Traits of plant communities in fragmented forests: The relative influence of habitat spatial configuration and local abiotic conditions.

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Running headline: Traits of plant communities in fragmented forests

Summary

1. The plant trait composition of forest fragments is thought to be partly determined by forest spatial properties, although the relative importance of habitat configuration and local abiotic drivers is poorly understood.
2. To address this issue, large-scale habitat extent data were combined with detailed field survey information for temperate broad-leaved deciduous forest patches to quantify the relative effects of spatial and abiotic filters on plant community mean trait values.
3. Local conditions such as shade and soil fertility had the largest effect on mean trait values, but aspects of habitat configuration also had significant partial effects on a number of traits.

4. Mean trait values within older forest patches were more strongly influenced by forest spatial configuration than in younger patches.
5. *Synthesis.* Results suggest that, in addition to the effects of greater light availability and competition in small patches and at forest edges, aspects of habitat configuration such as patch size and isolation are themselves important factors limiting the occurrence of forest specialist species. Large areas of core forest habitat contain a greater proportion of rare, poor dispersing species, although these effects were less visible in more recently established forest. This highlights the importance of maintaining existing large and old forest patches as a refuge for forest specialist plants. The results of this comparison of spatial and abiotic variables suggest that controlling the spatial properties of forest patches is likely to prove an effective way of managing plant species diversity, provided that sites with appropriate abiotic conditions are chosen.

Key-words: dispersal traits, environmental conditions, forest age, forest conservation, habitat fragmentation, patch area, rarity, seedbank persistence, specific leaf area.

Introduction

Forests, particularly those of long continuity, are a conservation priority in many areas due to their potential to act as a refuge for rare or threatened species (Peterken & Game, 1984; Wulf, 1997). An assessment of the way in which the spatial configuration of these habitats affects species with different life history traits is therefore essential to allow accurate modelling of the impacts of ongoing landscape change on forest specialist plants. Urbanisation and agricultural intensification have dramatically changed landscapes worldwide, causing the fragmentation and loss of many habitat types (Foley *et al.* 2005). In a fragmented landscape, habitat availability is reduced for target organisms, with favourable patches generally smaller and less well connected. Consequently the populations of species which are dependent on this habitat may be smaller and at greater risk of localised extinction (Fischer & Lindenmayer, 2007). Here, the effects of a number of variables describing forest configuration, condition and history upon plant community mean trait values were investigated. The aim was to quantify the partial covariance between mean trait values and forest spatial configuration given variation in patch age, soil quality and levels of shade, thus allowing the strength of the effects of both spatial properties and local abiotic conditions on mean trait values within forest patches to be compared.

Although species with particular life history traits exhibit a negative response to habitat loss and fragmentation, the occurrence of most plant species is dependent upon habitat quality rather than habitat configuration (Dupré & Ehrlén, 2002). Direct filters such as substrate pH, soil moisture and macronutrient availability within forests are strongly related to plant species occurrence (Critchley et al. 2002; Corney et al. 2006; Smart et al. 2010) and as such may be the biggest drivers of mean trait values. Light availability at ground level is also important, since a number of forest specialists possess traits such as high specific leaf area and small stature which make them well adapted to low light conditions (Hermy et al. 1999). It was therefore hypothesised that mean trait values in this study would be more strongly affected by local abiotic condition variables than forest spatial configuration.

Species that are most vulnerable to the effects of landscape fragmentation and habitat loss tend to be those that have characteristics that do not favour effective dispersal in space or time (Henle et al. 2004; Kolb & Diekmann, 2005; Ockinger et al. 2010). Species with fast falling seeds and no persistent seedbank are generally less able to rescue threatened populations through immigration from nearby patches (Jacquemyn et al. 2003; Ozinga et al. 2009; Schleicher et al. 2011; Jacquemyn et al. 2012). Dispersal method is also important, with abiotically dispersed species more prone to extinction in fragmented landscapes than those which are capable of dispersing via animal vectors (Marini et al. 2012). Consequently species possessing traits such as these occur less frequently in small, isolated habitat patches, which become dominated by a higher proportion of more persistent, longer lived and better dispersed species (Kolb and Diekmann 2005; Lindborg, 2007). Factors such as patch area and the amount of forest habitat in the surrounding landscape should therefore be important determinants of mean trait values within forest patches, as should distance to the nearest forest edge, since species dependent upon the interior of forest patches tend to possess traits linked to higher shade tolerance and lower dispersal capability (Hermy et al. 1999, Pellissier et al. 2013). The presence of lag effects, which result in a lack of coupling between contemporary habitat structure and species composition (Lindborg & Eriksson, 2001; Purschke et al. 2012) may however reduce the strength of this association.

