Drivers of vascular plant species area relationships in British broadleaved woodlands and their effects on the species area curve

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Summary

1. The loss of plant biodiversity in Great Britain is a major concern, with a fifth of species endangered or vulnerable according to the latest IUCN Red List. The Government's 25 Year Plan for the environment [Defra, 2018] aims to halt this loss and build new habitats, including new woodlands. To ensure that biodiversity loss is halted in existing woodlands and gain is maximised in new ones, we need to better understand which drivers have been most influential in controlling biodiversity. Here we focus on vascular plant species' richness.

2. Previous attempts to explain plant species richness have mainly focussed on alpha diversity in a consistent, fixed unit area. Here, we additionally undertake a novel analysis of the effects of environmental heterogeneity and abiotic factors on species-area relationships derived from 16 randomly placed quadrats in each of 103 semi-natural, broad-leaved woodlands across Britain. Species-area relationships were examined at two scales ($4m^2$ to $200m^2$ and $200m^2$ to $3200m^2$) to explore the relationship between the drivers of species richness and the exponent z, of the canonical species-area curve, $S = cA^z$. We also explore the use of a new metric ζ_r, based on zeta diversity to quantify heterogeneity.

3. Habitat heterogeneity increased species richness, as did the exposure of the woodlands to surrounding natural habitats. Higher levels of soil organic matter and the progression of woodlands to later successional stages, decreased species richness. Richness was also seen to have a unimodal response to soil acidity with a peak around pH6. At the smaller scale, heterogeneity elements in the woodland such as riparian zones or coppicing led to an increase in the value of the exponent of the species area curve. At the larger scale, species turnover led to an increase in the exponent of the curves while succession led to a decrease. At both scales, soil organic matter content had a negative effect. ζ_r was found to be a significant and important variable and to affect both species richness and the slope of the species accumulation curves at larger scales.

Synthesis. Habitat heterogeneity measures included the presence of coppicing, open areas such as rides and riparian zones and the difference between species assemblages in different plots in the woodland. Results suggest that to maximize vascular plant diversity, woodlands should be managed for heterogeneity. In addition, the increase in richness with exposure to surrounding natural habitats suggests that woodlands should be large and connected. This implies that if possible current woodlands should be increased in size, rather than creating new smaller disconnected sites.

Key words: biodiversity, species area curves, species richness, woodlands, zeta diversity.

Introduction

Biodiversity worldwide continues to decline [Butchart et al., 2010, Tittensor et al., 2014] and Britain is no exception to this trend [Hayhow et al., 2016]. The IUCN Red List for the UK shows 22% of plant taxa as critically endangered, endangered or vulnerable [Stroh et al., 2014]. Biodiversity is important for ecosystem function [Gaston & Spicer, 2004], with woodlands performing specific additional functions including the improvement of water quality, carbon sequestration [Slee and Kyle, n.d], nectar provision within farmed landscapes [Baude et al 2016] and the provision of habitats for other taxa [Amar et al., 2006, Fuller & Warren, 1993].

The aims of the new 25-Year Environment Plan [Defra, 2018] include achieving “thriving plants and wildlife”, planting 180,000 hectares of new woodland and ensuring that existing woodlands are better managed. However, more woodland is not necessarily the answer to biodiversity loss if we cannot ascertain why our current woodlands are not thriving.

This study was aimed at finding the main drivers of vascular plant species richness in British broad-leaved semi-natural woodlands to provide research-based evidence on how best to manage, maintain and increase their plant biodiversity. This research is the only work of its kind that analyses diversity as the slope of the species area relationship expressed across multiple samples at the national scale.

SUMMARY OF FACTORS THAT HAVE BEEN SHOWN TO AFFECT SPECIES RICHNESS

Table 1 summarises variables that have been shown in the literature to affect plant species richness and which can also be obtained from the CEH Woodland Survey database [Kirby et al., 1971]. This is not intended as a comprehensive review and only represents a small selection of the rich literature in this area. Indeed, the papers cited discuss results for multiple factors affecting species richness. The reason for this summary is to justify the selection of predictor variables by appealing to prior knowledge. This is important due to the model averaging procedure used as part of this analysis which is described in more detail below.

Table 1. Examples of abiotic factors which have been shown by previous authors to affect vascular plant species richness.

Factor	Relationship to species richness	Comments	Reference
pH	positive linear	Studies of beech and hornbeam woodlands report lower species richness with lower pH and increased SOM. This was true for both taxa, suggesting that the effect was not solely the result of the physical barrier created by slowly degrading beech litter.	Koojiman & Cammeraat, [2010]
Soil Organic Matter (SOM)	negative linear		
pH	Unimodal	Greatest richness in woodlands occurred on nutrient rich soils, with a peak around Ellenberg N of 7 for shade loving species.	Cornwell & Grubb, [2003]
Latitude	11% per degree latitude	Authors pointed to altitude as more important in this study on tree species richness. Understory richness was not affected, and this effect may not be evident given the	Ohlemuuler & Wilson, [2000]

		modest change in latitude in our data.	
Isolation	Connected habitat contained 13 – 18% more plant species.	Species were averaged across dispersal mechanism.	Brudvig et al., [2009]
Isolation	Negative trend with increasing isolation	Authors found that plant species richness in agricultural, fragmented landscapes increased with connectivity of landscape elements.	Thiele et al., [2018]
Isolation	Woodland patch area and isolation explained 20% of variation in observed species richness in lowland woodlands	In this study connectivity with wooded linear features indicated lower isolation.	Petit et al., [2004]
Isolation	Correlation coefficient -0.33 to -0.45	Distance to nearest woodlands used as isolation factor and was shown to be negatively correlated with woodland and shrub species richness	Dzwonko & Loster [1988]
Heterogeneity	Plant species richness up to 20% lower in unmanaged forests.	Presence of logging trails used as sign of disturbance in managed forests,	Boch et al., 2013
Heterogeneity	60% change in mean species richness in sites which experienced storm damage	In this work wind throw as a result of the 1987 hurricane generated heterogeneity	Smart et al., 2014

Materials and Methods

HABITAT HETEROGENEITY – THE USE OF ZETA DIVERSITY

Habitat heterogeneity is known to be important for biodiversity [Gardener, 2010], but it is not trivial to quantify and has been expressed in many ways. Honnay et al., [1999] used length of rides, number of soil types and a ratio of perimeter and area. Schmidt [2005] used the presence of logging trails, and Bàldi [2008] used the number of CORINE land cover codes. In this work several methods were used to quantify heterogeneity as shown in table 2. However, these methods have some weaknesses. PHI

(Positive Heterogeneity Index, see table 2 for more details) requires additional work to collect the information and does not indicate the concentration of elements. For example, if a woodland shows considerable signs of woodland management, only one code is entered, and the PHI increases by 1 for woodlands with both a large or a small amount of management. In addition, the number of elements included depend on the additional area of woodland that surveyors cover. A new metric was therefore generated based on zeta diversity [Hui & McGeoch, 2014] to provide a simple, objective measure.

