Kimberley, Adam; Blackburn, G. Alan; Whyatt, J. Duncan; Smart, Simon M. 2016. **How well is current plant trait composition predicted by modern and historical forest spatial configuration?** *Ecography*, 39 (1). 67-76. 10.1111/ecog.01607

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 species whose extinction debt is still to be paid, and faster 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.

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.

Although the impact of forest area, configuration and history has been investigated in previous studies (Dupré & Ehrlén, 2002, Lindborg et al, 2012), relatively little work has directly focussed on quantifying the extent of lag effects in forest habitat and determining whether they differ between plant traits in a predictable manner. Here, we combine a national scale dataset of plant species occurrence in forest patches with past and present forest extent data. We then used these data to investigate the degree to which current plant community composition is explained by historical rather than modern forest patch area.

Extinction debts are associated with species with low rates of population turnover such as those with long life spans or the ability to persist within the seedbank. Such species may remain as remnant populations for some time following unfavourable landscape change, even when their eventual local extinction is likely (Eriksson 1996, Lindborg 2007, Vellend et al. 2006). Forest habitat which has reduced in size may therefore still retain a disproportionate number of the rare, forest specialist species that survived in previously larger forest patches (Vellend et al, 2006, Kimberley et al, 2014). Conversely, immigration credits result from the slow colonisation of new forest area by poorly dispersing species (Verheyen et al. 2003, Jackson and Sax 2010). Forest patches which have been recently established or which have seen an increase in the amount of forest habitat may therefore still be dominated by better dispersing species; those with low seed weight and seed terminal velocity or seeds which persist within the seed bank, in the absence of forest specialist plants (Kimberley et al. 2014). Over time as the immigration credit is paid many of these forest specialists are likely to arrive, although the rate at which this occurs depends upon proximity to source populations and the permeability of the intervening habitat matrix (Peterken 2000, Brunet et al. 2011).

Where extinction debts and immigration credits exist in forest patches, the proportion of species with linked traits such as high seed weight and terminal velocity and high seedbank persistence are likely to lag behind landscape change. Combinations of life history characteristics such as high seed terminal velocity and high specific leaf area are also known to differentiate slow-dispersing, shade tolerant specialists largely restricted to long-continuity, ancient woodland from forest plants that are more readily dispersed and more typical of secondary forest (Kimberley et al. 2013). Such species are also more likely to be rare. Thus ancient forest species tend to be stress tolerant and poor colonisers of new habitat (Hermy et al. 1999) and therefore may be more prone to lag behind changes in forest configuration. Since lag effects in forest plants are long lasting and have been observed more than a century after forest fragmentation (Vellend et al. 2006), we hypothesised that present day forest community mean values for these traits would be better explained by historical rather than modern forest patch area in patches which have undergone area change. In addition to the trait-based approach, the relationships between both total species richness and ancient woodland specialist richness (based on the list of ancient woodland indicators in Kirby (2006)) and modern forest spatial configuration were also analysed in order to determine whether species-based patterns could be discerned alongside trait-based relationships with historical change in landscape structure.

In summary the following hypotheses were tested:

1. Plant community traits are better predicted by historical patch area than by modern patch area within forest patches greater than 100 years old.

2. Traits associated with restriction to ancient forest habitat such as seed terminal velocity and seedbank persistence are likely to be those most strongly linked to historical forest patch area.
3. Richness of species restricted to ancient forest will be more closely related to historical forest patch area than overall species richness.

Methods

Survey data

Digitised First Edition Ordnance Survey County Series (OS) maps (dated between 1849 and 1899) and data from the Countryside Survey, a national ecological surveillance programme for Great Britain (Norton *et al.* 2012), were used to identify 82 patches of British broadleaved forest which were established prior to 1899 and that were still recorded as forest in 2007. Forest understory plant species occurrence data were then obtained for 151 vegetation sampling plots within these patches, assessed as part of Countryside Survey 2007. Two types of vegetation sampling plot were employed in the analysis; linear plots (10 m^2 in area), located parallel to forest streamsides and forest tracks, and area plots (200 m^2 in area), located within the wider areal extent of each patch but not sampling a linear feature.

Species and plant trait data

Plant community mean trait values for a number of life history characteristics were calculated for each plot by averaging the individual traits of all species present. These mean values were then used as response variables in subsequent modelling. Mean trait values were left un-weighted by species abundance. This allowed both subordinate and dominant species to be considered equally, thus avoiding the confounding effect of variation in cover due to local competitive sorting. Plant trait information was obtained from the Electronic

Comparative Plant Ecology database (Grime *et al.* 1995), the LEDA traitbase (Kleyer *et al.* 2008), The British Flora (Stace 1997) and PLANTATT (Hill et al. 2004). Species rarity was obtained from PLANTATT as the number of occurrences in British 10 km squares in the period 1987-1999.

Excluding trees and shrubs, 250 species occurred across the vegetation plots. Since trait data were not available for all traits for all species, an approach was taken to minimise this problem by estimating the missing values using a Bayesian hierarchical model written in WinBUGs (Lunn et al. 2000), following the approach of Thompson and McCarthy (2008) as applied in Kimberley et al. (2014). Imputing missing values in this manner is preferable to removing them entirely, since estimated values take into account both between and within family similarity among those species with known trait values. The five traits tested, along with the percentage of species with missing values were; log natural seed weight (17.6%), seed terminal velocity (29.6%), specific leaf area (5.2%), seedbank persistence (24.8%) and rarity (0.4%). Seedbank persistence was assessed on a four point scale (1 = Transient seed, 2 = Persistent until next growing season, 3 = Small concentrations of persistent seeds, 4 = Large year round bank of persistent seeds). In addition to the mean trait values, counts of both overall plant species richness and ancient woodland indicator species richness were also obtained, using the list of indicator species in Kirby (2006).