Human activity has long lasting effects on abiotic conditions and therefore on patterns of species richness and composition within secondary forests (Dupouey et al. 2002; Vellend et al, 2007). As such, mean trait values within more recently established forest patches are likely to be more strongly determined by these historical environmental effects than by forest configuration, particularly where sited on former agricultural land with conditions which are unfavourable to many forest specialist species (Dupouey et al. 2002). Conversely, older patches are likely to contain a greater proportion of ancient woodland indicator species, characterised by poor competitive and colonising ability (Verheyen et al. 2003; Kimberley et al. 2013); traits which are likely to make them more vulnerable to habitat loss and fragmentation. These species should be more frequent in large patches or far from the edges of forests, but mainly in the long-established habitat in which they almost exclusively exist due to time lags caused by the slow colonisation of younger forests by ancient woodland specialists (Jacquemyn et al. 2003). For these reasons, trait values in older forests should be more dependent on habitat configuration than those in younger forests.

In summary the following hypotheses were tested;

1. Variation in abiotic conditions exerts a stronger selective filter on mean trait values than forest spatial configuration and age.
2. Relationships between forest spatial configuration, patch age and mean plant trait values in British forest patches are still detectable having accounted for variation in abiotic conditions.
3. The spatial properties of older forest patches have a stronger effect on mean trait values than those of younger patches.

Materials and methods

Plant trait data

Plant species occurrence data were collected in 406 randomly stratified sampling plots located in broadleaved deciduous forest habitat within 1 km^2 regions across Great Britain as part of the 2007 Countryside Survey (Norton et al. 2012). Mean values for a number of life history traits within each of these plots were then obtained by averaging available trait data across species present. The mean trait values obtained were then used as response variables in the subsequent modelling. To allow the amount of shade present to be included as an explanatory variable without introducing circularity to the analysis, trees and shrubs were excluded from this process. Mean trait values were left un-weighted by species' abundance. This approach places each species, whether subordinate or dominant, on an equal footing and avoids confounding the results by introducing the influence of variation in cover as a result of 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), Stace (1997) and PLANTATT (Hill, Preston & Roy, 2004). Species' rarity was obtained from PLANTATT (Hill, Preston & Roy, 2004) as the number of occurrences in British 10 km squares in the period 1987-1999.

In total, 445 species were present across the vegetation sampling plots. The difficulties in obtaining trait data for so many species meant that data were not available for all traits for all species. The five traits tested, along with the percentage of species with missing values were; log natural seed weight (23.4%), seed terminal velocity, (35.5%), specific leaf area (10.3%), seedbank persistence (39.6%) and rarity (0.9%). Following the Bayesian approach of Thompson & McCarthy (2008), missing trait values for species were drawn randomly from a posterior statistical distribution of trait values which was created based upon the distribution of known values for other species within the same genus and family, using a hierarchical model written in WinBUGS (Lunn et al. 2000). This approach is superior to simply imputing mean values since missing values were estimated taking into account all available information for related species.

Local conditions

The approach taken was to include measurement of influential abiotic conditions in the analysis but to treat them as "nuisance" covariates whose effects would be removed prior to estimating the magnitude of the effect of forest spatial configuration on mean trait values. By including both the spatial characteristics of forest patches and data on local conditions in the same analysis it was possible to evaluate the relative importance of these different sets of variables in determining the mean trait values within forest habitat.

Two types of Countryside Survey 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. 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 = 87) soil pH, volumetric soil moisture content 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 = 319) 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 three 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, thus avoiding the problem of circularity when the estimated soil variables were used to model mean trait values. 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).

Spatial woodland variables & Patch age

To determine the configuration of forest patches around vegetation samples, the geo-referenced Countryside Survey plot data was overlain with forest extent data obtained from Land Cover Map (LCM) 2007 using ArcMap 10.0 software (ESRI, 2011). LCM 2007 is a satellite-derived dataset containing information on the spatial extent of various habitat types across Great Britain (Morton et al. 2011). Use of this data set enabled the spatial configuration of broadleaved forest patches in the wider landscape around vegetation plots to be assessed.

Figure 1 illustrates the spatial variables obtained from the various data sources for an example Countryside Survey vegetation plot. These were “patch area” (the area of the forest patch containing the vegetation sampling plot), “distance to edge” (the Euclidean distance between each vegetation plot and the nearest point of forest edge) and “buffer forest” (the percentage of forest habitat within a 1 km buffer area around the vegetation plot). To reflect the fact that the majority of plant species have maximum dispersal distances of less than 1 km (Thompson et al. 2011), only forest habitat within 1 km of vegetation sampling plots was considered. Forest area further than this was therefore assumed to be too far away from vegetation plots to have a significant impact on trait values and therefore not included in this statistic, even where contiguous with patches within the 1 km area. Patch area and distance to edge were both natural log transformed prior to inclusion within the modelling, to reduce the positive skew in their distributions.