Zeta diversity is the average number of species shared between multiple plots, [Hui & McGeoch 2014] and can be used to show compositional change in species assemblages, [McGeogh et al., 2017] and model drivers of species turnover, [Latombe et al., 2017].

ζ_1 is the average number of species in each plot ζ_2, is the average number of species shared between every combination of two plots. If plots contain the same species, then $\zeta_1 - \zeta_2 = 0$. If all plots contain different species then $\zeta_1 - \zeta_2 = \zeta_1$.

A homogeneous woodland is more likely to contain species that occur in many plots, whereas a heterogeneous woodland is more likely to have plots containing different species. This suggests a method of comparing heterogeneity between woodlands using the ratio,

$$\zeta_r = \frac{\zeta_1 - \zeta_2}{\zeta_1},$$

The more homogeneous the woodland, the closer the value of ζ_r to zero. There is sometimes concern that the use of a diversity metric to predict richness introduces a circularity. This is not the case when using the ratio ζ_r. ζ_r can take values between 0 and 1. The value depends on the difference between average numbers of species in each plot to the average number shared between two plots and not on the richness of the plots. For example, in homogeneous species rich or species poor woodlands the values of ζ_1 and ζ_2 will be similar, and therefore ζ_r will approach 0. The converse occurs for a heterogeneous woodland. The ratio ζ_r is not, therefore, a predictor of richness, it can

take values between 0 and 1 for both species rich and species poor woodlands, it is a predictor of species turnover.

ζ_r can be seen to be like Jaccard's dissimilarity index, with the extension that here the use of ζ diversity calculations allows us to easily use multiple plots.

The zeta values for each woodland were calculated using the zetadiv function in R, [Latombe et al., 2018]. The ζ_r coefficient was calculated and added to the set of predictor variables.

DRIVERS OF VASCULAR PLANT SPECIES RICHNESS ACROSS ENTIRE WOODLANDS AND AT TWO DIFFERENT SCALES.

The drivers of vascular plant species richness were studied in two ways. Firstly, by examining the effect of a range of variables on the species richness of a fixed area within 103 different woodlands and, secondly, by looking at the scale dependence of species richness as expressed in the canonical species area curve (SAC), $S = cA^z$, and the effect of habitat heterogeneity and environmental conditions on the exponent, *z* of these curves.

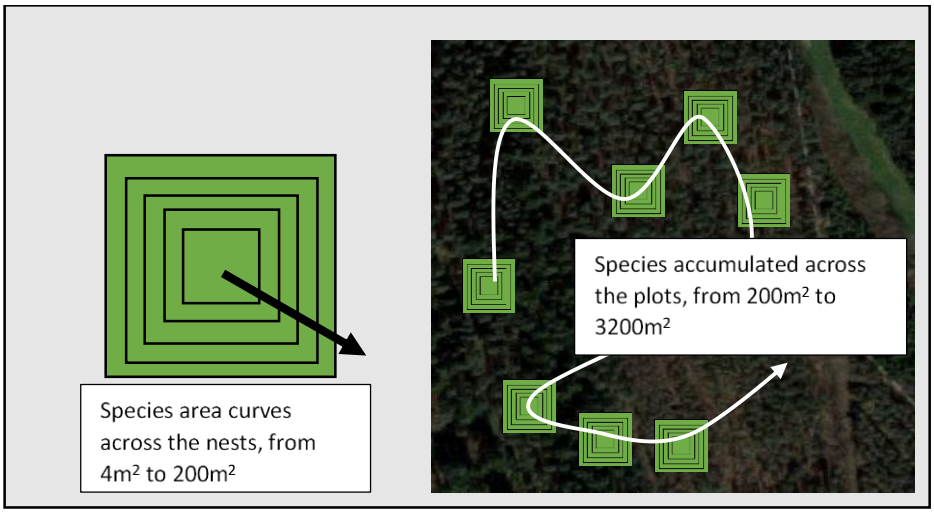

Figure 1. Two scales of species area dependence. At the nest scale species area curves were calculated for areas from 4m²to 200m². At the plot scales species were accumulated across the 16 plots such that area increased from 200m² to 3200m².

The smallest scale used species accumulated across a concentrically nested set of square quadrats. (This z value will be referred to as nest z). These are typically referred to as species area curves and z values of around 0.25 were first proposed by Preston [1960] as being the result of sampling from log-normal species distributions. Other authors have suggested that the z value at this scale has no biological meaning [Connor et al, 1983, Tjorve & Tjorve, 2017] but is a result of species distribution. Using neutral models Cencini et al [2012] predicted that population size affects the shape of the curve while Sugihara [1979] concludes that the value of 0.25 reflects community structure.

At the larger scale species were accumulated across all the non-contiguous nested quadrats in the site. (This z value will be referred to as plot z). These curves are referred to as species accumulation curves and at this scale habitat heterogeneity is likely to play a part in the z value [Storch et al, 2014]. In similar work, Shen et al [2009] considered the effect of tree density, soil nutrients, pH, slope, elevation and aspect and heterogeneity and concluded that dispersal and habitat heterogeneity jointly are required to explain the shape of species area curves. Baldi & Sadler [2017] concluded that habitat heterogeneity, as quantified by the number of habitat types as shown through CORINE land cover maps, was more important than area for expressing species richness.

The combined influence of local abiotic factors and woodland heterogeneity on the exponent of curves constructed over these two different scales, was examined.