Spatial data

Patch area data for forest patches around each Countryside Survey vegetation plot were derived for two periods; modern (2007) and historical (pre 1899), by overlaying forest extent data onto the geo-referenced Countryside Survey plot data using GIS techniques (ESRI, 2011). Modern forest patch area data were extracted from the satellite derived Land Cover

Map 2007 (Morton et al. 2011) whilst historical patch area data were digitised from First Series OS maps. These modern and historical area data were then natural log transformed to reduce the skew in their distribution.

Local abiotic conditions

Local conditions within forests are also important determinants of community composition (Dupré and Ehrlén 2002, Kimberley et al. 2014). In order to obtain a more realistic estimate of the effects of modern and historical forest configuration on mean community trait values we included a number of abiotic variables measured at the same locations as the plant species composition. Shade was estimated on a three point scale for all vegetation plots and plots designated unshaded, partially shaded or fully shaded by field surveyors. Within each of the area plots (n = 46) soil pH and carbon to nitrogen ratio were measured based on a 15 cm topsoil sample taken at the same time as the flora was recorded in each plot. In the linear plots (n = 105) directly measured soil data were not available. Values within these plots were estimated using published equations derived from a national calibration of observed values of the two soil variables against the mean Ellenberg values of plants in 1033 plots from a stratified, random sample of the range of British vegetation types (Smart et al. 2010). The mean Ellenberg values used in these equations to generate soil variables were derived only from the trees and shrubs which were excluded from the calculation of mean trait values for the herbaceous understorey (the dependent variables in the present study). This may result in a less accurate estimate of soil conditions present in vegetation plots due to the lower sample size of woody species present, however the problem of circularity when the estimated soil variables were used to model mean trait values is avoided through this method. In order to account for differences in response between the area and linear plots, plot type was included as a categorical explanatory variable. Climate and residual geographic variation across Britain were accounted for by the inclusion of the northing of each sample plot as a continuous explanatory variable (Corney et al. 2006).

Modelling approach

In order to determine the extent to which modern mean community trait values are better predicted by modern or historical patch area data, the spatial data from the two time periods were combined into two new variables; one describing the mean patch area and the other the change in the patch area between the historical and modern period. The amount of change observed in patch area across forest patches is shown in Appendix 1 (Fig. A1). These variables were then used as explanatory variables in models of present day mean values of life history traits and species richness data within forest habitat. Since spatial data was replicated over time but only modern plant species data were available, this modelling approach allowed the effect of modern and historical forest spatial structure to be assessed in a single model for each response variable.

Results from the models can be interpreted as follows: the relationship between trait and mean patch area indicates whether the trait in question is significantly affected by forest patch area. In cases where a significant effect exists, the parameter estimate for the change in patch area versus modern trait relationship can then be used to indicate whether the trait is better modelled using the modern or historical spatial data. Where the relationship between mean patch area and trait is positive, a value for the change in area parameter of greater than zero will indicate a community that is better predicted by the modern spatial data. If the change in area parameter is negative, the results indicate present day trait data are more strongly correlated with historical patch area (this is reversed where the relationship between mean patch area and trait is negative). Where a significant effect of mean patch area is observed but the change in patch area regression coefficient is close to zero, the results indicate an intermediate community which is equally well explained by both modern and historical spatial data, suggesting an intermediate amount of lag. Since high, low and intermediate values for this metric all indicate important results, testing for a significant difference from zero is not appropriate for the change in patch area term. Confidence intervals are therefore not shown around results for this measure (Figures 3 and 4).

Both present and past spatial data would be expected to predict plant composition equally well where the plant composition is in an intermediate state, having moved away from the historic forest configuration following landscape change but not yet well predicted by current spatial data. However modern and historical patch area would also be expected to be equivalent in their ability to predict modern trait values where only small amounts of spatial change has occurred. In order to prevent any lag effects being obscured by a lack of change between time periods it was therefore important to ensure that the dataset was not dominated by patches which were stable in area between historical and modern data sources. To reduce this problem 40 plots, randomly selected from those present in patches which had undergone less than a 10% change in patch area, were removed from the dataset prior to the analysis. This provided a set of patches with an approximately even distribution of amount of change which could be used in subsequent modelling (Supplementary material Appendix 1, Fig. A1).

The analysis allowed the identification of traits which are similarly well predicted by both modern and historical patch area as well as permitting the amount of change between time periods to be taken into account in the analysis. Use of the mean patch area rather than the historical value avoids collinearity problems where historical patch area is correlated with the amount of change. Thus the two spatial variables used in the analysis were statistically independent.

The approach can be demonstrated using simulated examples. An artificial dataset was created with information on modern trait composition, modern patch area and historical patch area, where all patches had undergone a randomly allocated amount of change (either positive or negative). The data were constructed such that modern values for a hypothetical life history trait were strongly correlated with historical patch area but had no relationship with a modern patch area (Figure 1a, b). Figure 1 shows the result of fitting the mean patch area (Figure 1c) and change in patch area (Figure 1d) terms against the trait values. The trait values which were associated with spatial variable values in the historical data have not changed despite these patches having undergone change. Thus the patch area has changed – high becoming low and low becoming high – but the trait values have not (Fig 1a). In such a situation a relationship between trait and mean spatial variable is observed (Figure 1c), and necessarily results in a strong negative correlation between change in the spatial variable and the modern trait variable (Fig 1d), from which the stronger relationship between trait and historical patch area can be inferred. If the historical patch area versus trait relationship had been negative then this effect would have resulted in a positive slope in Fig 1d.

