How well is current plant trait composition predicted by modern and historical forest spatial configuration?

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Abstract

There is increasing evidence to suggest that a delayed response of many forest species to habitat loss and fragmentation leads to the development of extinction debts and immigration credits in affected forest habitat. These time lags result in plant communities which are not well predicted by present day landscape structure, reducing the accuracy of biodiversity assessments and predictions for future change. Here, species richness data and mean values for five life history characteristics within deciduous broadleaved forest habitat across Great Britain were used to quantify the degree to which aspects of present day forest plant composition are best explained by modern or historical forest patch area. Ancient forest specialist richness, mean rarity and mean seed terminal velocity were not well predicted by modern patch area, implying the existence of a degree of lag in British forest patches. Mean seedbank persistence values were more closely related to modern patch area than historical, particularly in larger patches. The variation in response for different mean trait values suggests that species respond to landscape change at different rates depending upon their combinations of different trait states. Current forest understorey communities are therefore likely to consist of a mixture of declining extinction debt species and colonising immigrant species. These results indicate that without management action, rare and threatened species of plant are likely to be lost in the future as a result of changes in forest spatial configuration that have already taken place. The lag seen here for rare specialist plants suggests however that there may still be scope to protect such species before they are lost from forest patches.

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1. **Introduction**

The spatial configuration of forest habitat is an important determinant of the richness and composition of forest understorey plant communities (Jacquemyn et al. 2003, Lindborg 2007, Kimberley et al. 2014). Large, well connected patches support greater numbers of rare species and species which possess low dispersal and competitive ability (Kolb and Diekmann 2005). This is particularly the case where such forests are of long continuity (Kimberley *et al.* 2014). Species with fast falling seeds and which are unable to persist within the seedbank tend to be lost from forest habitat following landscape fragmentation and habitat loss, partly because they are less able to rescue threatened populations through immigration or through regeneration from the seedbank (Ozinga et al. 2009, Jacquemyn et al. 2012, Lindborg et al, 2012).

Recent evidence suggests that the response of forest communities to landscape change is not immediate, with many species taking years to be lost from fragmented habitat or to colonise expanding forest areas. This results in the formation of "extinction debts" and "immigration credits" (Lindborg and Eriksson 2004, Metzger et al. 2009), where species assemblages remain more strongly correlated with historical landscape structure than modern habitat configurations (Kuussaari et al. 2009, Jackson and Sax 2010, Purschke et al. 2012). The consequent lack of coupling between biodiversity estimates and present day landscape configuration is likely to reduce the ability of present day forest configuration to explain and predict future patterns of plant species occurrence (Jackson and Sax 2010). This has important implications for forest conservation and management strategies which depend on accurate estimates of current biodiversity.

70   Although the impact of forest area, configuration and history has been investigated in

71   previous studies (Dupré & Ehrlén, 2002, Lindborg et al, 2012), relatively little work has

72   directly focussed on quantifying the extent of lag effects in forest habitat and determining

73   whether they differ between plant traits in a predictable manner. Here, we combine a

74   national scale dataset of plant species occurrence in forest patches with past and present

75   forest extent data. We then used these data to investigate the degree to which current plant

76   community composition is explained by historical rather than modern forest patch area.

77   Extinction debts are associated with species with low rates of population turnover such as

78   those with long life spans or the ability to persist within the seedbank. Such species may

79   remain as remnant populations for some time following unfavourable landscape change,

80   even when their eventual local extinction is likely (Eriksson 1996, Lindborg 2007, Vellend et

81   al. 2011). Forest habitat which has reduced in size may therefore still retain a

82   disproportionate number of the rare, forest specialist species that survived in previously

83   larger forest patches (Vellend et al, 2006, Kimberley et al, 2014). Conversely, immigration

84   credits result from the slow colonisation of new forest area by poorly dispersing species

85   (Verheyen et al. 2003, Jackson and Sax 2010). Forest patches which have been recently

86   established or which have seen an increase in the amount of forest habitat may therefore

87   still be dominated by better dispersing species; those with low seed weight and seed

88   terminal velocity or seeds which persist within the seed bank, in the absence of forest

89   specialist plants (Kimberley et al. 2014). Over time as the immigration credit is paid, many of

90   these forest specialists are likely to arrive, although the rate at which this occurs depends

91   upon proximity to source populations and the permeability of the intervening habitat matrix

92   (Peterken 2000, Brunet et al. 2011).

93   Where extinction debts and immigration credits exist in forest patches, the proportion of

94   species with linked traits such as high seed weight and terminal velocity and high seedbank

95   persistence are likely to lag behind landscape change. Combinations of life history

96   characteristics such as high seed terminal velocity and high specific leaf area are also known

97   to differentiate slow-dispersing, shade tolerant specialists largely restricted to long-

98   continuity, ancient woodland from forest plants that are more readily dispersed and more

99   typical of secondary forest (Kimberley et al. 2013). Such species are also more likely to be

100   rare. Thus ancient forest species tend to be stress tolerant and poor colonisers of new

101   habitat (Hermy et al. 1999) and therefore may be more prone to lag behind changes in forest

102   configuration. Lag effects in forest plants are often long lasting and have been observed

103   more than a century after forest fragmentation (Vellend et al. 2011). We therefore

104   hypothesised that present day forest community mean values for these traits would be

105   better explained by historical rather than modern forest patch area in patches which have

106   undergone area change. In addition to the trait-based approach, the relationships between

107   both total species richness and ancient woodland specialist richness (based on the list of

108   ancient woodland indicators in Kirby (2006)) and modern forest spatial configuration were

109   also analysed in order to determine whether species-based patterns could be discerned

110   alongside trait-based relationships with historical change in landscape structure.

111   In summary the following hypotheses were tested:

112   1. Plant community traits are better predicted by historical patch area than by modern

113   patch area within forest patches greater than 100 years old.

114   2. Traits associated with restriction to ancient forest habitat such as seed terminal

115   velocity and seedbank persistence are likely to be those most strongly linked to

116   historical forest patch area.

117   3. Richness of species restricted to ancient forest will be more closely related to

118   historical forest patch area than overall species richness.

119 **2. Methods**

120   **2.1. Survey data**

121 Digitised First Edition Ordnance Survey County Series (OS) maps (dated between 1849 and

122 1899) and data from the Countryside Survey, a national ecological surveillance programme

123 for Great Britain (Norton *et al.* 2012), were used to identify 82 patches of British

124 broadleaved forest which were established prior to 1899 and that were still recorded as

125 forest in 2007. Forest understory plant species occurrence data were then obtained for 151

126 vegetation sampling plots within these patches, assessed as part of Countryside Survey

127 2007. Two types of vegetation sampling plot were employed in the analysis; linear plots (10

128 m^2 in area), located parallel to forest streamsides and forest tracks, and area plots (200 m^2 in

129 area), located within the wider areal extent of each patch but not sampling a linear feature.

130   **2.2. Species and plant trait data**

131 Plant community mean trait values for a number of life history characteristics were

132 calculated for each plot by averaging the individual traits of all species present. These mean

133 values were then used as response variables in subsequent modelling. Mean trait values

134 were left un-weighted by species abundance. This allowed both subordinate and dominant

135 species to be considered equally, thus avoiding the confounding effect of variation in cover

136 due to local competitive sorting. Plant trait information was obtained from the Electronic

137 Comparative Plant Ecology database (Grime *et al.* 1995), the LEDA traitbase (Kleyer *et al.*

138   2008), The British Flora (Stace 1997) and PLANTATT (Hill et al. 2004). Species rarity was

139   obtained from PLANTATT as the number of occurrences in British 10 km squares in the

140   period 1987-1999.