DATA

The data were taken from the Centre for Ecology and Hydrology's woodland survey database [Smart et al., 2013]. One hundred and three woodlands across Great Britain were surveyed between 2000 and 2003. Sixteen plots were randomly located in each woodland, each plot had a total area of 200m^2. Further, each plot was itself nested with sub-areas of 4m^2, 25m^2, 50m^2, 100m^2 and 200m^2 (see figure 1).

All flora was recorded within each plot. Additional plot data were collected, including diameter at breast height (DBH) of trees, live basal area (LBA) of trees and shrubs, soil pH, soil organic matter (SOM) content, National Vegetation Classification (NVC) code, and major soil group (MSG). Additional woodland information was also recorded, such as whether there were signs of woodland management, the presence of riparian zones and open areas such as glades or rides. Table 2 summarises the information taken from the dataset and details how it was transformed to create predictor variables.

The richness for each woodland was calculated to be the unique number of species in the total 16 plots surveyed. The variables within the database were at different scales, plot level and woodland level. Plot level variables, such as pH, DBH or SOM, were scaled appropriately to the richness by taking the mean per woodland. Site level variables were buffer, number of NVC codes, number of major soil groups, area ratio and PHI. The variables fall into two categories; those which represent heterogeneity and those which describe average site conditions. The bold code H or S in column 2 of table 2 denotes the former and latter respectively.

Table 2 Summary of predictors created from the variables in the dataset. Column 2 denotes either a site level variable, S, where means of plot level values have been taken, or a variable used to represent heterogeneity, H.

Variable	Variable type	Description
Positive Heterogeneity Index (PHI)	**H**	Codes were recorded for each woodland to show the presence of other elements such as ponds, ditches, buildings, dead wood etc. The sum of codes that corresponded to an element that has been shown by previous authors to be positively correlated with vascular plant species richness. This sum was used as an explanatory variable - PHI. The greater the PHI, the more elements within the woodland that could increase richness by increasing heterogeneity of conditions.
Northing	**S**	Latitude
Buffer	**H**	The proportion of land around the wood (to 3500m from the edge) that is not arable, improved grassland or urban. The larger the buffer, the more the surrounding area can be considered as positive for species richness. This variable therefore equates to the inverse of isolation and measures the favourability of the matrix within which each woodland was embedded.
Number of major soil groups (MSG)	**S**	The number of major soil group codes in each woodland.
Number of National Vegetation Classification (NVC) codes	**H**	The number of different NVC codes in each woodland. The NVC code represents the assignment of the plant species assemblage to a phyto-sociological classification of British plant communities. The number of different NVC codes therefore describes the number of different plant assemblages present. This is equivalent to the number of CORINE land cover codes used by Baldi [2008]. Although the NVC code might correlate with richness, the number of codes will not, since it is possible that each code could represent a low richness assemblage. However, since NVC codes represent a different species assemblage with different abiotic factors, if there are more codes, it is more likely that the woodland has greater heterogeneity.
pH	**S**	The pH for the plot
Soil Organic Matter (SOM) content	**H**	The SOM content for a plot
Live Basal Area (LBA)	**S**	The LBA of all saplings, trees and shrubs recorded in a plot
Diameter at breast height (DBH)	**S**	The DBH of all trees recorded in each plot
Tree Density (TD)	**S**	Count of trees per plot
Area ratio	**H**	The ratio of area to perimeter of the site. This is a measure of the number of habitats the woodland is exposed to [Honnay et al, 1999].
ζ_r	**H**	The ratio of ζ_1-ζ_2 to ζ_1, quantifying species turnover between plots.

MODELLING

The modelling was designed to answer three questions as follows:

1) Which variables had most influence on species richness of the entire woodland?

2) Which variables had most influence on the exponent of the species area curve and did this change with scale?

3) Is the zeta diversity metric ζ_r useful as a measure of heterogeneity?

To answer the first question, model averaging and a gradient boosting machine (GBM) were used to examine which of the predictor variables had the greatest effect on the species richness of the same area, 3200m^2, in each of the 103 woodlands. To explore the second, the response of the exponent, z, of the species area curves to the same set of variables was explored at two scales; 4m^2-200m^2 (nest level) and 200 – 3200m^2 (plot level) using model averaging. Finally, significance and importance of ζ_r was observed in the above models as compared to the alternative heterogeneity metrics employed.

MODEL AVERAGING

Model averaging is an ideal method for isolating variables which are most important for predicting a response when the relationships are linear, [Kimberley et al, 2014; Symonds & Moussalli, 2010]. The Akaike Information Criteria (AIC) is used to rank a set of competing models, [Burnham, Anderson, & Huyvaert, 2010]. A subset of these models with the lowest Akaike weights are selected, and parameters averaged across this set.

Since highly correlated predictor variables are undesirable [Freckleton, 2010] the correlation coefficients of all variables were examined, and it was found that all variables had Spearman and Pearson correlation coefficients below 0.54. The variance inflation factors of the models were also examined and were all below 2.

Once the predictor variables were selected the dataset was standardized as suggested by Gelman, [2008]. This gives parameter effect sizes that can be compared directly (two standard deviations of change in the predictor variable will result in the effect size change in the response). A linear model was created using all the variables. The dredge function in the MuMin package in R [Barton, 2018] was used to create a set of models containing all permutations of the variable set. These were ranked according to the AIC. The model with the lowest AIC is considered the model that best represents the data. This method will always produce a best model, but that model is only "best" relative to all the other models generated. It is therefore important to ascertain the goodness of fit of the initial linear model used [Symonds & Moussalli, 2010]. The goodness of fit of the models using all the parameters was ascertained by examining the fitted values against the residuals and by considering the value of R^2. None of the models showed any pattern in the residuals. For the species richness models R^2 was 0.47. For nest z, 0.33 and for plot z, 0.47.

All models within an AIC of between two to seven can be considered as equally good [Burnham et al., 2010] and used to create a model set. The parameter effect sizes are then averaged across this model set and a 95% confidence interval obtained. If this confidence interval does not cross zero, these predictors are considered significant, [Kimberley et al., 2014]. In this work, models within AIC of 2 ($\delta < 2$) of the highest ranked model were initially selected. The effect of increasing δ was then examined. If more variables were introduced which had confidence intervals that crossed zero, the lower value was used to avoid including redundant models [Grueber et al., 2011]. The relative importance of each effect size was also obtained, [Burnham, 2015]. Relative importance is a measure of the probability that a variable is present in the model set. A relative importance of 1 means that a variable appears in every model in the model set.