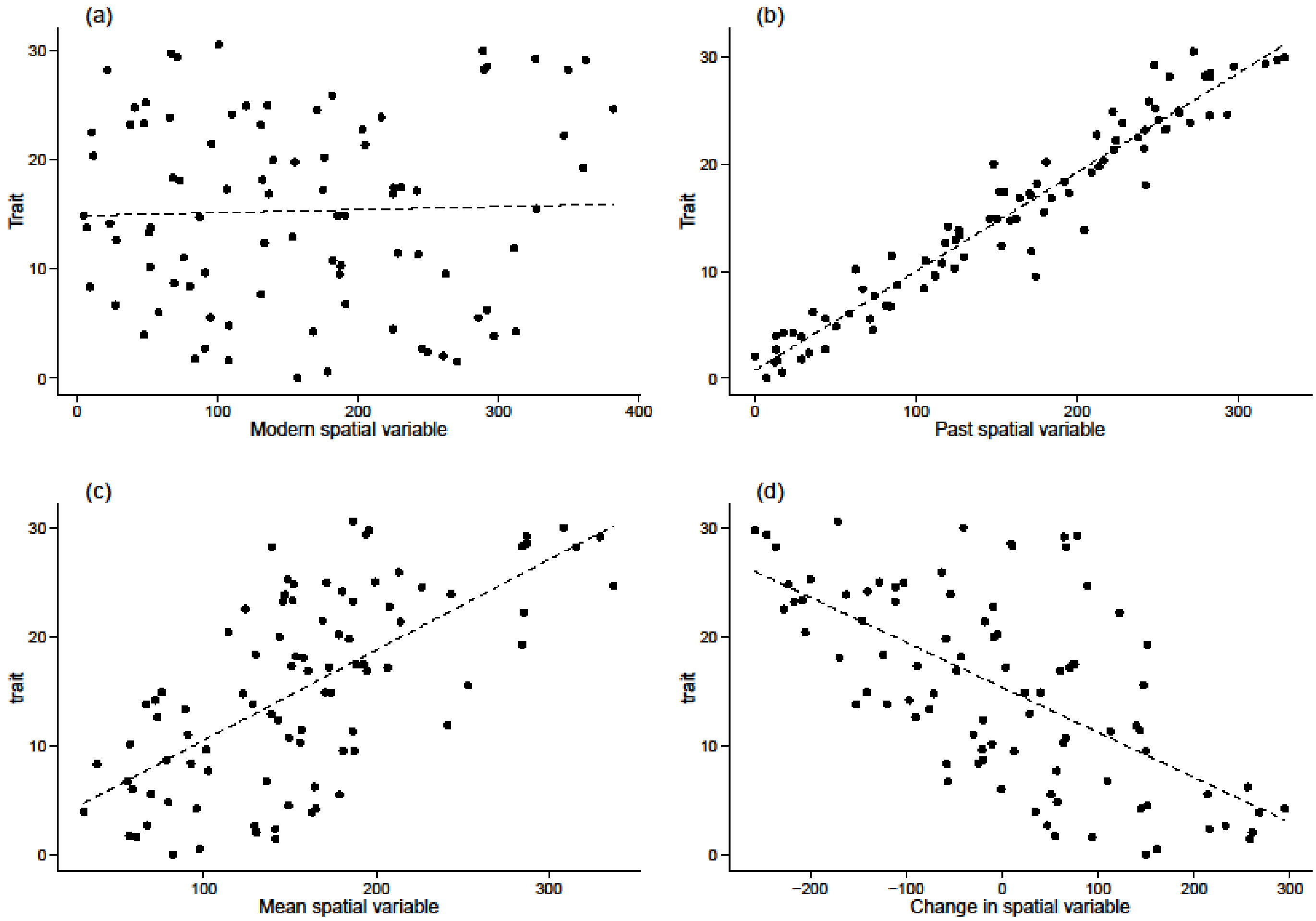

Figure 1. Simulated data showing the relationships between hypothetical mean trait values and (a) a modern spatial variable, (b) a historical spatial variable, (c) mean across modern and historical spatial variables and (d) change between modern and historical spatial variables, where trait data is best 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 modern patch area is revealed by the positive relationship between trait and change in patch area (Figure 2d).