141   Excluding trees and shrubs, 250 species occurred across the vegetation plots. Since trait data

142   were not available for all traits for all species, an approach was taken to minimise this

143   problem by estimating the missing values using a Bayesian hierarchical model written in

144   WinBUGs (Lunn et al. 2000), following the approach of Thompson and McCarthy (2008) as

145   applied in Kimberley et al. (2014). Imputing missing values in this manner is preferable to

146   removing them entirely, since estimated values take into account both between and within

147   family similarity among those species with known trait values. The five traits tested, along

148   with the percentage of species with missing values were; log natural seed weight (17.6%),

149   seed terminal velocity (29.6%), specific leaf area (5.2%), seedbank persistence (24.8%) and

150   rarity (0.4%). Seedbank persistence was assessed on a four point scale (1 = Transient seed, 2

151   = Persistent until next growing season, 3 = Small concentrations of persistent seeds, 4 =

152   Large year round bank of persistent seeds). In addition to the mean trait values, counts of

153   both overall plant species richness and ancient woodland indicator (AWI) species richness

154   were also obtained, using the list of AWIs in Kirby (2006).

155   **2.3.   Spatial data**

156   Patch area data for forest patches around each Countryside Survey vegetation plot were

157   derived for two periods; modern (2007) and historical (pre 1899), by overlaying forest extent

158   data onto the geo-referenced Countryside Survey plot data using GIS techniques (ESRI,

159   2011). Modern forest patch area data were extracted from the satellite derived Land Cover

160   Map 2007 (Morton et al. 2011) whilst historical patch area data were digitised from First

161   Series OS maps. These modern and historical area data were then natural log transformed to

162   reduce the skew in their distribution.

163   **2.4.   Local abiotic conditions**

164   Local conditions within forests are also important determinants of community composition

165   (Dupré and Ehrlén 2002, Kimberley et al. 2014). In order to obtain a more realistic estimate

166   of the effects of modern and historical forest configuration on mean community trait values

167   we included a number of abiotic variables measured at the same locations as the plant

168   species composition. Shade was estimated on a three point scale for all vegetation plots and

169   plots designated unshaded, partially shaded or fully shaded by field surveyors. Within each

170   of the area plots (n = 46) soil pH and carbon to nitrogen ratio were measured based on a 15

171   cm topsoil sample taken at the same time as the flora was recorded in each plot. In the

172   linear plots (n = 105) directly measured soil data were not available. Values within these

173   plots were estimated using published equations derived from a national calibration of

174   observed values of the three soil variables against the mean Ellenberg values of plants in

175   1033 plots from a stratified, random sample of the range of British vegetation types (Smart

176   et al. 2010). The mean Ellenberg values used in these equations to generate soil variables

177   were derived only from the trees and shrubs which were excluded from the calculation of

178   mean trait values for the herbaceous understorey (the dependent variables in the present

179   study). This may result in a less accurate estimate of soil conditions present in vegetation

180   plots due to the lower sample size of woody species present, however the problem of

181   circularity when the estimated soil variables were used to model mean trait values is

182   avoided through this method. In order to account for differences in response between the

183   area and linear plots, plot type was included as a categorical explanatory variable. Climate

184 and residual geographic variation across Britain were accounted for by the inclusion of the

185 northing of each sample plot as a continuous explanatory variable (Corney et al. 2006).

186 **2.5.   Modelling approach**

187 In order to determine the extent to which modern mean community trait values are better

188 predicted by modern or historical patch area data, the spatial data from the two time

189 periods were combined into two new variables; one describing the mean patch area and the

190 other the change in the patch area between the historical and modern period. The amount

191 of change observed in patch area across forest patches is shown in Appendix 1 (Fig. A1).

192 These variables were then used as explanatory variables in models of present day mean

193 values of life history traits and species richness data within forest habitat. Since spatial data

194 was replicated over time but only modern plant species data were available, this modelling

195 approach allowed the effect of modern and historical forest spatial structure to be assessed

196 in a single model for each response variable.

197 Results from the models can be interpreted as follows: the relationship between trait and

198 mean patch area indicates whether the trait in question is significantly affected by forest

199 patch area. In cases where a significant effect exists, the parameter estimate for the change

200 in patch area versus modern trait relationship can then be used to indicate whether the trait

201 is better modelled using the modern or historical spatial data. Where the relationship

202 between mean patch area and trait is positive, a value for the change in area parameter of

203 greater than zero will indicate a community that is better predicted by the modern spatial

204 data. If the change in area parameter is negative, the results indicate present day trait data

205 are more strongly correlated with historical patch area (this is reversed where the

206 relationship between mean patch area and trait is negative). Where a significant effect of

207   mean patch area is observed but the change in patch area regression coefficient is close to

208   zero, the results indicate an intermediate community which is equally well explained by both

209   modern and historical spatial data, suggesting an intermediate amount of lag. Since high,

210   low and intermediate values for this metric all indicate important results, testing for a

211   significant difference from zero is not appropriate for the change in patch area term.

212   Confidence intervals are therefore not shown around this measure.

213   Both present and past spatial data would be expected to predict plant composition equally

214   well where the plant composition is in an intermediate state, having moved away from the

215   historic forest configuration following landscape change but not yet well predicted by

216   current spatial data. However modern and historical patch area would also be expected to

217   be equivalent in their ability to predict modern trait values where only small amounts of

218   spatial change has occurred. In order to prevent any lag effects being obscured by a lack of

219   change between time periods it was therefore important to ensure that the dataset was not

220   dominated by patches which were stable in area between historical and modern data

221   sources. To reduce this problem 40 plots, randomly selected from those present in patches

222   which had undergone less than a 10% change in patch area, were removed from the dataset

223   prior to the analysis. This provided a set of patches with an approximately even distribution

224   of amount of change which could be used in subsequent modelling (Supplementary material

225   Appendix 1, Fig. A1).

226   The analysis allowed the identification of traits which are similarly well predicted by both

227   modern and historical patch area as well as permitting the amount of change between time

228   periods to be taken into account in the analysis. Use of the mean patch area rather than the

229   historical value avoids collinearity problems where historical patch area is correlated with

230   the amount of change. Thus the two spatial variables used in the analysis were statistically

231   independent.

232   The approach can be demonstrated using simulated examples. An artificial dataset was

233   created with information on modern trait composition, modern patch area and historical

234   patch area, where all patches had undergone a randomly allocated amount of change (either

235   positive or negative). The data were constructed such that modern values for a hypothetical

236   life history trait were strongly correlated with historical patch area but had no relationship

237   with a modern patch area (Figure 1a, b). Figure 1 shows the result of fitting the mean patch

238   area (Figure 1c) and change in patch area (Figure 1d) terms against the trait values. The trait

239   values which were associated with spatial variable values in the historical data have not

240   changed despite these patches having undergone change. Thus the patch area has changed

241   – high becoming low and low becoming high – but the trait values have not (Fig 1a). In such

242   a situation a relationship between trait and mean spatial variable is observed (Figure 1c),

243   and necessarily results in a strong negative correlation between change in the spatial

244   variable and the modern trait variable (Fig 1d), from which the stronger relationship

245   between trait and historical patch area can be inferred. If the historical patch area versus