GRADIENT BOOSTING MACHINES

Gradient Boosting Machines (GBMs) are ensemble decision tree algorithms where recursive binary splits divide the data into regions, such that the root mean square error (rmse) of the response variable is minimized, [James et al., 2013. In addition, GBMs weight the observations such that those which were difficult to classify after a split are given increased weight. The next tree is then generated using these weighted observations. GBMs are suited to analysing complex ecological datasets because they can fit non-linear relationships and are not sensitive to scale, [De'Ath & Fabricius, 2000; Elith et al., 2008]. They have been shown to be successful, for example, in finding environmental variables which explain species richness of vertebrate groups [Mouchet et al., 2015]. In this analysis the gbm package in R was used, [Ridgeway, 2017].

The data was split into train and test sets using a 75/25 ratio. The GBM also uses a random subset of training data and so automatically provides a validation set. The values that are not selected can be used to give an "out of bag" (OOB) prediction error for the model.

Hyper parameters define the structure of the GBM and must be chosen to optimise the model performance. This was achieved through a hyper parameter tuning grid; a matrix containing a set of permutations of hyper parameters. The model was run across the hyper parameter tuning grid and the hyper parameters which minimized the OOB error were used in the final model.

Over fitting was addressed using the ntrees function of the gbm library. This function looks at the prediction error on the OOB set, and the number of trees is set as the value when this error stops decreasing and starts to increase. The rmse error of the train was half that of the test set, suggesting some overfitting. However, the test set rmse was comparable to that obtained using model-averaging.

To extract the variables which most influence species richness the relative influence (RI) of each variable was used, [Natekin & Knoll, 2013]. The percentage decrease in rmse is averaged for each variable over each time a variable was chosen to make a binary split in the data. The variable which has greatest RI is best at splitting the data and predicting the response.

Decision tree methods such as GBMs sometimes do not give stable results for RI, [Nicodemus et al., 2007]. Therefore, each model was repeated 100 times and the variables ranked by the average values of RI. The value of RI is relative and therefore subjective. In this work variables which had RI above 10% were selected as important for species richness.

The benefit of using these two modelling methods is their ability to detect different responses. Model-averaging detects linear relationship whereas the GBM can detect more complex patterns in the data, [James et al, 2013].

SCALE DEPENDENCE OF SPECIES RICHNESS

This part of the work involved calculating species area curves across the nests from $4m^2$ to $200m^2$. These correspond to type I nested curves as described by Scheiner [2003]. At the larger scale species were accumulated across the plots from $200m^2$ to $3200m^2$, as shown in figure 1.

At the larger scale, species can be accumulated in 16! alternative ways. The average of a subset of these accumulation curves is often used to calculate the slope of the species area curve. However, there are potential problems with this method when the area over which the accumulation occurs is heterogeneous, [Bacaro et al, 2012; Bevilacqua et al, 2018, Chiarucci et al, 2009]. This method is effectively selecting all species for accumulation as if they have equal probabilities of occurring in any plot in the woodland, i.e. the woodland is homogeneous. This is not the case for this data, the species are grouped into assemblages. Therefore, we took a different approach to maintain this spatial information. First, species were accumulated in such a way as to give a minimum gradient to the species accumulation curve. This is equivalent to grouping all similar species assemblages together. Secondly, species were accumulated to give a maximum gradient. This is equivalent to arranging the plots in the most heterogeneous manner. Since these two cases represent two extremes in the woodland (the most homogenous and the most heterogeneous) an average was taken of the two resulting curves. This spatially explicit method is similar to a type III curve, as described by Scheiner

[2003], where mean diversities of adjacent plots are calculated, but here adjacency is in terms of species assemblage's similarity or dissimilarity. In order to check the fit of this method the R^2 value of the log/log transform was calculated and found to be greater than 0.94 for three quarters of the woodlands. At both scales the gradients of the log/log transform of the curves were used as z (see supplementary material for more information). The z values at the two scales were then modelled with the same variables used to model species richness, as listed in table 2.

Results

SPECIES RICHNESS OF FIXED AREA OF 3200M^2

Figure 2 shows the model-averaged effect sizes and 95% confidence intervals for the total richness of all the 16 200m^2 plots in each woodland. Buffer, number of NVC codes, PHI and ζ_r have a positive effect on species richness with similar effect sizes. Mean diameter at breast height and mean SOM have a negative effect, again, with similar effect size. All significant variables are included in every model in the model set except ζ_r which shows an 80% probability of inclusion. The effect sizes of all significant variables are similar, with no one parameter clearly having a greater influence on richness than any other.