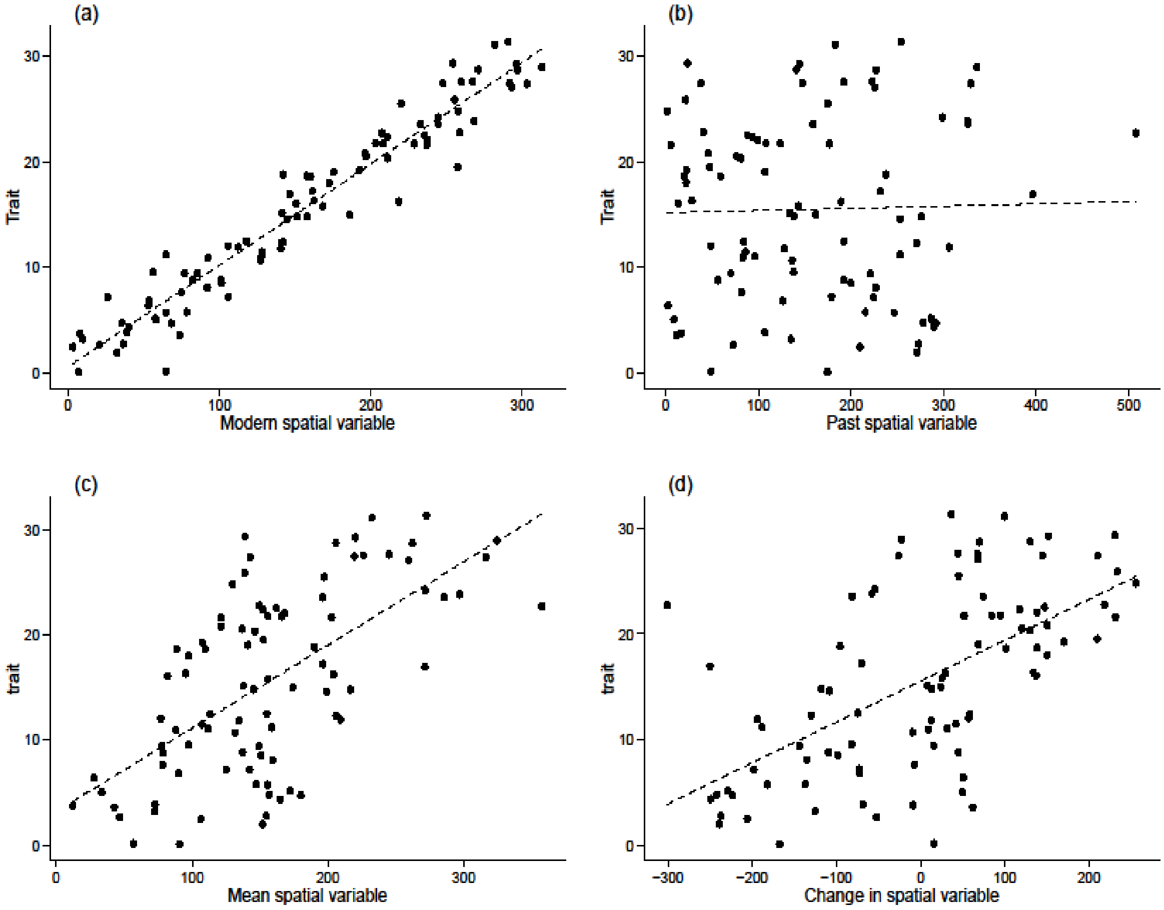

Figure 2. Simulated data showing the relationships between hypothetical mean trait values and (a) a modern spatial variable, (b) a historical spatial variable, (c) mean across modern and historical spatial variables and (d) change between modern and historical spatial variables, where trait data is best explained by modern spatial conditions. Dashed lines show linear models between trait and each individual explanatory variable.

The modelling approach demonstrated in the simulated examples was applied to the real data for the 111 vegetation sampling plots used. A single model was fitted for each mean plant trait, along with species richness and ancient woodland indicator richness. These models contained the mean patch area, the change in patch area and the interaction between these two variables, in addition to all local condition variables described above. The interaction term was included in each model to investigate whether patches with varying mean area differ in the extent to which modern spatial data can be used to predict trait composition. A mixed-effects modelling approach was taken, including site (Countryside Survey 1 km square) as a random intercept, using the package lme4 in the statistical software R. This accounted for the spatial autocorrelation introduced by analysing a number of vegetation sampling plots located within the same Countryside Survey sample square. Mean trait values were modelled by linear mixed effects models while generalised linear mixed effects models with a Poisson error distribution were used for species richness and ancient woodland indicator richness models, to account for the count data response. All models were scaled and centred using the R package arm, to produce comparable regression coefficients. These allowed an estimate of the effect sizes of each spatial variable on each plant trait to be made. 95% confidence intervals around these effect sizes were calculated using the bootstrap method in lme4. For linear models response values were also treated in this way to produce standardised effect sizes bounded by ±1. For models of count data this was not possible due to the link function used in the generalised linear models. Parameter estimates from the different model types are therefore not directly comparable. The resulting effect sizes and confidence intervals allowed the extent to which present day mean values for different life history traits are better predicted by modern or historical forest spatial configuration to be assessed.

A number of significant effects of the abiotic variables, northing and plot type were detected, discussion of which is beyond the scope of this article. Here we focus on partial spatial relationships with trait composition having accounted for variation explained by local environmental conditions. Full modelling results are however shown in Appendix 2 (Appendix 2, Table A2).

Results

Trait data

Mean patch area was a significant predictor for three of the five community mean response variables tested; seedbank persistence, seed terminal velocity and species rarity (Figure 3). Rarer species with faster falling seeds and less persistent seedbanks were found in patches with a high average area across the two time periods, suggesting that forest configuration has an important effect on the occurrence of species with these traits. The lag metric was close to zero for both seed terminal velocity and rarity (change in area term, Figure 3a,b), suggesting that both modern and historical patch area explain these traits equally well, despite the gradient of change in patch area present across the sampled woodlands. This must therefore mean that communities have not remained static and hence stayed correlated with historic patch configuration, but neither have they completely readjusted to the modern patch configuration. The lag metric for seedbank persistence however was less than zero (Figure 3e). Given the negative relationship between mean patch area and this trait this indicates that mean seedbank persistence values were better predicted by the modern patch area than the historical.

The interaction between mean patch area and change in patch area had a significant negative effect on mean seed bank persistence values (Figure 3e). As mean patch area increases, the negative relationship between trait and change in area becomes stronger. This suggests that mean seedbank persistence was better predicted by modern patch area in forest patches with a larger mean area across the two time periods than in patches with a smaller mean area.

