Fig. 1:** Location of the 36 2 x 2 km study tetrads in central southern England and a thematic representation of
692 landscape change, comparing the historical and contemporary landscapes for one study tetrad.

693 **Fig. 2:** Partial Canonical Correspondence Analysis (pCCA) bi-plot illustrating the response of carabid
694 communities to contemporary landscape composition variables. Key explanatory variables identified by partial
695 Interactive Forward Selection (pIFS). For legibility, bi-plot displays the 25 species that are well described by the
696 first two ordination axes (which together explain 11.6% of the total variation) and are shown using bi-plot
697 scaling. Refer to Table 1 for variable abbreviations and Table S3 for full species names.

698 **Fig. 3:** Partial Canonical Correspondence Analysis (pCCA) bi-plot illustrating the response of carabid
699 communities to historical landscape composition variables. Key explanatory variables identified by partial
700 Interactive Forward Selection (pIFS). For legibility, bi-plot displays the 25 species that are well described by the
701 first two ordination axes (which together explain 10.2% of the total variation) and are shown using bi-plot
702 scaling. Refer to Table 1 for variable abbreviations and Table S3 for full species names.

703 **Fig. 4:** Partial Canonical Correspondence Analysis (pCCA) bi-plot illustrating the response of carabid
704 communities to contemporary landscape configuration variables. Key explanatory variables identified by partial
705 Interactive Forward Selection (pIFS). For legibility, bi-plot displays the 25 species that are well described by the
706 first two ordination axes (which together explain 9.0% of the total variation) and are shown using bi-plot
707 scaling. Refer to Table 1 for variable abbreviations and Table S3 for full species names.

708 **Fig. 5:** Partial Canonical Correspondence Analysis (pCCA) bi-plot illustrating the response of carabid
709 communities to historical landscape configuration variables. Key explanatory variables identified by partial
710 Interactive Forward Selection (pIFS). For legibility, bi-plot displays the 25 species that are well described by the
711 first two ordination axes (which together explain 11.0% of the total variation) and are shown using bi-plot
712 scaling. Refer to Table 1 for variable abbreviations and Table S3 for full species names.

713 **Supporting Information**

714 Additional Supporting Information may be found in the online version of this article:

715 **Table S1:** Creation of Broad Habitat categories derived from LCM2007 and OSMM data.

716 **Table S2:** Pearson correlation matrices for landscape variables in each year and between time periods.

717 **Table S3:** Record of carabid species, bi-plot codes and species characteristics.