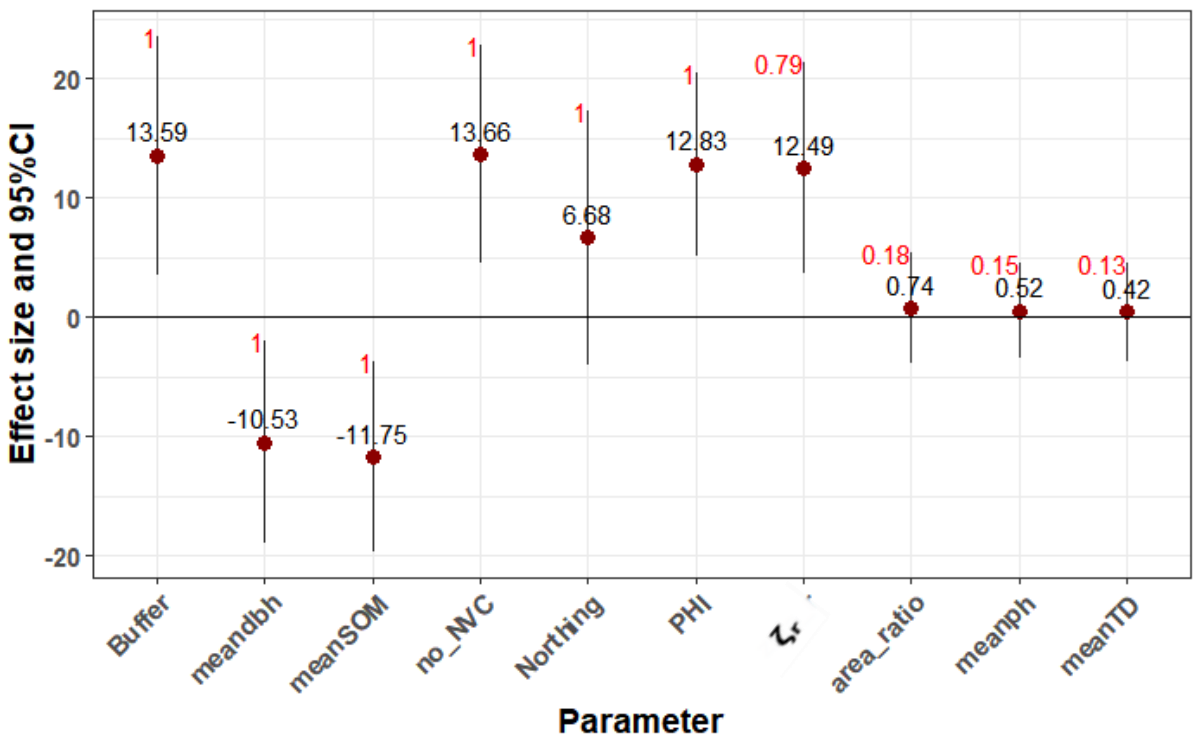

Figure 2. Model averaged effect sizes for woodland richness modelled with all variables using δ < 2 for the model set. Variable importance is in red. The points show the average effect size and the bars show the 95% confidence intervals.

Table 3 shows the parameters with relative influence of 10 or above in the GBM. ζ_r and PHI are again selected as important for predicting richness. The GBM also selects mean LBA, mean pH and Northing.

Table 3. Most influential variables from the gradient boosted machine

Parameter	Relative influence
ζ	16.37
Northing	13.25
meanLBA	11.42
PHI	10.88
mean pH	9.92

SCALE DEPENDENCE OF SPECIES RICHNESS

Figure 3 shows the distributions of nest z and plot z at the two scales. At the smaller nest scale the exponents are distributed around 0.25, whilst at the larger scale they are distributed around 0.5.

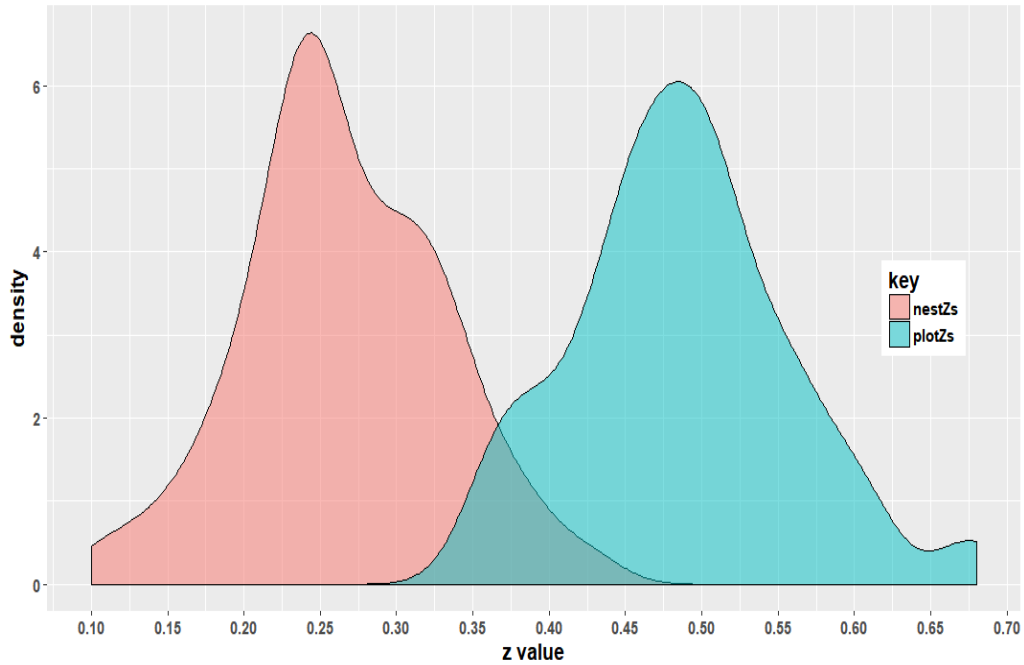

Figure 3. Distribution of z values at two scales. The pink distribution shows nest scale – 4m^2 to 200m ^{2}. The blue distribution shows plot scale – 200m^2 to 3200m^2

Figure 4 shows the model-average effect sizes for nest z. The heterogeneity parameters PHI and ζ_r have a positive effect on the value of z while mean SOM has a negative effect. The mean SOM is contained in every model in the model set, but the probability of inclusion of PHI is 82% and for ζ_r only 57%, this implies that ζ_r is not an important parameter at nest scale. PHI is the most significant parameter, the effect size double that of mean SOM.