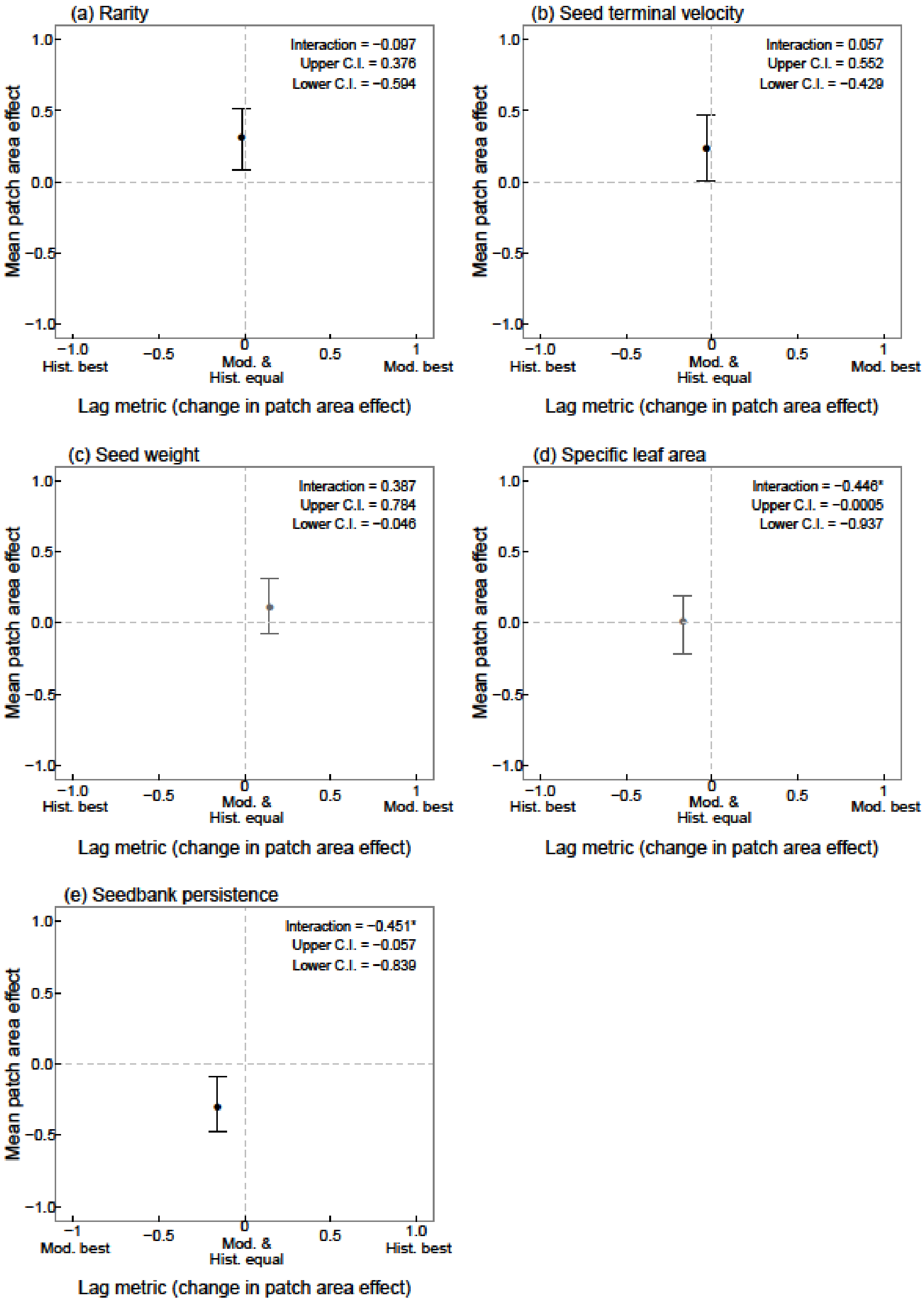

Figure 3. Standardised effect sizes quantifying the influence of patch area in models of five mean trait values in forest vegetation sampling plots. Error bars represent 95% confidence intervals. Where displayed confidence intervals do not overlap 0 a significant effect of patch area is indicated. The 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.

Species data

Mean patch area had a significant effect on ancient woodland indicator 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 ancient woodland indicator richness, indicating that the number of ancient forest specialists is slightly better predicted by historical patch area than modern.