246   trait relationship had been negative then this effect would have resulted in a positive slope
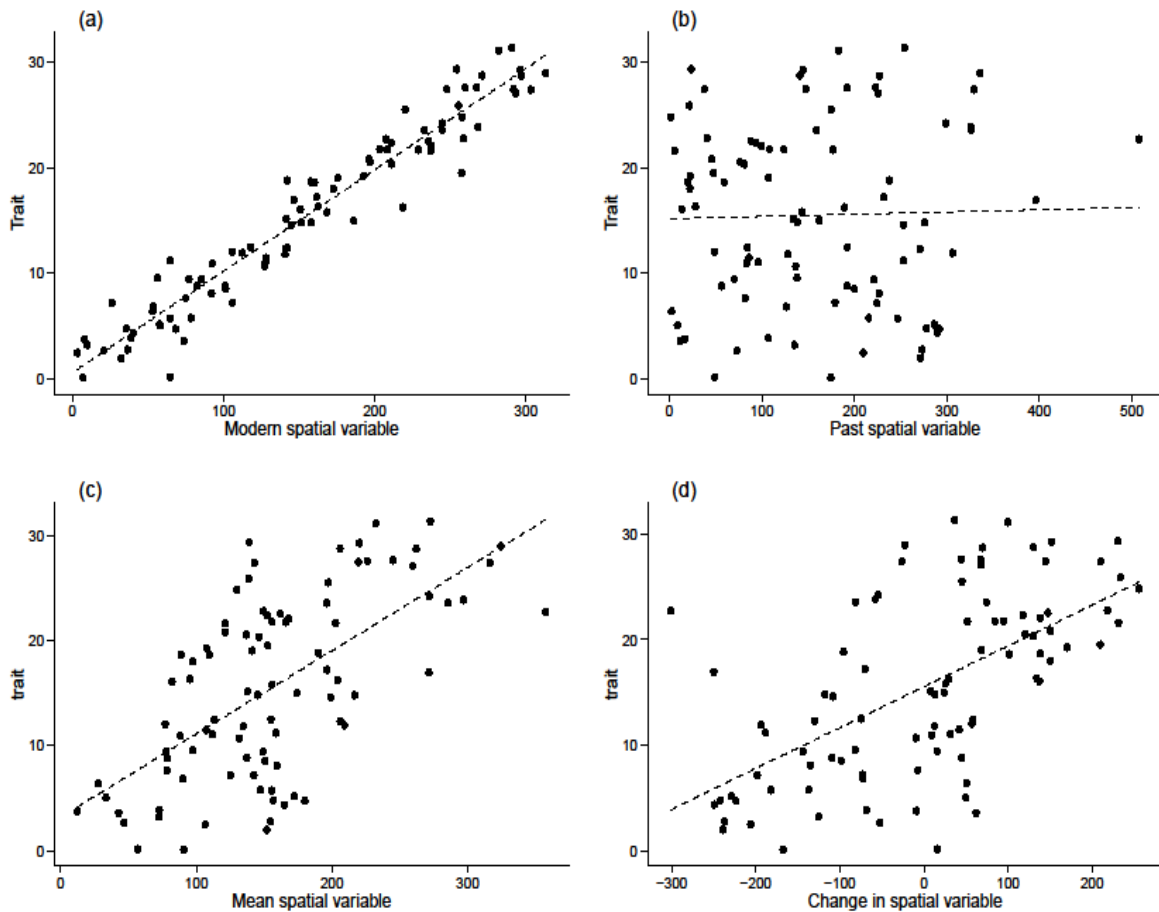
247   in Fig 1d.

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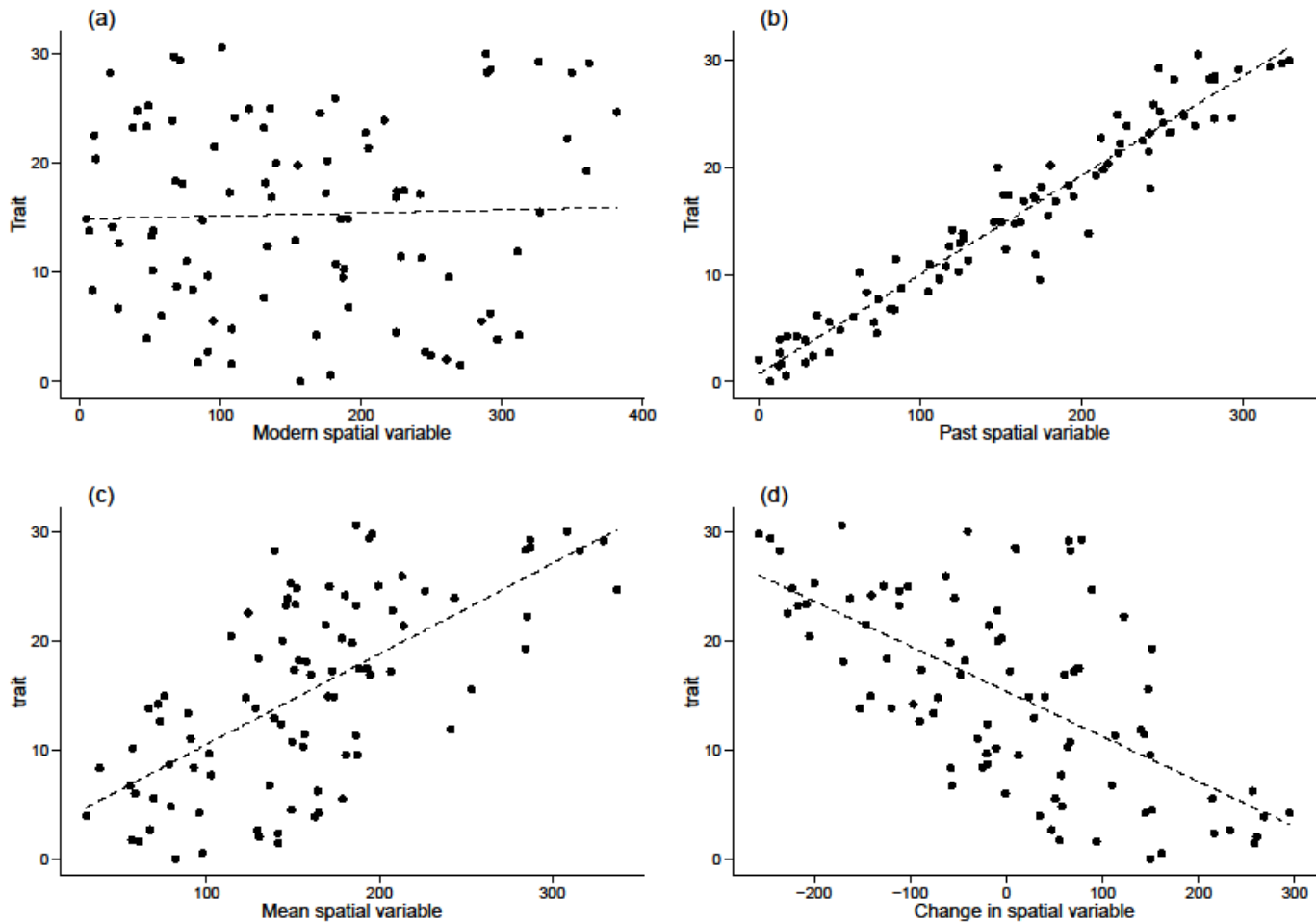
Figure 1. Simulated data showing the relationships between hypothetical mean trait values and (a) a modern spatial variable, (b) a historical spatial variable, (c) mean across modern and historical spatial variables and (d) change between modern and historical spatial variables, where trait data is best explained by historical spatial conditions. Dashed lines show linear models between trait and each individual explanatory variable.