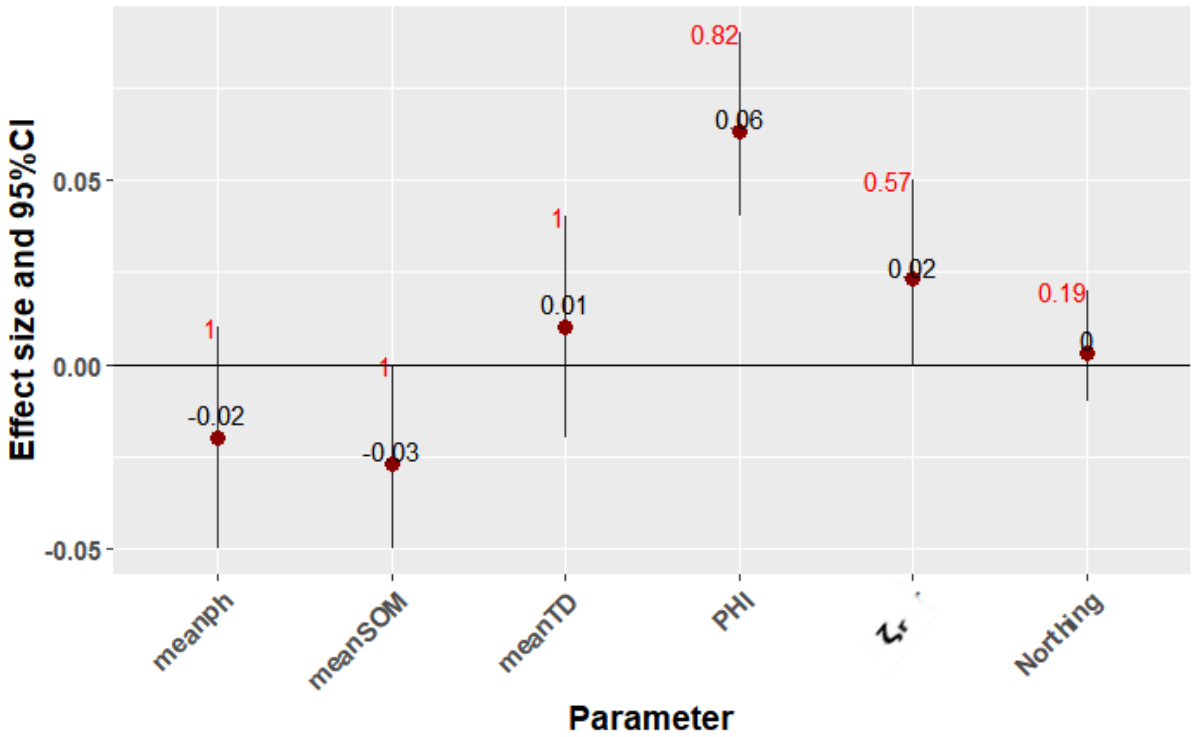

Figure 4. Model averaged effect sizes for nest z modelled with all variables using δ < 1.5 for the model set.

Figure 5 shows the model-average effect sizes for plot z. ζ_r is highly significant and has a positive effect on plot z. At this larger scale the effect of ζ_r, which quantifies species turnover across the woodland, has much greater significance than at the smaller nest scale. Mean tree density and mean SOM are also significant, although less so than ζ_r and their effect sizes are less than a third of ζ_r. Both mean SOM and mean tree density have a negative effect on plot z.

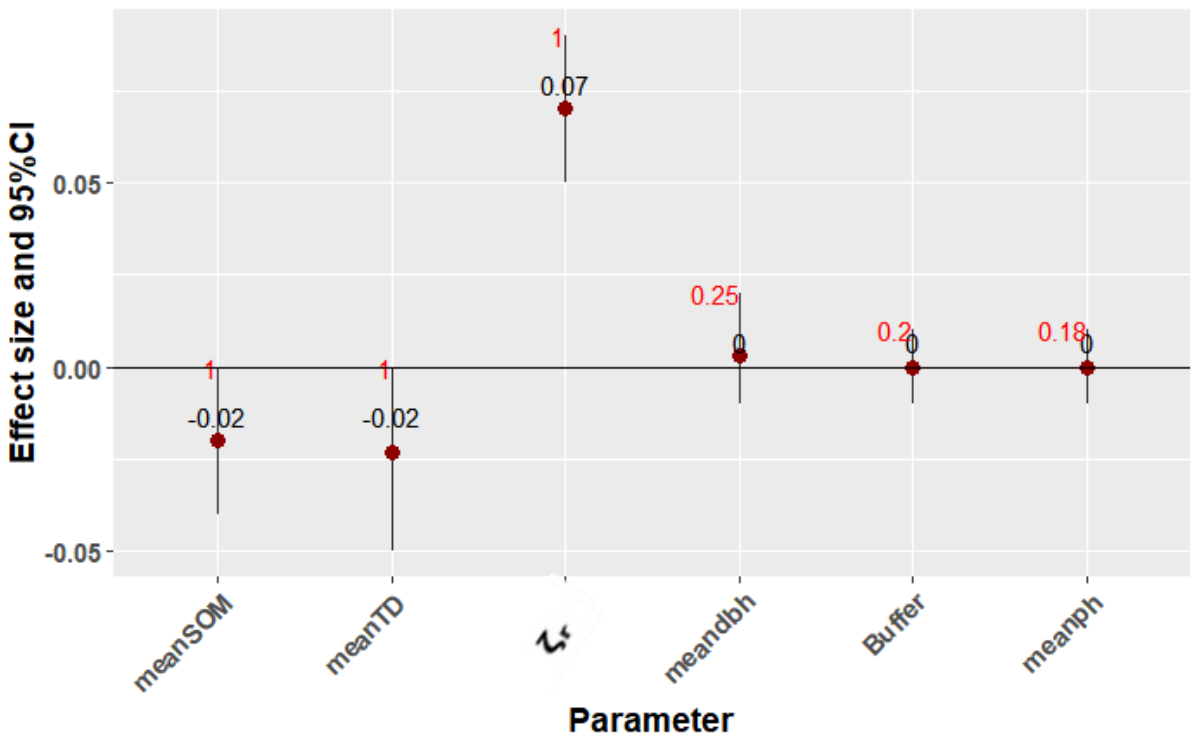

Figure 5. Model averaged effect sizes for plot z modelled with all the variables using δ < 1.5 for the model set. Variable importance is in red.

Discussion

VARIABLES AFFECTING SPECIES RICHNESS

HETEROGENEITY

Model-averaging and the GBM showed nine variables as affecting richness of the woodlands. Three of these represent heterogeneity: ζr, number of NVC codes and PHI. Of these, number of NVC codes and PHI are present in every model in the model set and ζr is present in 80% of the models. The GBM selects ζ_r as the most influential variable.

The greater PHI, the more evidence there is of woodland management, open areas and riparian zones. This implies that all these features are required to maximise richness. The number of NVC codes and ζr quantify the number of different species assemblages. Different species assemblages are more likely to occur if environmental conditions differ across the woodland – for example, different levels of soil

moisture or different light levels, again stressing the importance of heterogeneity within the woodlands.

MEAN-DBH AND MEAN-LBA

Model-averaging shows mean DBH to have a negative effect on richness and the GBM selected mean LBA as influential. This is to be expected, as an increase in either variable implies succession in the woodland [Packham et al., 2001; Smart et al., 2014] which leads to increased homogeneity because of a strengthening of the shading filter on the understorey species pool [Keith et al., 2009], again indicating the importance of woodland management schemes, such as coppicing, to vary the successional status of the woodland.