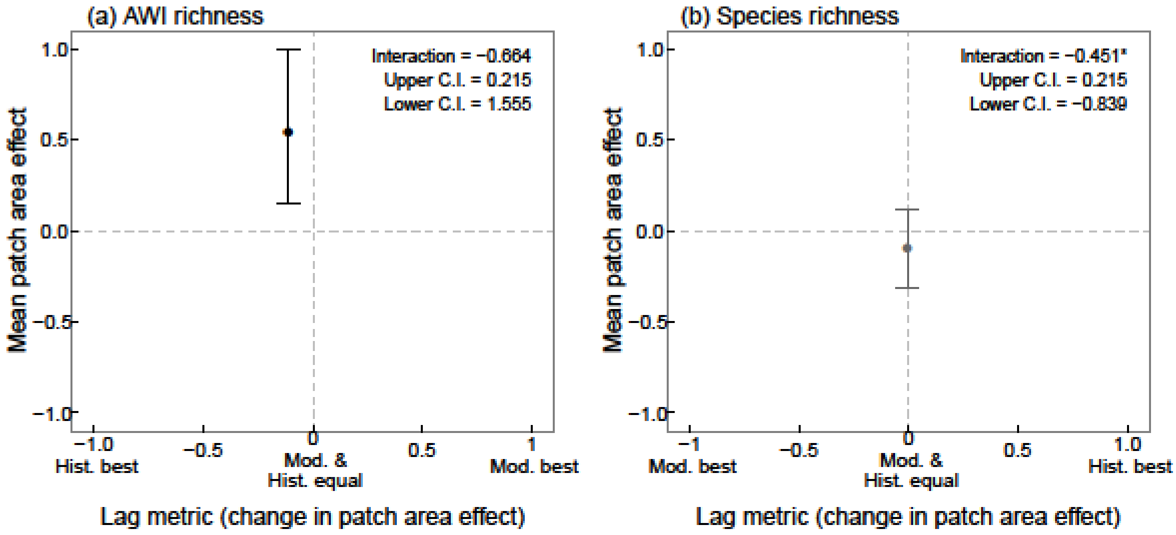

Figure 4. Standardised parameter estimates quantifying the influence of patch area in models of overall species richness and ancient woodland indicator (AWI) richness in forest vegetation sampling plots. Error bars represent 95% confidence intervals. Where displayed confidence intervals do not overlap 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.

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 characteristics. This supports previous studies which have found that plant communities take time to respond following landscape change (Lindborg and Eriksson 2004, Metzger et al. 2009, Saar et al. 2012). Rare species and those with heavy, fast falling seeds are likely to be less able to disperse effectively and rescue threatened populations through immigration (Kolb & Diekmann, 2005). Many such species are therefore unlikely to be able to persist long-term following the loss of forest patch area. Since many rare, forest specialist plants are perennial species however (Kimberley et al, 2013), they may survive in remnant populations for some time following landscape change (Eriksson, 1996). The slow loss of species with these characteristics may explain why mean seed terminal velocity and rarity were equally well predicted by modern and historical patch area. This is further evidenced by the fact that ancient woodland indicator richness within forest patches was more closely related to historical patch area than modern. Hence there is likely to be a disproportionate drop in the occurrence of these vulnerable plant species in the future as existing extinction debts are paid in patches which have decreased in area. In many cases these species are also likely to be slow to colonise forest patches which have increased in size, particularly in isolated patches (Brunet, 2011). Hence maintaining large areas of older forest is important to avoid the loss of populations of rare or poorly dispersing ancient woodland specialist plants (Kimberley *et al.* 2013).

Although existing time lags are likely to lead to ongoing change in forest community composition, if the amount of change in forest extent between time periods is small the degree of future change in plant composition is also likely to be limited, even where this change takes some time to occur. It is therefore also important to consider the amount of change which occurred between time periods when interpreting these results. It is likely that a large alteration in patch size is needed to produce a significant, long lasting time lag. Here only a weak lag was identified for mean rarity and seed terminal velocity, possibly due to a modest amount of change between historical and modern patch area for many patches. Further application of this method to forests which have undergone more substantial or very recent changes in area may reveal whether this is indeed the case. If so, the greatest benefit of increasing forest patch area may be seen in patches which have recently undergone a large reduction in area. The time lag identified here for rarity and seed terminal velocity may also be weak due to the difference in species richness and composition between area and linear plots used in this analysis. If linear plots contain a higher proportion of ruderal species with characteristics consistent with a more rapid response to landscape change, communities are likely to be closer to those predicted by modern forest patch area.

The variation in the degree to which modern or historical forest patch area best explains mean trait values suggests that different species are responsible for each individual trait relationship. For a species to persist but be bound for extinction it requires both strong ability to persist and weak dispersal capability. Any lag observed in patches which have lost area may be due to forest specialist species which have a particular combination of established phase traits (slow, shade-tolerant vegetative growth) and regenerative traits (poor dispersal) and therefore have the potential to persist for some time after landscape change (Saar et al, 2012, Kimberley et al, 2013). Forest specialist species without this trait combination are likely to be lost relatively quickly from fragmented patches while species with these characteristics remain until they are either out-competed by more ruderal immigrants or otherwise suffer mortality from disturbance, herbivory or disease (Grime, 2001, Jackson & Sax 2010). On the other hand immigrant species must be both rapidly dispersed and shade-tolerant slow growers to truly survive in undisturbed forest understorey. For example ruderal species with high investment in many small seeds with low terminal velocity, high relative growth rates and high seedbank persistence can respond more rapidly to landscape change, quickly colonising new forest edges, new small areas of secondary woodland including previously larger patches which have lost forest area (Tabarelli et al. 1999).

What we see integrated into the mean trait values is likely to be the trait-controlled sum of the dynamics of fast-responding species more rapidly dispersed in time (through persistent seedbanks) and space (through light, slower falling seeds) arriving at different rates from surrounding habitats, coexisting with extinction debt species that are better fitted to historical spatial configurations and hence are likely to decline further. These two processes may occur at different rates however, with extinction debts in forest understorey plants being paid sooner (after around 160 years) (Kolk & Naaf, 2015) than immigration credits (which can remain for much longer) (Naaf & Kolk, 2015). If extinction debts in forest patches which have lost area have largely been paid in this analysis, this may partly explain why only weak lags were identified here for mean seed terminal velocity and rarity.