A further simulation shows the pattern recovered by the analysis where the same strong positive spatial-trait relationship occurs but in this case with modern patch area. A second dataset was created; this time such that modern values for the hypothetical life history trait were strongly correlated with modern patch area but had no relationship with historical patch area (Figure 2a, b). The same modelling approach of fitting mean and change in patch area against trait was then applied. This again results in a relationship between trait and mean patch area (Figure 2c); however in this case the relationship between trait and

264   modern patch area is revealed by the positive relationship between trait and change in

265   patch area (Figure 2d).

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Figure 2. Simulated data showing the relationships between hypothetical mean trait

values and (a) a modern spatial variable, (b) a historical spatial variable, (c) mean across

modern and historical spatial variables and (d) change between modern and historical

spatial variables, where trait data is best explained by modern spatial conditions. Dashed

lines show linear models between trait and each individual explanatory variable.

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274   The modelling approach demonstrated in the simulated examples was applied to the real

275   data for the 111 vegetation sampling plots used. A single model was fitted for each mean

276   plant trait, along with species richness and AWI richness. These models contained the mean

277   patch area, the change in patch area and the interaction between these two variables, in

278   addition to all local condition variables described above. The interaction term was included

279   in each model to investigate whether patches with varying mean area differ in the extent to

280   which modern spatial data can be used to predict trait composition. A mixed-effects

281   modelling approach was taken, including site (Countryside Survey 1 km square) as a random

282   intercept, using the package lme4 in the statistical software R. This accounted for the spatial

283   autocorrelation introduced by analysing a number of vegetation sampling plots located

284   within the same Countryside Survey sample square. Mean trait values were modelled by

285   linear mixed effects models while generalised linear mixed effects models with a Poisson

286   error distribution were used for species richness and AWI richness models, to account for

287   the count data response. All models were scaled and centred using the R package arm, to

288   produce comparable regression coefficients. These allowed an estimate of the effect sizes of

289   each spatial variable on each plant trait to be made. 95% confidence intervals around these

290   effect sizes were calculated using the bootstrap method in lme4. For linear models response

291   values were also treated in this way to produce standardised effect sizes bounded by ±1. For

292   models of count data this was not possible due to the link function used in the generalised

293   linear models. Parameter estimates from the different model types are therefore not directly

294   comparable. The resulting effect sizes and confidence intervals allowed the extent to which

295   present day mean values for different life history traits are better predicted by modern or

296   historical forest spatial configuration to be assessed.

297 A number of significant effects of the abiotic variables, northing and plot type were

298 detected, discussion of which is beyond the scope of this article. Here we focus on partial

299 spatial relationships with trait composition having accounted for variation explained by local

300 environmental conditions. Full modelling results are however shown in Appendix 2

301 (Appendix 2, Table A2).

3. Results

3.1. Trait data

304 Mean patch area was a significant predictor for three of the five community mean response

305 variables tested; seedbank persistence, seed terminal velocity and species rarity (Figure 3).

306 Rarer species with faster falling seeds and less persistent seedbanks were found in patches

307 with a high average area across the two time periods, suggesting that forest configuration

308 has an important effect on the occurrence of species with these traits. The lag metric was

309 close to zero for both seed terminal velocity and rarity (change in area term, Figure 3a,b),

310 suggesting that both modern and historical patch area explain these traits equally well,

311 despite the gradient of change in patch area present across the sampled woodlands. This

312 must therefore mean that communities have not remained static and hence stayed

313 correlated with historic patch configuration, but neither have they completely readjusted to

314 the modern patch configuration. The lag metric for seedbank persistence however was less

315 than zero (Figure 3e). Given the negative relationship between mean patch area and this

316 trait this indicates that mean seedbank persistence values were better predicted by the

317 modern patch area than the historical.

318   The interaction between mean patch area and change in patch area had a significant

319   negative effect on mean seed bank persistence values (Figure 3e). As mean patch area

320   increases, the negative relationship between trait and change in area becomes stronger. This

321   suggests that mean seedbank persistence was better predicted by modern patch area in

322   forest patches with a larger mean area across the two time periods than in patches with a

323   smaller mean area.

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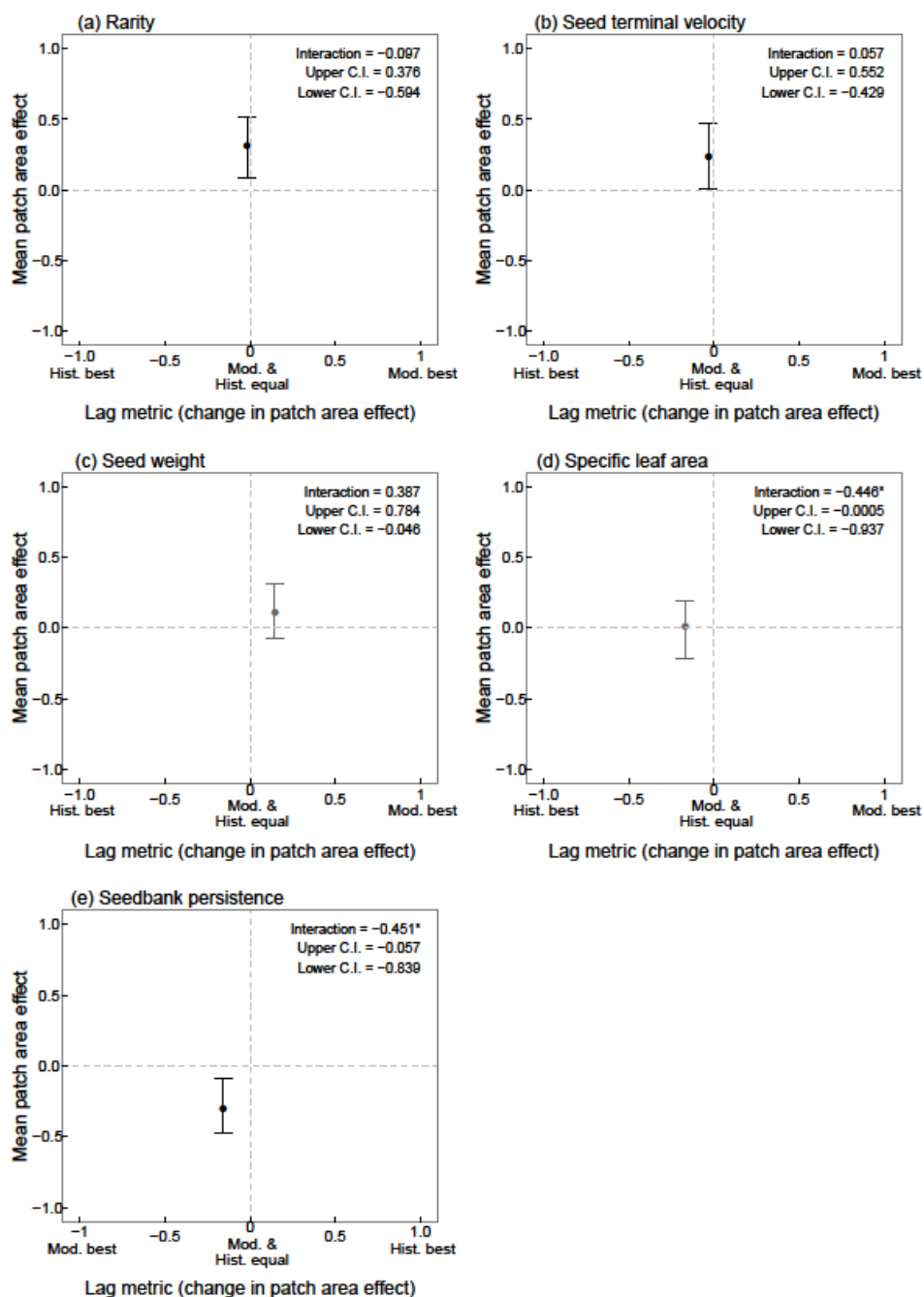
Figure 3. Standardised effect sizes quantifying the influence of patch area in models of five mean trait values in forest vegetation sampling plots. Error bars represent 95% confidence intervals. Where displayed confidence intervals do not overlap 0 a significant effect of patch area is indicated. The position of the point on the x axis shows the extent to which present day trait values are best predicted by historical or modern patch area. Text in the top right of each panel shows the parameter estimate and upper and lower confidence intervals for interaction terms. Parameter estimates for local abiotic variables (also included in models) are not shown here.