Finally, the age of forest patches was estimated using First Edition Ordnance Survey maps (County Series) dated from 1849 to 1899. Presence or absence of woodland patches on these historical maps was used to divide present day woodland patches into either younger woodland (established after 1899, n = 255) or older woodland patches (established before 1899, n = 151).

Statistical modelling

Mean trait values within forest patches were modelled using the various local conditions and forest spatial properties described earlier. For each trait a full linear mixed effects model, containing all of the spatial and abiotic explanatory variables, was built. Interactions between forest age and patch area, buffer woodland and distance to edge were also included and all models were fitted using the Countryside Survey 1 km square identifier as a random intercept. This accounted for spatial autocorrelation caused by the presence of multiple plots within the same 1 km sampling region.

The R package MuMIn (Barton, 2012) was then used to fit all subsets nested within the full model described above. Models were standardised following the procedure of Grueber et al. (2011), in order to provide effect sizes on a comparable scale. To avoid bias resulting from the low ratio of observations to parameters, models were compared using an adjusted Akaike information criterion (AICc) statistic, as recommended by Burnham and Anderson (2002). AICc is a measure of model performance which compares the maximum likelihood estimate of models, adjusted for increasing model complexity. The model with the lowest AICc value is considered the best performing model (of the set tested). All models with AICc values within 4 of the lowest value were then selected as a “confidence set”, thus including possible models possessing a considerable level of empirical support (Burnham and Anderson, 2002). These confidence sets were then used to derive relative importance values and model averaged effect sizes for each explanatory variable. Relative importance represents the probability of a variable being present in the best performing model for a particular trait, and was calculated in MuMIn using the relative Akaike weights of models within the confidence set (Burnham and Anderson, 2002). Model averaged effect sizes were calculated for each explanatory variable by averaging the parameter estimates across each model in which a given variable occurred. 95% confidence intervals were also generated for these effect sizes and a significant effect of a variable is indicated where the confidence intervals do not overlap with zero (Grueber et al. 2011). The resulting statistics provide a way of assessing which spatial, age and local variables affect each trait, and the magnitude of these effects.

Recent work on the same plant species pool showed that their traits helped discriminate ancient woodland specialists from other woodland species yet segregation of species into either group was not explained at all by phylogeny (Kimberley et al. 2013). It is therefore unlikely that ancestral relatedness is responsible for artefactual correlations between traits and the explanatory variables used to quantify forest age and patch geometry. For this reason phylogeny was not included in any analyses.

Results

Selection probability

The relative importance values shown in Table 1 indicate the probability of each explanatory variable being selected in the best performing model (of the set tested) for each plant trait. Where a selection probability > 0.50 the variable in question is more likely to be included in the best performing model than not, and is therefore considered an important predictor. Abiotic predictors had a selection probability > 0.50 in a higher proportion of cases (20 out of 30) than the spatial/age predictors (11 out of 35) although both sets of variables were important predictors across the range of traits. This suggests that a strong local filtering effect is operating upon mean plant trait values but that forest spatial configuration is still an important driving factor.

Model averaged effect sizes

Seed weight

Amount of shade present had the strongest effect on mean seed weight values in vegetation sampling plots, with significantly heavier seeds found in plots which were fully shaded compared to plots which were fully lit (Fig 2a and Table S1 in Supporting information). Increasing northing and C: N ratio were both found to lead to a significant reduction in mean seed weight, albeit with an effect size of lesser magnitude. Despite distance to nearest edge having a high probability of inclusion in the best performing model it was only found to have a weak effect on mean seed weight values.

Seed terminal velocity

Seed terminal velocity was significantly affected by a number of the local condition variables, with amount of shade again having the strongest effect (Fig 2b, Table S2). More shaded plots were found to contain sets of species with faster falling seeds, as were plots with a low soil moisture content and a high soil pH value. Although the local condition variables had the strongest effect on mean seed terminal velocity values, the amount of buffer forest also had a significant effect on this trait, with species with faster falling seeds found in patches with more forest habitat in the 1 km buffer area. Furthermore, the effect size observed for this spatial variable was similar in magnitude to the effects of soil moisture and soil pH. This suggests that the spatial structure of forest habitat is influencing plant species composition with a similar degree of strength to the local conditions.

A significant effect was also found for the interaction between forest patch age and distance to nearest patch edge. This suggests that the influence of core forest habitat depends upon the age of the patch in question. As Figure 3 suggests, the relationship between mean seed terminal velocity of plots and increasing distance to the edge is slightly stronger in older habitat than in younger.