Mean seedbank persistence values lag less behind changes in patch area than mean seed terminal velocity and rarity, particularly in large forest patches. High seedbank persistence allows species to regenerate vulnerable or locally extinct populations from the soil seedbank. The absence of such persistent species in larger forest patches (Kimberley et al, 2014) may result in a community which is faster to respond to changing patch area because more species present in the vegetation possess no persistent seedbank. Such species are likely to be quickly lost when habitat area is reduced. The species present above-ground are also often poorly correlated with the species present in the seedbank (Bossuyt et al. 2002). Many species present in forest seedbanks may therefore be rapidly growing species and widely dispersed which are absent from the above-ground vegetation but likely to appear and thrive following disturbance to the soil or canopy (Bossuyt et al. 2002). When forest patches lose area or are newly disturbed they may swiftly gain these ruderal species from the existing seedbank, reducing the lag for this trait (Smart et al 2014). In smaller patches this effect may be weaker due to a higher original proportion of species with a persistent seedbank (Kimberley et al, 2014). This suggests that large patches are likely to be quickest to pay their extinction debts when they are reduced in size and further confirms the fact that species which are particularly dependent on large, core areas of habitat may be first to become extinct following the loss and fragmentation of forest habitat. The creation of small patches of new forest is therefore likely to be of less benefit than extending existing forest habitat (Peterken 2000).

One limitation of analysing the data in this way is that there is no way of knowing when changes in spatial properties between the two time periods have occurred. Interpretation of the results must therefore be done with care, since modern forest configuration would be expected to have a stronger effect than historical if most of the spatial change was longer ago. The large number of data points from across a wide geographic area used here however ensured that a realistic assessment of current patterns in British forests could be made. Furthermore, because the same forest habitats were analysed for all traits tested, comparisons of the relative strength with which modern forest configuration affects different mean trait values are still valid. Mean trait values were analysed separately to allow differences in the response of traits to important variables to be detected. As such however, the inter-correlation between pairs of traits must be taken into account. For example, part of the observed effect of patch area on seedbank persistence may be due to the close relationship between this trait and seed mass (Westoby et al. 2002). Correlations between mean trait values are shown in Appendix 3 (Appendix 3, Fig. A5).

Although only forest patch area was tested here, this variable is often correlated with a number of other forest configuration variables such as the amount of forest present in the landscape or the amount of core forest habitat (Fahrig, 2003). In reality, time lags in forest habitat are likely to depend on interactions between the size of patches, the amount of nearby forest (particularly that of long continuity) and the amount of edge habitat present. For example, newly created forest patches within a short distance of ancient forest habitat have been shown to accumulate forest specialist species more quickly (Brunet *et al.* 2011), while young forest patches which are highly isolated from ancient forest habitat mostly accumulate species adapted for effective dispersal which tend not to be ancient woodland specialists (Brunet 2007). Hedges and other semi-natural habitat types also have some ability to act as a refuge for forest specialist species (McCollin et al. 2000, Smart et al. 2001), potentially enabling such species to persist for longer, and therefore exhibit a stronger lag effect, in landscapes where such features are common. The landscape context of changing forest habitat is therefore also likely to be an important determinant of the extent to which time lags develop. High intensity agriculture in neighbouring land use has been shown to reduce the ability of forest specialist species to exist near forest edge habitat (Chabrerie et al. 2013). Where forest patches are surrounded by intensive agricultural land, forest edge is likely to be quickly colonised and dominated by weedy generalist species with higher seedbank persistence (Willi et al. 2005). Where forest edge is buffered by less intensive land uses however, stronger lags may be occurring as forest specialist species take longer to be out-competed by immigrants. Hence, some forest specialist species may still be able to persist even in small patches or at forest edges, so long as they are already established before fragmentation and that the forest patch is appropriately surrounded by non-intensive land. Buffering forest habitat with less intensive habitat types and linear refuges may therefore allow many vulnerable forest species to persist following landscape change, but this issue requires further research.

In future, as existing immigration credits and extinction debts are paid, forest species composition is likely to shift towards present day patterns of habitat configuration, with fragmented forest likely to lose shade tolerant, poor dispersers and gain populations of immigrant species. Likewise forest patches which are increasing in size will begin to recruit suitable populations of forest plants and lose species more fitted to smaller patches with a high edge to area ratio. The fact that mean rarity and seed terminal velocity were equally strongly affected by modern and historical forest configuration in long established British forest patches highlights the importance of accounting for historical forest spatial configuration when modelling patterns of plant species occurrence (Ewers et al. 2013). Failure to do so risks both underestimating the strength with which forest configuration affects species and failing to identify species which are at risk of local extinction (Helm et al. 2006). However extinction debts in particular do present an opportunity to initiate measures to prevent the loss of threatened species (Kuussaari *et al.* 2009) and the time lag identified here for rare species and inefficient dispersers suggests that many vulnerable species could benefit from well targeted management action.

Acknowledgements

This research was funded through a NERC algorithm studentship to A.K., project code NEC03454. Ordnance Survey County Series maps (1st Edition: 1849-1899) were obtained from the EDINA Historic Digimap Service, http://edina.ac.uk/digimap, Landmark Information Group, UK.

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Supplementary Materials

Appendix 1: Histograms showing the amount of change in each spatial variable for forests patches.