3.2 Species data

Mean patch area had a significant effect on AWI species richness but no effect on overall species richness (Figure 4). This suggests that ancient forest specialists are more sensitive to patch area than other forest plants. Change in patch area had a weak negative effect on AWI species richness, indicating that the number of ancient forest specialists is slightly better predicted by historical patch area than modern.
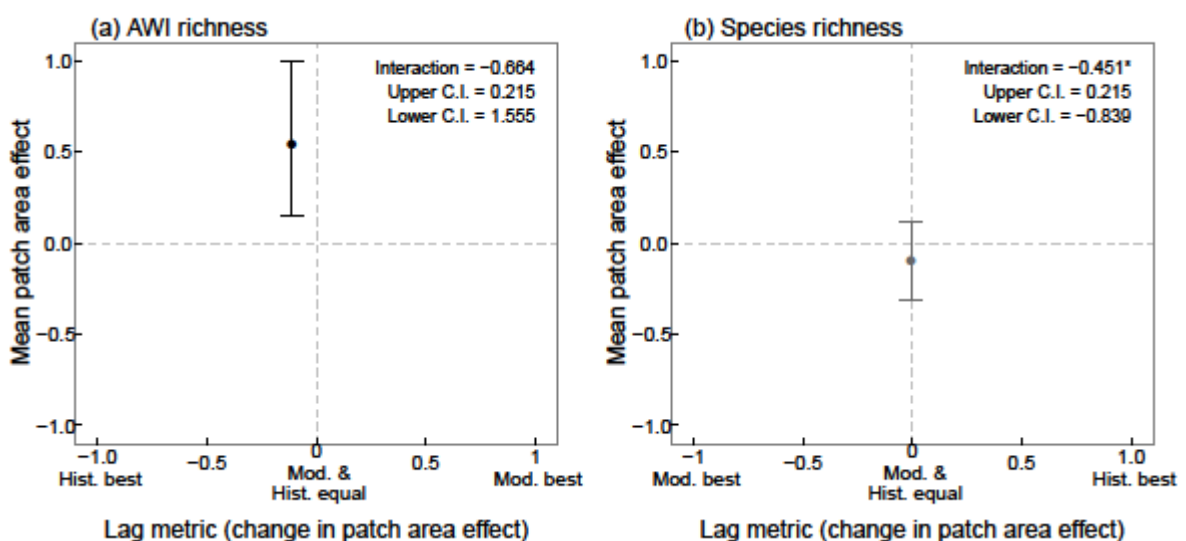
Figure 4. Standardised parameter estimates quantifying the influence of patch area in

models of overall species richness and ancient woodland indicator (AWI) richness in forest

vegetation sampling plots. Error bars represent 95% confidence intervals. Where displayed

confidence intervals do not overlap 0 a significant effect of patch area is indicated. The

position of the point on the x axis shows the extent to which present day trait values are

best predicted by historical or modern patch area. Text in the top right of each panel

shows the parameter estimate and upper and lower confidence intervals for interaction

terms.   Parameter estimates for local abiotic variables (also included in models) are not

shown here.

4. Discussion

The important effects of forest spatial configuration on understorey plant composition

within forest patches were confirmed by the relationships identified here between mean

patch area and three of the five mean community values tested here. The strength with

which different traits could be predicted by modern rather than historical forest patch area

varied, indicating that while some species may be quickly lost from fragmented habitat,

many are likely to persist for some time following landscape change. Such variation in

response to changes in habitat fragmentation has important consequences for conservation

planning because it suggests that there may be a window of time in which to introduce

measures to help vulnerable species (Wearn et al. 2012).

The analytical approach taken here allowed intermediate situations to be identified, where a

mean trait value is affected by patch area but the trait is equally well predicted by both

modern and historical forest extent. Results suggest that this is the current case for both

rarity and seed terminal velocity, implying the existence of weak time lags for these

363 characteristics. This supports previous studies which have found that plant communities take

364 time to respond following landscape change (Lindborg and Eriksson 2004, Metzger et al.

365 2009, Saar et al. 2012). Rare species and those with heavy, fast falling seeds are likely to be

366 less able to disperse effectively and rescue threatened populations through immigration

367 (Kolb & Diekmann, 2005). Many such species are therefore unlikely to be able to persist

368 long-term following the loss of forest patch area. Since many rare, forest specialist plants are

369 perennial species however (Kimberley et al, 2013), they may survive in remnant populations

370 for some time following landscape change (Eriksson, 1996). The slow loss of species with

371 these characteristics may explain why mean seed terminal velocity and rarity were equally

372 well predicted by modern and historical patch area. This is further evidenced by the fact that

373 AWI richness within forest patches was more closely related to historical patch area than

374 modern. Hence there is likely to be a disproportionate drop in the occurrence of these

375 vulnerable plant species in the future as existing extinction debts are paid in patches which

376 have decreased in area. In many cases these species are also likely to be slow to colonise

377 forest patches which have increased in size, particularly in isolated patches (Brunet, 2011).

378 Hence maintaining large areas of older forest is important to avoid the loss of populations of

379 rare or poorly dispersing ancient woodland specialist plants (Kimberley *et al.* 2013).

380 Although existing time lags are likely to lead to ongoing change in forest community

381 composition, if the amount of change in forest extent between time periods is small the

382 degree of future change in plant composition is also likely to be limited, even where this

383 change takes some time to occur. It is therefore also important to consider the amount of

384 change which occurred between time periods when interpreting these results. It is likely that

385 a large alteration in patch size is needed to produce a significant, long lasting time lag. Here

386   only a weak lag was identified for mean rarity and seed terminal velocity, possibly due to a

387   small amount of change between historical and modern patch area for many patches.

388   Further application of this method to forests which have undergone more substantial or very

389   recent changes in area may reveal whether this is indeed the case. If so, the greatest benefit

390   of increasing forest patch area may be seen in patches which have recently undergone a

391   large reduction in area. The time lag identified here for rarity and seed terminal velocity may

392   also be weak due to the difference in species richness and composition between area and

393   linear plots used in this analysis. If linear plots contain a higher proportion of ruderal species

394   with characteristics consistent with a more rapid response to landscape change,

395   communities are likely to be closer to those predicted by modern forest patch area.