Specific leaf area

Although none of the spatial variables tested were found to influence mean specific leaf area (SLA) values within plots (Figure 2c and Table S3), a strong relationship was identified between the levels of soil carbon present and mean SLA. Where soil C: N was high, lower SLA values were observed within plots. Increasing shade also had a significant, albeit smaller effect on this trait, with heavily shaded plots containing species with a higher mean SLA than more open plots. Mean SLA values were also higher in more northerly plots and in plots with lower soil moisture.

Seedbank persistence

The amount of shade present was found to have the strongest effect on mean seedbank persistence values, with fully-shaded plots containing species with a less persistent mean seedbank than non-shaded plots (Figure 2d). Weak but still significant relationships were also found between increasing soil pH and increasing Northing and higher mean seedbank persistence.

The interaction between age and patch area had a weak but non-significant (at the 95% confidence level) effect on mean seedbank persistence values within vegetation sampling plots (Figure 2d and Table S4) suggesting that the relationship between patch area and mean seedbank persistence may be stronger in older forests than younger forests. This is supported by Figure 3, where mean seedbank persistence decreases with increasing patch area in old forest patches but shows little response in younger forest patches.

Rarity

Forest patches with high levels of shade and soil C: N contained a greater proportion of rare species. Conversely, plots in the north of Britain were found to have, on average, species which are more common (Figure 2e and Table S5). Again, the spatial variables did not have a significant effect on rarity considering all forests together, but patch area was found to have a stronger effect on mean rarity in older forests, shown by the significant effect of the interaction between patch area and patch age in Figure 2e. Figure 3 suggests that, in older forest patches, as the area of forest patches increases, the average rarity of species present increases.

Discussion

Abiotic conditions

As expected, abiotic conditions within forest patches were found to be key determinants of plant species composition. Principal amongst these was the amount of shade in vegetation plots, which had the strongest effect on four of the five traits tested. These patterns likely reflect the different strategies needed to survive in relatively open woodlands compared with more dense forest habitat. For example, greater light availability has been shown to favour species possessing traits associated with a high relative growth rate, such as lower seed mass (Reich et al. 1998). Such patterns were observed in this study; well lit forests contained species with significantly lower mean seed weights and mean seed terminal velocities compared to plots which were fully shaded. Species found in shadier patches had a less persistent seedbank on average, possibly since soil turnover is an unpredictable and rare event in forest environments. Persistent banks of buried seeds are a less common regenerative strategy in these conditions than, for example, non-flowering ramets or cohorts of persistent juveniles (Grime, 2001).

The effect of increasing shade on mean SLA values supports previous work showing that, under low light conditions, shade tolerant species possess higher SLA (Hodgson et al. 2011). In temperate broadleaf forests such as those studied here, thinner leaves, and hence higher SLA, promote greater light capture for least expenditure on structural tissues which can then afford to be shed every autumn. This is in contrast to tropical forest trees where the longer growing season favours year round photosynthesis and growth but at a cost of greater investment in structural tissue, resulting in lower SLA (Baltzer & Thomas, 2010).

Increasing soil C: N ratio had the strongest effect on mean SLA values; on more productive soils (those with a low C: N ratio) mean SLA values were higher. Under these conditions high macronutrient availability can fund growth strategies that divert resources into rapidly accumulating plant biomass comprising leaves of low longevity and higher tissue nitrogen content (Ordoñez et al. 2009). This is consistent with the link between soil fertility and leaf mass per unit area revealed by the Leaf Economics Spectrum (Wright et al. 2004). Thus in temperate forests high SLA is not a reliable indicator of shade-tolerance associated with ancient forest because in some areas high SLA can also indicate the presence of nutrient-demanding generalist herbs (Hodgson et al. 2011).

Other multivariate studies have assessed the effects of spatial and abiotic factors on community composition using species occurrence data, thus only accounting for their overall effect on various different traits (Foster et al. 1998; Vellend et al. 2007). In this study mean trait values were analysed separately, allowing the differences in the way traits respond to important variables to be detected. Care must be taken when interpreting these results however, due to correlations between pairs of traits. For example, part of the observed effect of shade on seedbank persistence may be due to the close relationship between this trait and seed mass (Westoby et al. 2002) which is also linked to light availability.