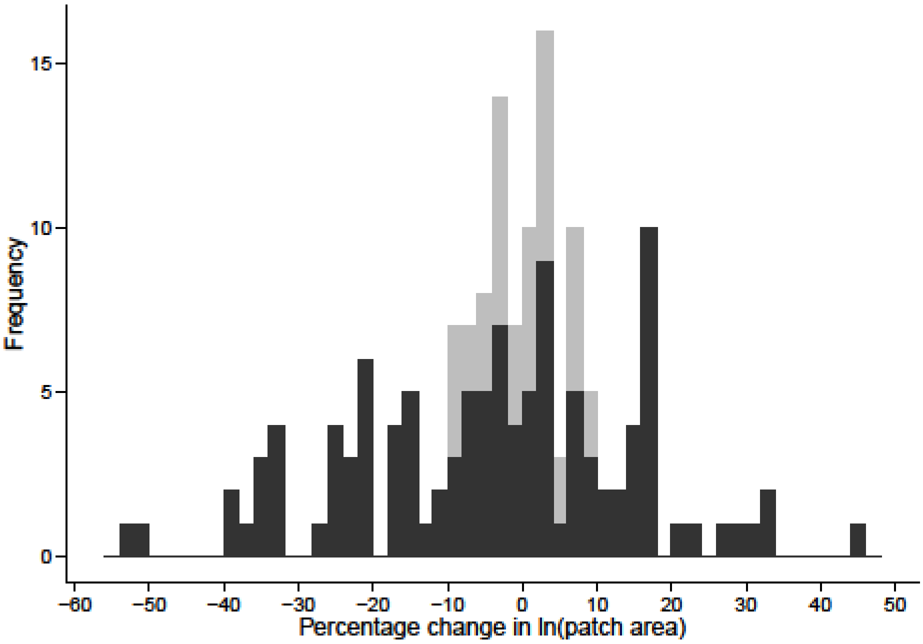

Figure A1: Histograms showing the amount of change observed for three aspects of forest spatial configuration between 1899 and 2007 in forest patches over 100 years in age across Great Britain, around 151 vegetation sampling plots. Grey area shows the data removed prior to modelling.

Appendix 2: Effect sizes and 95% confidence intervals for explanatory variables in models of mean trait values and species richness.

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

Appendix 3: Pairs plot displaying correlations between mean trait values within 151 vegetation sampling plots.

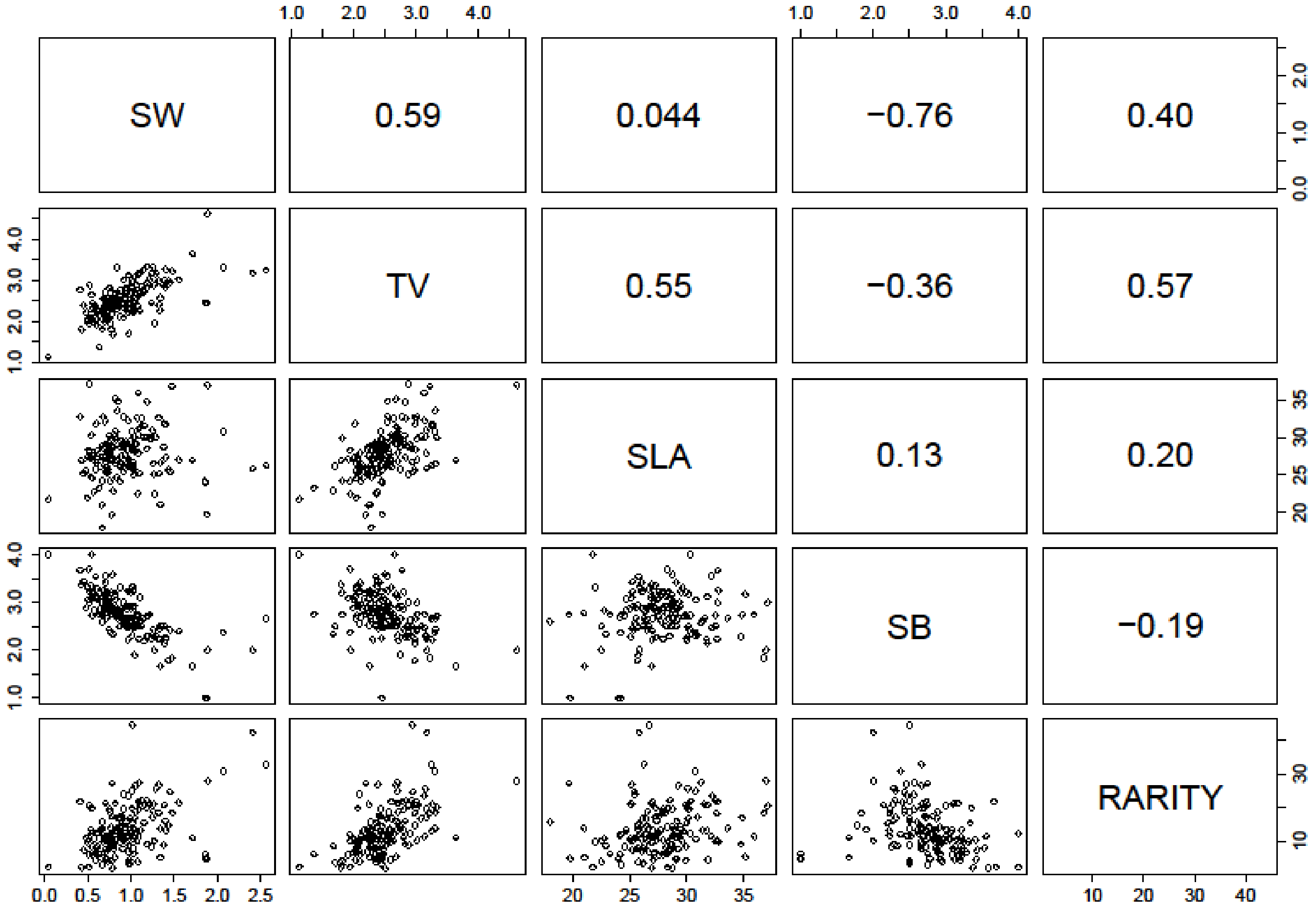

Figure A3: Pairs plot displaying correlations between mean trait values within vegetation sampling plots.