396   The variation in the degree to which modern or historical forest patch area best explains

397   mean trait values suggests that different species are responsible for each individual trait

398   relationship. For a species to persist but be bound for extinction it requires both strong

399   ability to persist and weak dispersal capability. Any lag observed in patches which have lost

400   area may be due to forest specialist species which have a particular combination of

401   established phase traits (slow, shade-tolerant vegetative growth) and regenerative traits

402   (poor dispersal) and therefore have the potential to persist for some time after landscape

403   change (Kimberley et al, 2013, Saar et al, 2012). Forest specialist species without this trait

404   combination are likely to be lost relatively quickly from fragmented patches while species

405   with these characteristics remain until they are either out-competed by more ruderal

406   immigrants or otherwise suffer mortality from disturbance, herbivory or disease (Grime,

407   2001, Jackson & Sax 2010). On the other hand immigrant species must be both rapidly

408   dispersed and shade-tolerant slow growers to truly survive in undisturbed forest

409 understorey. For example ruderal species with high investment in many small seeds with low

410 terminal velocity, high relative growth rates and high seedbank persistence can respond

411 more rapidly to landscape change, quickly colonising new forest edges, new small areas of

412 secondary woodland including previously larger patches which have lost forest area

413 (Tabarelli et al. 1999).

414 What we see integrated into the mean trait values is likely to be the trait-controlled sum of

415 the dynamics of fast-responding species more rapidly dispersed in time (through persistent

416 seedbanks) and space (through light, slower falling seeds) arriving at different rates from

417 surrounding habitats, coexisting with extinction debt species that are better fitted to

418 historical spatial configurations and hence are likely to decline further. These two processes

419 may occur at different rates however, with extinction debts in forest understorey plants

420 being paid sooner (after around 160 years) (Kolk & Naaf, 2015) than immigration credits

421 (which can remain for much longer) (Naaf & Kolk, 2015). If extinction debts in forest patches

422 in this analysis which have lost area have largely been paid, this may partly explain why only

423 weak lags were identified here for mean seed terminal velocity and rarity.

424 Mean seedbank persistence values lag less behind changes in patch area than mean seed

425 terminal velocity and rarity, particularly in large forest patches. High seedbank persistence

426 allows species to regenerate vulnerable or locally extinct populations from the soil

427 seedbank. The absence of such persistent species in larger forest patches (Kimberley et al,

428 2014) may result in a community which is faster to respond to changing patch area because

429 more species present in the vegetation possess no persistent seedbank. Such species are

430 likely to be quickly lost when habitat area is reduced. The species present above-ground are

431 also often poorly correlated with the species present in the seedbank (Bossuyt et al. 2002).

432   Many species present in forest seedbanks may therefore be rapidly growing species and

433   widely dispersed which are absent from the above-ground vegetation but likely to appear

434   and thrive following disturbance to the soil or canopy (Bossuyt et al. 2002). When forest

435   patches lose area or are newly disturbed they may swiftly gain these ruderal species from

436   the existing seedbank, reducing the lag for this trait (Smart et al 2014). In smaller patches

437   this effect may be weaker due to a higher original proportion of species with a persistent

438   seedbank (Kimberley et al, 2014). This suggests that large patches are likely to be quickest to

439   pay their extinction debts when they are reduced in size and further confirms the fact that

440   species which are particularly dependent on large, core areas of habitat may be first to

441   become extinct following the loss and fragmentation of forest habitat. The creation of small

442   patches of new forest is therefore likely to be of less benefit than extending existing forest

443   habitat (Peterken 2000).

444   One limitation of analysing the data in this way is that there is no way of knowing when

445   changes in spatial properties between the two time periods have occurred. Interpretation of

446   the results must therefore be done with care, since modern forest configuration would be

447   expected to have a stronger effect than historical if most of the spatial change was longer

448   ago. The large number of data points from across a wide geographic area used here however

449   ensured that a realistic assessment of current patterns in British forests could be made.

450   Furthermore, because the same forest habitats were analysed for all traits tested,

451   comparisons of the relative strength with which modern forest configuration affects

452   different mean trait values are still valid. Mean trait values were analysed separately to allow

453   differences in the response of traits to important variables to be detected. As such however,

454   the inter-correlation between pairs of traits must be taken into account. For example, part of

22

455   the observed effect of patch area on seedbank persistence may be due to the close

456   relationship between this trait and seed mass (Westoby et al. 2002). Correlations between

457   mean trait values are shown in Appendix 3 (Appendix 3, Fig. A5).

458   Although only forest patch area was tested here, this variable is often correlated with a

459   number of other forest configuration variables such as the amount of forest present in the

460   landscape or the amount of core forest habitat (Fahrig, 2003). In reality, time lags in forest

461   habitat are likely to depend on interactions between the size of patches, the amount of

462   nearby forest (particularly that of long continuity) and the amount of edge habitat present.

463   For example, newly created forest patches within a short distance of ancient forest habitat

464   have been shown to accumulate forest specialist species more quickly (Brunet *et al.* 2011),

465   while young forest patches which are highly isolated from ancient forest habitat mostly

466   accumulate species adapted for effective dispersal which tend not to be ancient woodland

467   specialists (Brunet 2007). Hedges and other semi-natural habitat types also have some

468   ability to act as a refuge for forest specialist species (McCollin et al. 2000, Smart et al. 2001),

469   potentially enabling such species to persist for longer, and therefore exhibit a stronger lag

470   effect, in landscapes where such features are common. The landscape context of changing

471   forest habitat is therefore also likely to be an important determinant of the extent to which

472   time lags develop. High intensity agriculture in neighbouring land use has been shown to

473   reduce the ability of forest specialist species to exist near forest edge habitat (Chabrerie et

474   al. 2013). Where forest patches are surrounded by intensive agricultural land, forest edge is

475   likely to be quickly colonised and dominated by weedy generalist species with higher

476   seedbank persistence (Willi et al. 2005). Where forest edge is buffered by less intensive land

477   uses however, stronger lags may be occurring as forest specialist species take longer to be

478   out-competed by immigrants. Hence, some forest specialist species may still be able to

479   persist even in small patches or at forest edges, so long as they are already established

480   before fragmentation and that the forest patch is appropriately surrounded by non-intensive

481   land. Hence buffering forest habitat with less intensive habitat types and linear refuges may

482   allow many vulnerable forest species to persist following landscape change, but this issue

483   requires further research.

484   In future, as existing immigration credits and extinction debts are paid, forest species

485   composition is likely to shift towards present day patterns of habitat configuration, with

486   fragmented forest likely to lose shade tolerant, poor dispersers and gain populations of

487   immigrant species. Likewise forest patches which are increasing in size will begin to recruit

488   suitable populations of forest plants and lose species more fitted to smaller patches with a

489   high edge to area ratio. The fact that mean rarity and seed terminal velocity were equally

490   strongly affected by modern and historical forest configuration in long established British

491   forest patches highlights the importance of accounting for historical forest spatial

492   configuration when modelling patterns of plant species occurrence (Ewers et al. 2013).

493   Failure to do so risks both underestimating the strength with which forest configuration

494   affects species and failing to identify species which are at risk of local extinction (Helm et al.

495   2006). However extinction debts in particular do present an opportunity to initiate measures

496   to prevent the loss of threatened species (Kuussaari *et al.* 2009) and the time lag identified

497   here for rare species and inefficient dispersers suggests that many vulnerable species could

498   benefit from well targeted management action.

499   5. **Acknowledgements**

References

505   Bossuyt, B. et al. 2002. Seed bank and vegetation composition of forest stands of varying age
506   in central Belgium: consequences for regeneration of ancient forest vegetation. Plant
507   Ecol. 162: 33-48.

508   Brunet, J. 2007. Plant colonization in heterogeneous landscapes: an 80-year perspective on
509   restoration of broadleaved forest vegetation. J. Appl. Ecol. 44: 563–572.

510   Brunet, J. et al. 2011. Understory succession in post-agricultural oak forests: Habitat
511   fragmentation affects forest specialists and generalists differently. For. Ecol. Manage.
512   262: 1863–1871.