Importance of habitat configuration

Previous studies have related changes in the composition of forest vegetation with alterations in environmental conditions and levels of disturbance following land use changes (Foster et al. 1998). Our findings confirm the links between prevailing abiotic conditions within forest patches and mean community trait values, but also indicate that forest habitat configuration has an important effect. Rare species with fast falling seeds and no persistent seedbank responded to both the area of forest patches and the amount of surrounding forest habitat, even when abiotic factors were accounted for. This suggests that such species are not restricted to large, old forest fragments solely due to the increased disturbance and competition at the edges of small or young patches, but also because aspects of landscape context such as patch size and isolation are acting as important filters on the occurrence of these species.

Conservation strategies often centre on protecting and increasing areas of existing forest habitat (e.g. Forestry Commission, 2011); particularly in land sparing scenarios where large habitat reserves, separate from an agricultural matrix, are the main focus of effects to conserve biodiversity (Phalan et al. 2011). The results of this study provide some support for such measures, since positive relationships were found between the presence of large core forest areas and the occurrence of rare, poorly dispersing species, even after accounting for abiotic environmental conditions. Increasing the size of forest patches should therefore help to promote the occurrence of many forest specialist species. The effects of patch area and buffer forest however were often secondary to those of abiotic factors such as shade and soil C: N ratio. This suggests that the maximum benefit to these species will be obtained by focussing conservation and restoration efforts on areas where the soil and shade conditions are most favourable. Attempts to increase characteristic forest biodiversity on unfavourable sites may lead to any positive effects of extra available tree cover being negated by the stronger effects of soil fertility and light availability. In addition to the effects of forest configuration observed here, other aspects of landscape structure may also be important determinants of mean trait values. The heterogeneity of the matrix landscape around forest patches for example is likely to affect the ability of poorly dispersing species to colonise habitat patches (Matlack & Monde, 2004), while large amounts of nearby woody linear features may act as a refuge for forest specialist plants, increasing resilience to patch area and isolation (Petit et al. 2004). In addition to these other important possible covariates, the high levels of noise relative to signal found in large-scale randomised survey samples such as Countryside Survey (Smart et al. 2012), may explain the small effect sizes seen here for most variables.

As hypothesised, plant community mean trait values within younger forest patches were not strongly affected by forest spatial structure, possibly due to the absence of the inefficient dispersers which are most affected by habitat structure and typify older forests (Verheyen et al. 2003; Schleicher et al. 2011). Large areas of young forest habitat may be missing many of these species, despite providing suitable habitat. This immigration credit (Jackson & Sax, 2010) may result in a future change in trait composition towards one that more strongly reflects patch spatial characteristics, as the recently established forest is gradually colonised by poorer dispersers. Any newly created habitat however is likely to take time to realise benefits to biodiversity, with studies suggesting that secondary woodlands take around 70 years to develop a similar level of species diversity to ancient forests (Flinn & Vellend, 2005). Achieving this rate of community assembly also critically depends upon adjacency to existing ancient forest (Brunet et al. 2011).

Ancient forest habitat is generally thought to be of higher conservation value due to its ability to sustain a large number of rare species that are considered less capable of colonising isolated younger forest (Peterken & Game, 1984). Our results suggest that this is, on average, only the case for large older patches. Smaller forests, even where they are of long continuity, are less able to support these rare species (Figure 3). Although ruderal species possessing lighter seeds and more persistent seedbanks are not characteristic of the flora of long continuity forest habitat, they were still found to dominate the flora of older yet smaller forest patches. Moreover, species with no persistent seedbank were more frequent only in forest patches which were both large and old (Figure 2d, Figure 3). Higher mean values for seed terminal velocity were also observed at greater distances to forest edge in older forests (Figure 2b, Figure 3), suggesting a clear distinction between core and periphery species. In order to obtain the conservation benefits of old growth forest, such habitat must also be large in size and contain a high proportion of core habitat. Priority should therefore be given to measures that maintain and increase the area of old growth forest habitat where the aim is to conserve rare, poorly dispersing ancient forest specialist species.

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Table 1. Probabilities of spatial and local abiotic explanatory variables being included in the best performing model of the model set tested for five life history traits. Variables with a selection probability of greater than 0.5 are shown in bold

Explanatory variable	**Seed weight**	**Seed terminal velocity**	**Specific leaf area**	**Seedbank Persistence**	**Rarity**	**Important responses**
Spatial/age variables						