BUFFER

Buffer size had a significant positive effect on richness and occurred in every model in the model set. The size of the buffer relates to the amount of the woodland that is exposed to natural habitats and therefore has two potential effects. Firstly, the larger the buffer the more connected the woodland (habitat fragmentation is known to have a negative impact on biodiversity, [Quine, 2011, Watts et al 2008]). Secondly, the larger the buffer, the more protected the woodland from agrochemicals and airborne environmental pollutants; particularly around the edges [Draaijers, et al., 1988], which are linked to reduced species richness [Bobbink et al., 1998; Pallet et al., 2016, Simkin et al., 2016; Stevens et al., 2016]. Previous research has suggested that buffer regions should be included around woodlands for various reasons, including protection from anthropogenic influences [McWilliam et al., 2010] and vehicle pollution [Bignal et al., 2008]. It is not possible within this dataset to ascertain the mechanism for the increase in richness with buffer, but this work agrees with previous authors; larger more connected woodlands tend to have greater plant species richness.

NORTHING

Northing is selected as an influential variable by the GBM. This is in contradiction to previous authors, [Gilman et al., 2014; Ohlemuller & Wilson, 2000]. A bivariate plot of Northing with mean TD (figure 6) shows a negative correlation, suggesting that the increased richness could be due to the addition of light-demanding species.

The Scottish woodlands might also consist of plant communities which tend to be richer. For example, if Scottish woodlands were predominantly W6 eutrophic Alder woodlands, they would be richer than W14 beech woods which are common in the South. However, figure 7 shows that this is not the case. The distribution of NVC communities is similar in the North and South. What is noticeable, however, is that for the same community, richness tends to be greater in Scotland (figure 8). This suggests that other variables, not availabe in this dataset, may be responsible for the increased richness in Scottish woodlands, or that a combination of positive predictors is more likely to co-occur in the more Northern woodlands.

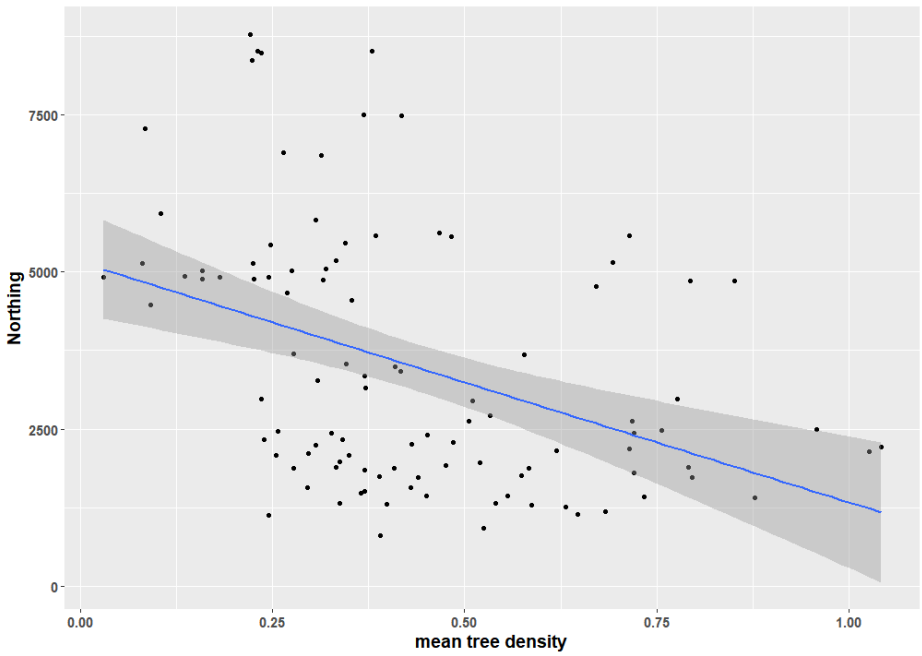

Figure 6. Scatter plot of northing with mean tree density suggests that the northern woodlands are more open. This could allow the inclusion of more light-loving species assemblages and hence add to species richness.

Distribution of NVC codes in English and Welsh woodlands

Distribution of NVC codes in Scottish woodlands

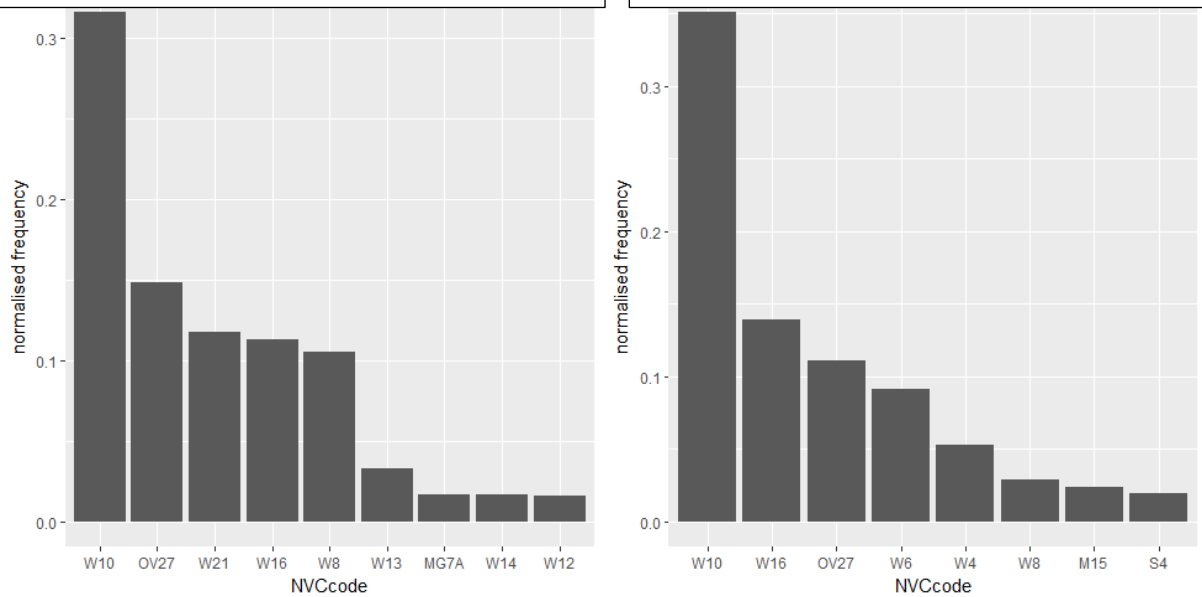

Figure 7. Distribution of NVC codes in Scotland and England and Wales. In both areas 30% of communities are W10, Quercus robur woodlands. These communities have one of the widest range of species richnesses of all NVC communities in this dataset.