513   Chabrerie, O. et al. 2013. Maturation of forest edges is constrained by neighbouring
514   agricultural land management. J. Veg. Sci. 24: 58–69.

515   Cohen. 1988. Statistical Power Analysis for the Behavioral Sciences, 2nd edn. Lawrence
516   Erlbaum Associates Ltd., New Jersey.

517   Corney, P.M. et al. 2006. Relationships between the species composition of forest field-layer
518   vegetation and environmental drivers, assessed using a national scale survey. J. Ecol. 94;
519   383–401.

520   Dupré, C. and Ehrlén, J. 2002. Habitat configuration, species traits and plant distributions. J.

521   Ecol. 90; 796–805.

522   Eriksson, O. 1996 Regional dynamics of plants: A review of evidence for remnant, source-

523   sink and metapopulations. Oikos 77:248-258.

524   ESRI. 2011. ArcGIS Desktop: Release 10. Environmental Systems Research Institute,

525   Redlands, CA.

526   Ewers, R. M. et al. 2013. Using landscape history to predict biodiversity patterns in

527   fragmented landscapes. - Ecol. Lett. 16: 1221–33.

528   Fahrig, L. 2003. Effects of Habitat Fragmentation on Biodiversity. Annu. Rev. Ecol. Evol. Syst.

529   34: 487-515.

530   Grime, J.P. et al. 1995. The Electronic Comparative Plant Ecology. Chapman & Hall, London.

531   Grime, J. P. 2001. Plant strategies, vegetation processes, and ecosystem properties. Second

532   edn. John Wiley and Sons, Chichester, UK.

533   Helm, A. et al. 2006. Slow response of plant species richness to habitat loss and

534   fragmentation. - Ecol. Lett. 9: 72–7.

535   Hermy, M. et al. 1999. An ecological comparison between ancient and other forest plant

536   species of Europe, and the implications for forest conservation. Biol. Cons. 91: 9-22.

537   Hill, M. O. et al. 2004. PLANTATT - attributes of British and Irish plants: status, size, life

538   history, geography and habitats. Centre for Ecology and Hydrology, Huntingdon.

539   Jackson, S. T. and Sax, D. F. 2010. Balancing biodiversity in a changing environment:

540   extinction debt, immigration credit and species turnover. Trends Ecol. Evol. 25: 153–60.

541   Jacquemyn, H. et al. 2003. Influence of environmental and spatial variables on regional

542   distribution of forest plant species in a fragmented and changing landscape. Ecography.

543   26: 768–776.

544   Jacquemyn, H. et al. 2012. Evolutionary changes in plant reproductive traits following habitat

545   fragmentation and their consequences for population fitness. J. Ecol. 100: 76–87.

546   Kimberley, A. et al. 2013. Identifying the trait syndromes of conservation indicator species:

547   how distinct are British ancient woodland indicator plants from other woodland

548   species? - Appl. Veg. Sci. 16: 667–675.

549   Kimberley, A. et al. 2014. Traits of plant communities in fragmented forests: The relative

550   influence of habitat spatial configuration and local abiotic conditions. J. Ecol. 102: 632–

551   640.

552   Kirby, K. 2006. Ancient Woodland Indicator (AWI) plants, in Rose, F. (ed) The wildflower key.

553   Penguin Group, London, pp. 558–561.

554   Kleyer, M. et al. 2008. The LEDA Traitbase: a database of life-history traits of the Northwest

555   European flora. J. Ecol. 96: 1266–1274.

556   Kolb, A. and Diekmann, M. 2005. Effects of Life-History Traits on Responses of Plant Species

557   to Forest Fragmentation. Conserv. Biol. 19: 929–938.

558   Kolk, J. and Naaf, T. 2015. Herb layer extinction debt in highly fragmented temperate forests

559   – Completely paid after 160 years? Biol. Cons. 182: 164-172.

560   Kuussaari, M. et al. 2009. Extinction debt: a challenge for biodiversity conservation. Trends

561   Ecol. Evol. 24: 564–71.

562   Lindborg, R. 2007. Evaluating the distribution of plant life-history traits in relation to current

563   and historical landscape configurations. J. Ecol. 95: 555–564.

564   Lindborg, R. et al. 2012. Effect of habitat area and isolation on plant trait distribution in

565   European forests and grasslands. Ecography 34:1-8.

566   Lindborg, R. and Eriksson, O. 2004. Historical Landscape Connectivity Affects Present Plant

567   Species Diversity. Ecology 85: 1840–1845.

568   Lunn, D.J., Thomas, A., Best, N. & Spiegelhalter, D. 2000. WinBUGS - a Bayesian modelling

569   framework: concepts, structure, and extensibility. Stat. Comput. 10: 325–337.

570   McCollin, D. et al. 2000. Hedgerows as habitat for woodland plants. J. Environ. Manage. 60:

571   77–90.

572   Metzger, J. P. et al. 2009. Time-lag in biological responses to landscape changes in a highly

573   dynamic Atlantic forest region. Biol. Conserv. 142: 1166–1177.

574   Morton, R.D. et al. 2011. Final Report for LCM2007 - the new UK land cover map.

575   Countryside Survey Technical Report No 11/07. NERC/Centre for Ecology & Hydrology

576   pp. 112.

577   Naaf, T. and Kolk, J. 20150. Colonization credit of post-agricultural forest patches in NE

578   Germany remains 130–230 years after reforestation, Biol. Cons. 182: 155-163.

579   Norton, L. R. et al. 2012. Measuring stock and change in the GB countryside for policy--key

580   findings and developments from the Countryside Survey 2007 field survey. J. Environ.

581   Manage. 113: 117–27.

582   Ozinga, W. et al. 2009. Dispersal failure contributes to plant losses in NW Europe. Ecol. Lett.

583   12: 66–74.

584   Peterken, G. F. 2000. Rebuilding Networks of Forest Habitats in Lowland England. Landsc.

585   Res. 25: 291–303.

586   Purschke, O. et al. 2012. Linking landscape history and dispersal traits in grassland plant

587   communities. Oecologia 168: 773–83.

588   Saar, L. et al. 2012. Which plant traits predict species loss in calcareous grasslands with

589   extinction debt? - Divers. Distrib. 18: 808–817.

590   Smart, S. M. et al. 2001. An assessment of the potential of British hedges to act as corridors

591   and refuges for Ancient Woodland Indicator plants. In Barr, C., Petit, S. (eds) Hedgerows

592   of the world: their ecological functions in different landscapes. Proceedings of the 10th

593   Annual Conference of the International Association for Landscape Ecology, pp 137–146.

594   Smart, S.M. et al. 2010. Empirical realised niche models for British higher and lower plants –

595   development and preliminary testing. J. Veg. Sci. 21: 643–656.

596   Smart, S. M. et al. 2014. Quantifying the impact of an extreme climate event on species

597   diversity in fragmented temperate forests: the effect of the October 1987 storm on

598   British broadleaved woodlands. J. Ecol. 102: 1273–1287.

599   Stace, C. 1997. New Flora of the British Isles. Cambridge University Press.

600   Tabarelli, M. et al. 1999. Effects of habitat fragmentation on plant guild structure in the

601   montane Atlantic forest of southeastern Brazil. Biol. Conserv. 91: 119-127

602   Thompson, K. & McCarthy, M.A. 2008. Traits of British alien and native urban plants. J. Ecol.

603   96: 853–859.

604   Thomson, F. J. et al. 2011. Seed dispersal distance is more strongly correlated with plant

605   height than with seed mass. J. Ecol. 99: 1299–1307.