Distance to edge	**0.53**	**0.77**	0.40	0.34	**0.52**	3
Patch area	0.18	0.31	0.19	**0.91**	**0.82**	2
Buffer forest	0.21	**1.00**	0.19	0.44	0.28	1
Age	0.35	**0.78**	**0.58**	**0.65**	**0.58**	4
Age x Distance to edge	0.11	**0.74**	0.05	0.17	0.13	1
Age x Patch area	0.14	0.04	0.01	0.47	0.43	0
Age x Buffer forest	0.01	0.14	0.00	0.06	0.05	0
Abiotic variables						
Shade	**1.00**	**1.00**	**0.94**	**1.00**	**1.00**	5
C:N ratio	**0.75**	0.17	**1.00**	0.18	**1.00**	3
Soil moisture	**0.58**	**1.00**	**1.00**	0.19	0.47	3
Soil pH	0.20	**1.00**	**0.50**	**1.00**	**0.72**	4
Plot type	0.16	**1.00**	**1.00**	0.10	0.21	2
Northing	**1.00**	0.49	0.22	**0.81**	**1.00**	3

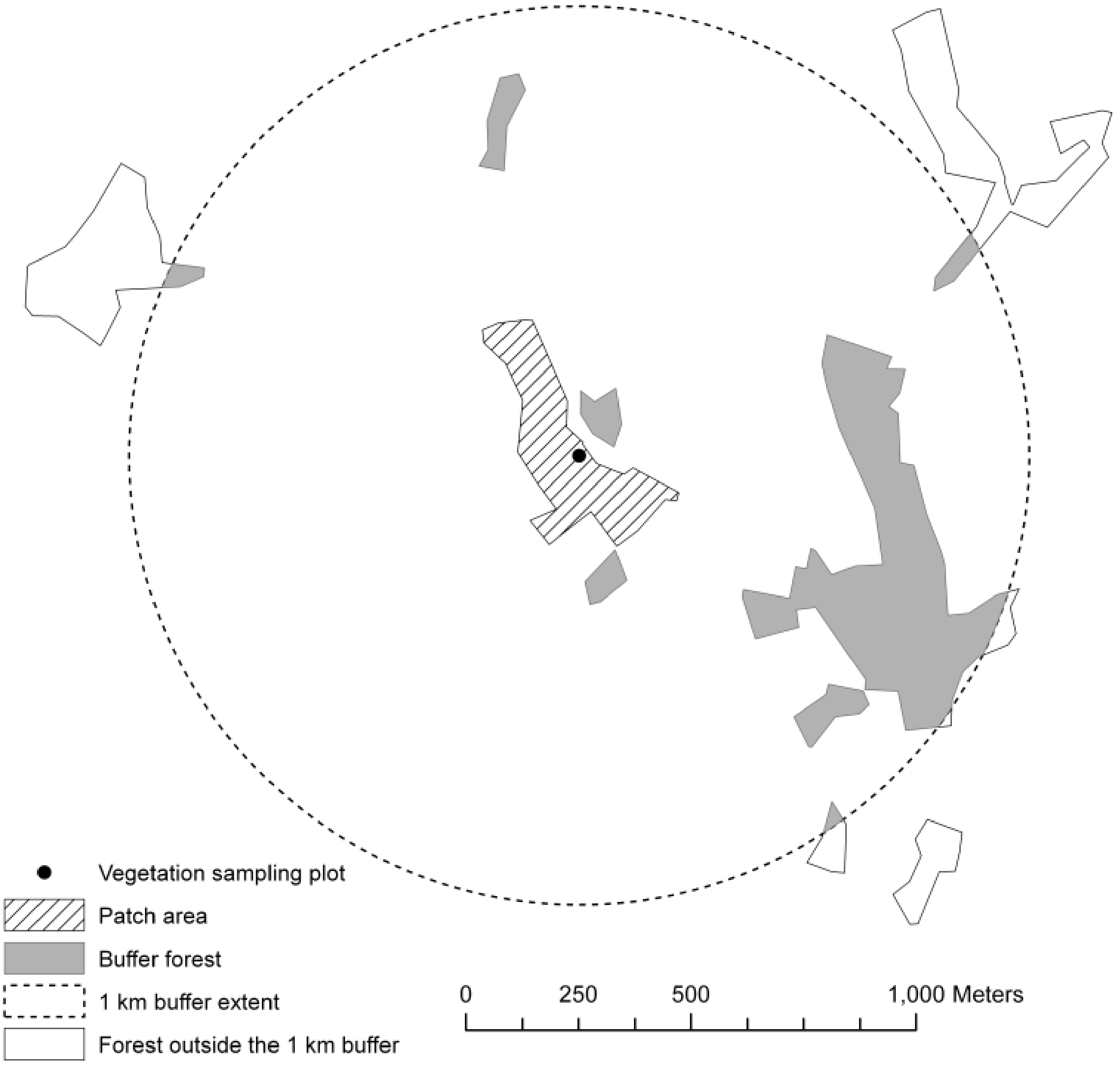


Fig 1. Map showing an example Countryside Survey vegetation sampling plot and surrounding Land Cover Map forest data. These data were used to calculate the various spatial metrics for the patch in which the plot occurs. The hatched area of forest habitat shows “Patch area” while the grey shaded area represents “Buffer forest”. Forest habitat outside the 1km buffer area was not considered within the Buffer forest variable, even where contiguous with patches inside the buffer.

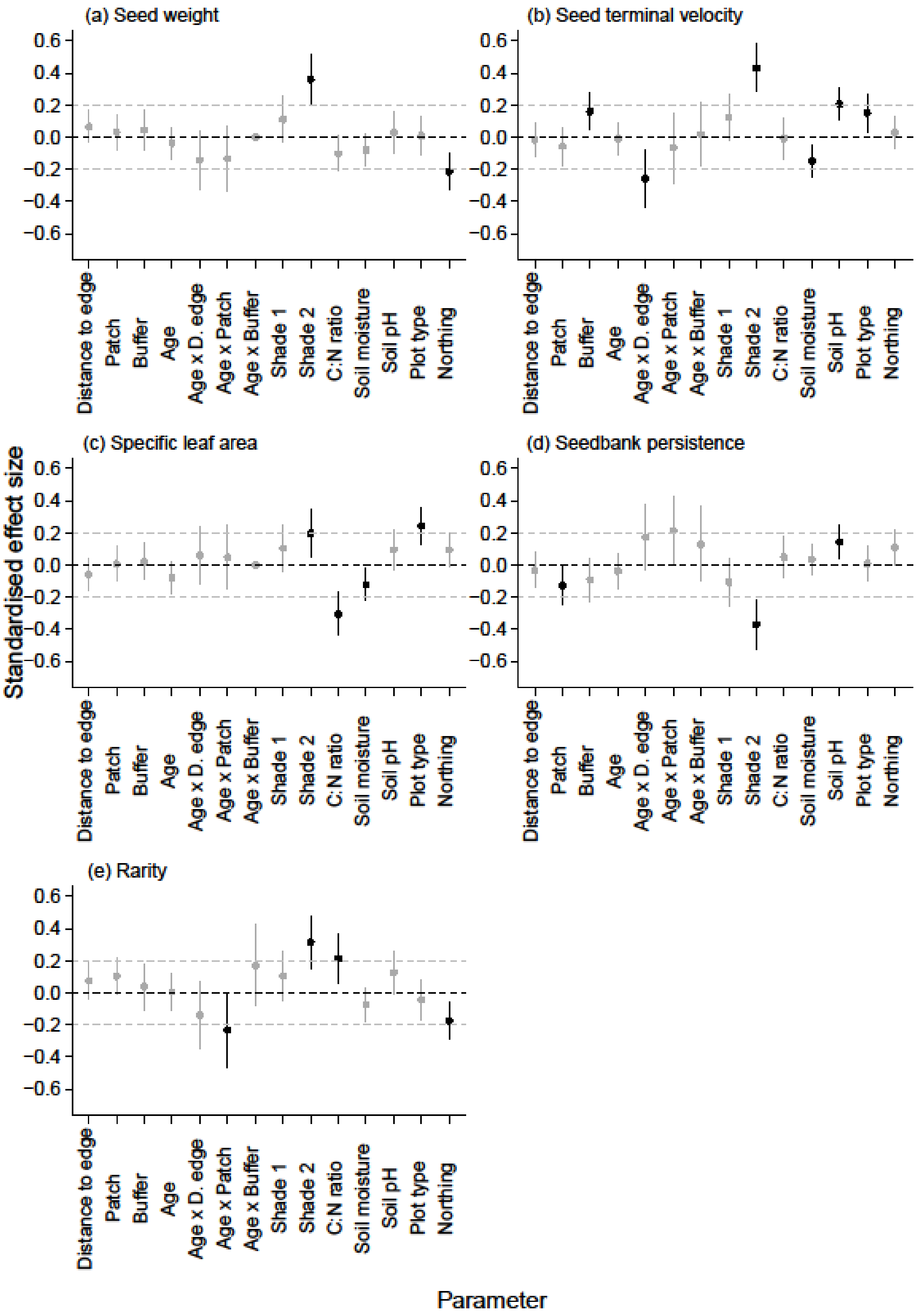
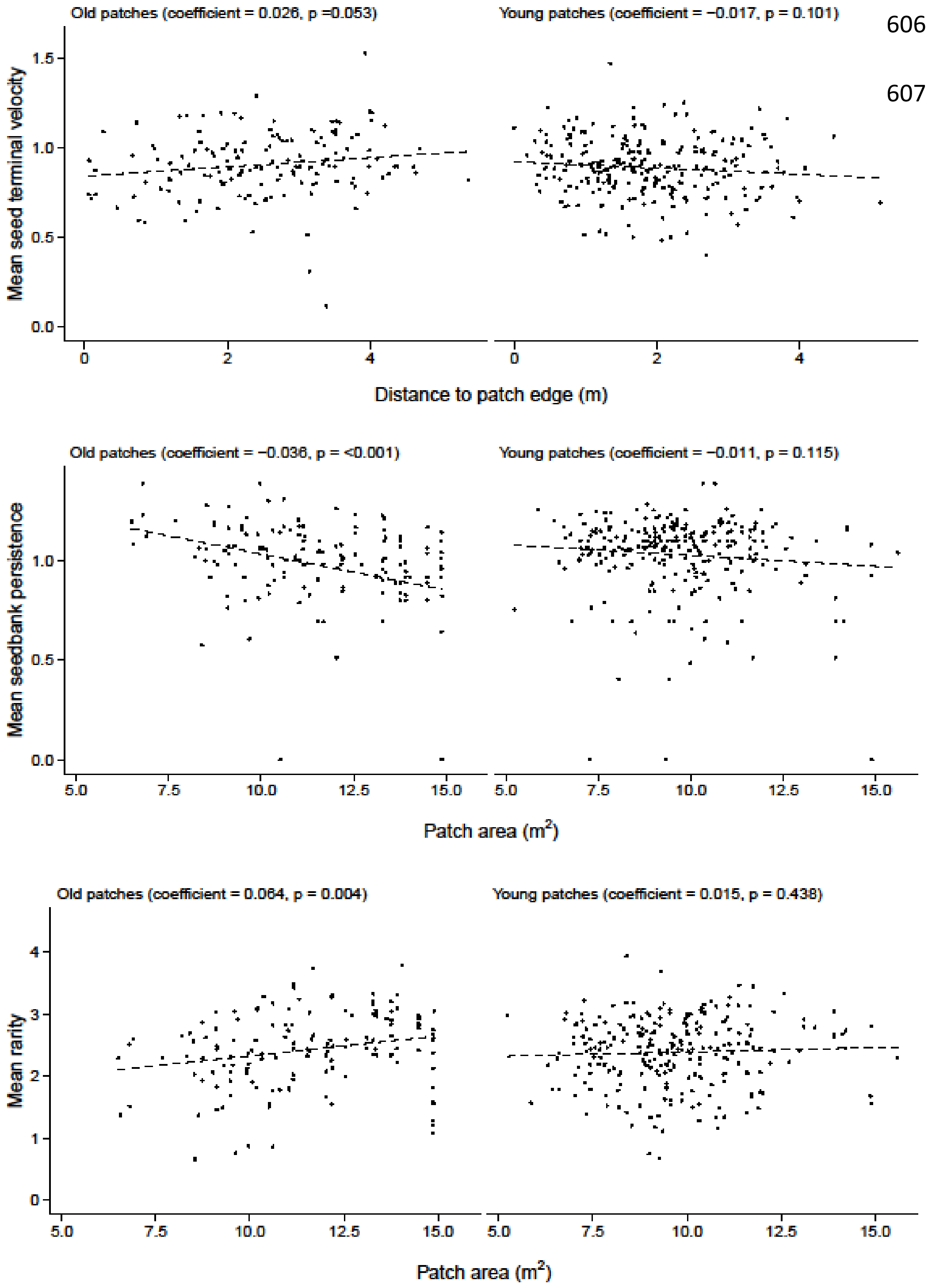


Fig 2. Model averaged effect sizes of 14 explanatory variables on mean trait values in forest plots. Points show the average effect size taken from multimodel inference analysis, while the error bars indicate 95 percent confidence intervals. Where the confidence intervals do not overlap zero (black points), a significant effect is indicated. The further a point is from

zero, the stronger the effect. Dashed horizontal lines at +0.2 and -0.2 delimit small from medium sized effects according to Cohen (1988). Shade 1 shows the difference between unshaded and partially shaded plots, Shade 2 the difference between unshaded and fully shaded.

Fig 3.



Relationships between spatial variables and mean trait values in older forest and young forest patches. Patch area and distance to patch edge were both log transformed. Dashed lines represent a linear model of trait versus spatial predictor. Regression co-efficients and *P* values for these models are also displayed.

Supporting information

Appendix S1: Model averaged effect sizes and selection probability values of explanatory variables.

Table S1: Model averaged effect sizes and selection probability values for seed weight

Table S2: Model averaged effect sizes and selection probability values for seed terminal velocity

Table S3: Model averaged effect sizes and selection probability values for specific leaf area

Table S4: Model averaged effect sizes and selection probability values for seedbank persistence

Table S5: Model averaged effect sizes and selection probability values for species rarity