606   Vellend, M. et al. 2006. Extinction Debt of Forest Plants Persists for More than a Century

607   following Habitat Fragmentation. Ecology. 87: 542-548

608   Verheyen, K. et al. 2003. Herbaceous plant community structure of ancient and recent

609   forests in two contrasting forest types. Basic Appl. Ecol. 4: 537–546.

610   Wearn, O. R. et al. 2012. Extinction debt and windows of conservation opportunity in the

611   Brazilian Amazon. Science. 337: 228–32.

612   Westoby, M. et al. 2002. Plant ecological strategies: some leading dimensions of variation

613   between species. Annu. Rev. Ecol. Syst., 33: 125–159.

614   Willi, J. C. et al. 2005. The Modification of Ancient Woodland Ground Flora at Arable Edges.

615   Biodivers. Conserv. 14: 3215–3233.

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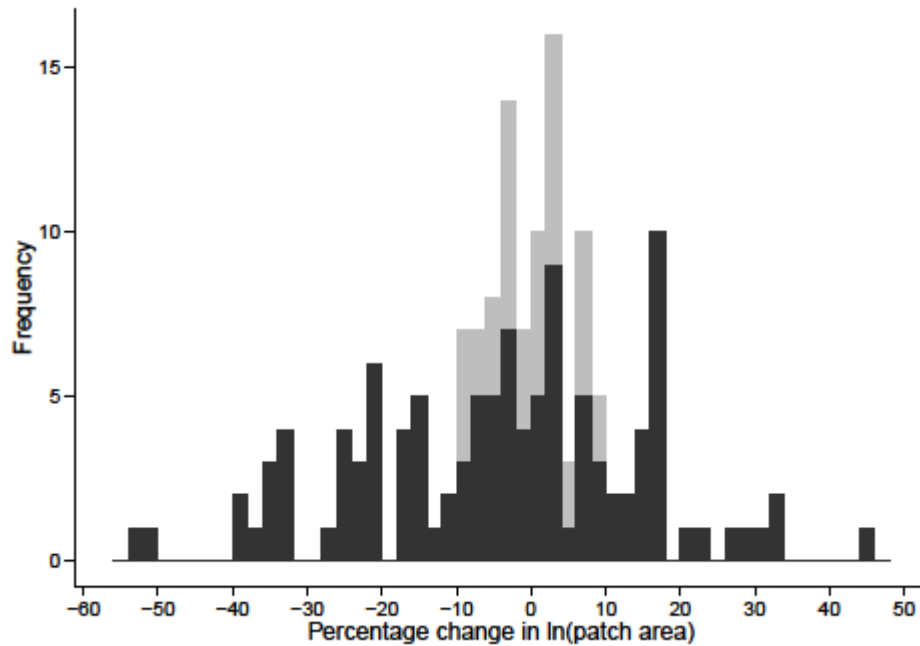
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632 **Supplementary Materials**

633 **Appendix 1: Histograms showing the amount of change in each spatial variable for forests**

634 **patches.**

635

636 **Figure A1: Histograms showing the amount of change observed for three aspects of forest**

637 **spatial configuration between 1899 and 2007 in forest patches over 100 years in age across**

638 **Great Britain, around 151 vegetation sampling plots. Grey area shows the data removed**

639 **prior to modelling.**

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644 **Appendix 2: Effect sizes and 95% confidence intervals for explanatory variables in models**

645 **of mean trait values and species richness.**

646 Table A2: Effect sizes and 95% confidence intervals for explanatory variables in patch area

647 models for different traits
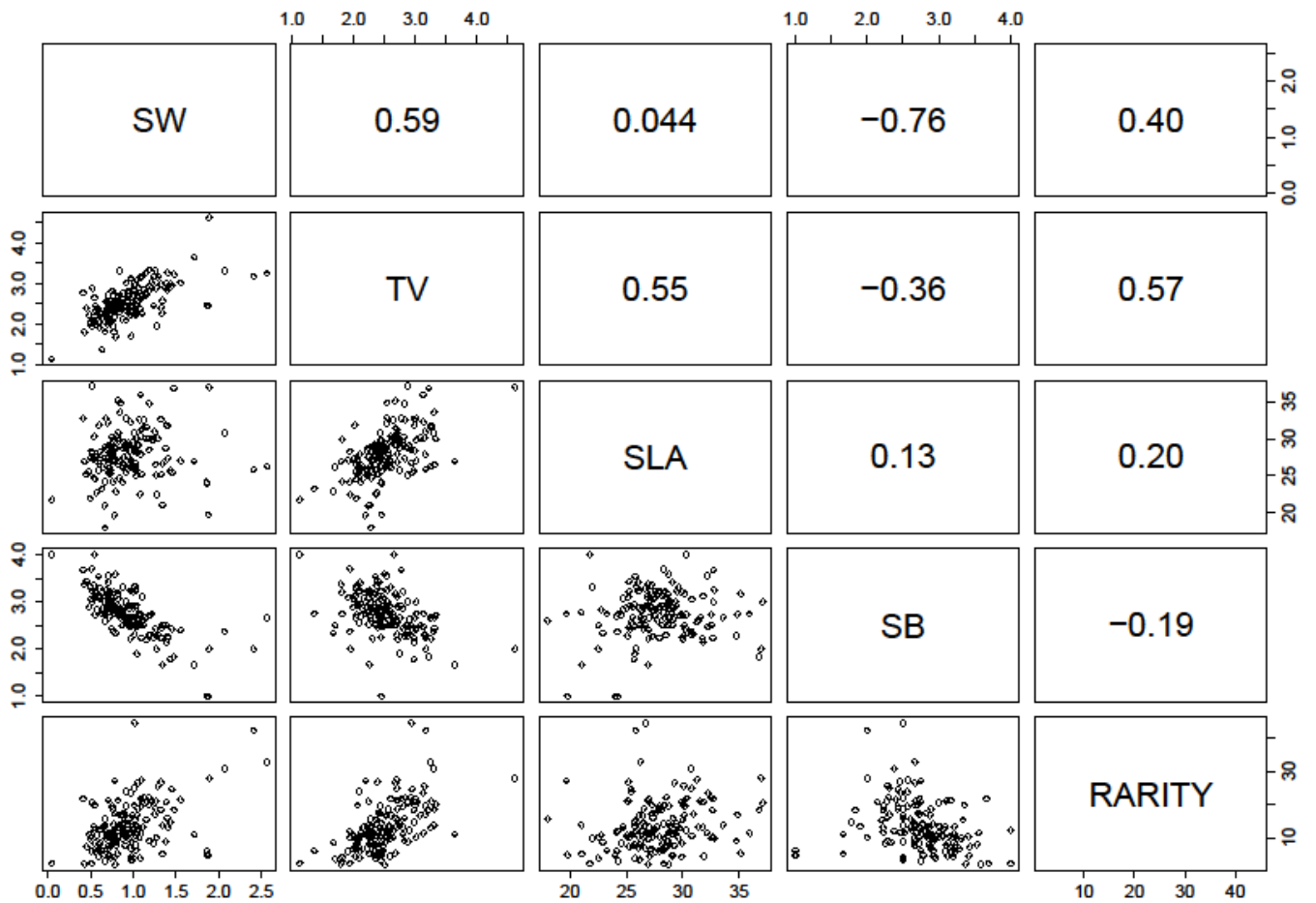
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Appendix 3: Pairs plot displaying correlations between mean trait values within 151 vegetation sampling plots.

658   **Figure A5: Pairs plot displaying correlations between mean trait values within vegetation**

659   **sampling plots.**

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