351

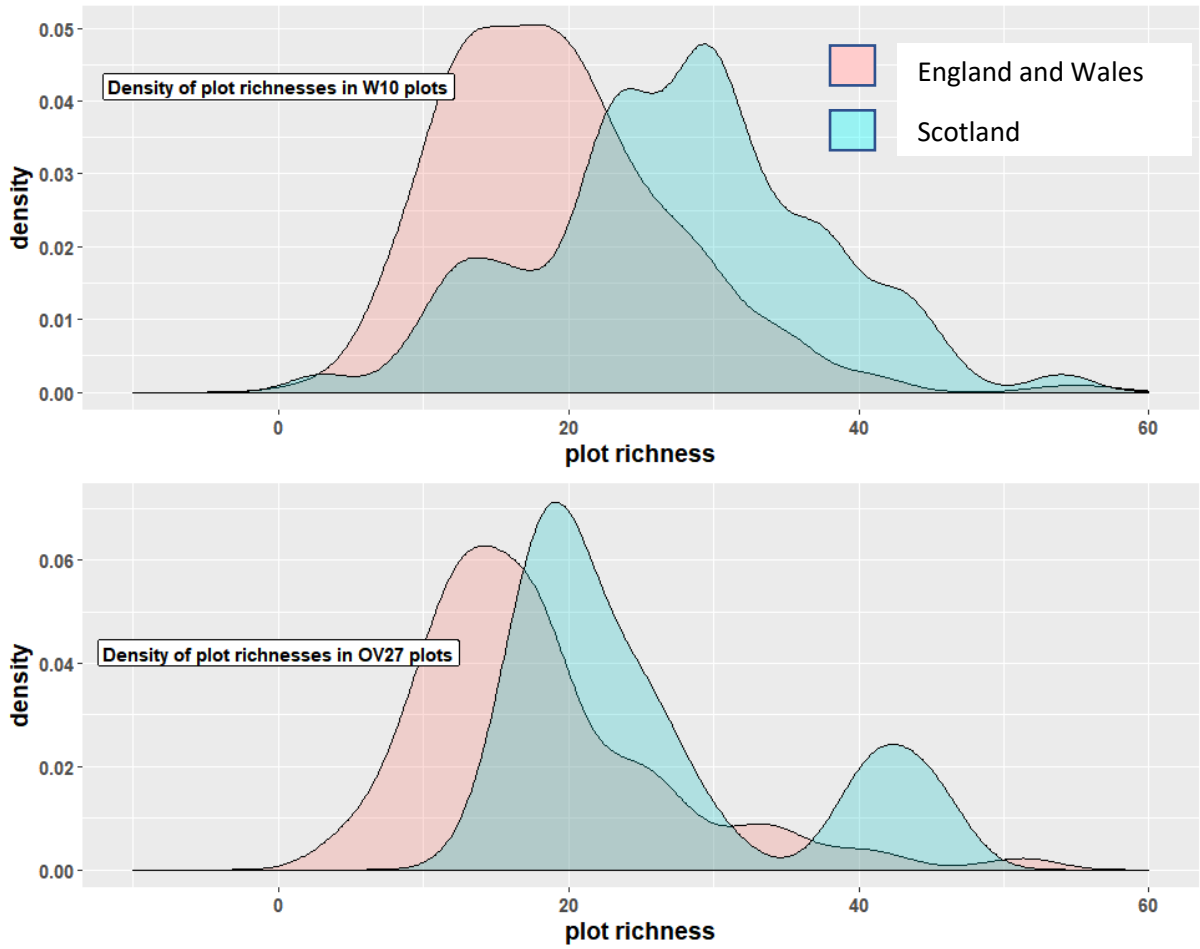

Figure 8. Density of plot richness for the most common NVC codes in the dataset in Scotland and England and Wales. Given the same NVC community, richness tends to be greater in Scotland for these common communities. Although OV27 is not a woodland community, it was was common in this dataset, demonstrating open areas within the wood.

SOIL ORGANIC MATTER

SOM content was shown to have a significant and important negative effect on species richness in agreement with Koojiman & Cammeraat [2010]. Organic soils have low pH and low pH soils in woodlands results in low species richness, [Cornwell & Grubb, 2003]. However, in this data, very few of the plots were located on organic soils. The six NVC codes shown in table 3 represent 82% of all plots surveyed and give an indication of the majority of soil types.

Table 3. Soil types for the most common NVC codes in this data

NVC code	% of plots	Soil type
W6 *Alnus glutinosa-Urtica diocica*	5%	Eutrophic moist soil alluvial or on flood fen peat
W8 *Fraxinus excelsior – Acer campestre – Mercurialis perennis*	9.5%	Dry calcareous soils
W21 *Crataegus monogyna – Hedera helix* scrub	10%	Various, base rich
W16 *Quercus* spp. – *Betula* spp. – *Deschampsia flexuosa*	11.5%	Very acidic, oligotrophic, pH<4, sandy podzolic
OV27 *Epilobium angustifolium* Open habitat	14%	Various, fertile, damp
W10 *Quercus robur – Pteridium aquilinum – Rubus fruticosus*	32%	Neutral brown earths

Of these, only W6, 5% of the total, are potentially on peat, but W6 is a high nutrient, high richness community. It is therefore unlikely that the reduced richness with SOM is caused by reduced richness expected on organic soils.

The reduced richness could be due to low pH on other soil types since increased SOM has been shown to decrease pH [Russell, 1960; Williams & McDonald, 1960]. On the other hand, adding SOM can also increase pH, depending on the initial acidity of the soil and the nature of the litter [Ritchie & Dolling, 1985]. In this analysis, increased SOM appears to correlate with either decreased or no change in pH (figure 9).

Figure 10 shows that all the common NVC communities tend to show reduced richness as SOM increases, regardless of soil type. Given also that the NVC code represents a community with similar physical conditions, such as nutrient levels, soil pH and light levels, and while the response to richness with increased SOM is seen across all communities, this finding implies that the variation in richness

with SOM is unlikely to be due solely to one of those physical conditions, but perhaps to another factor not measured in this dataset.

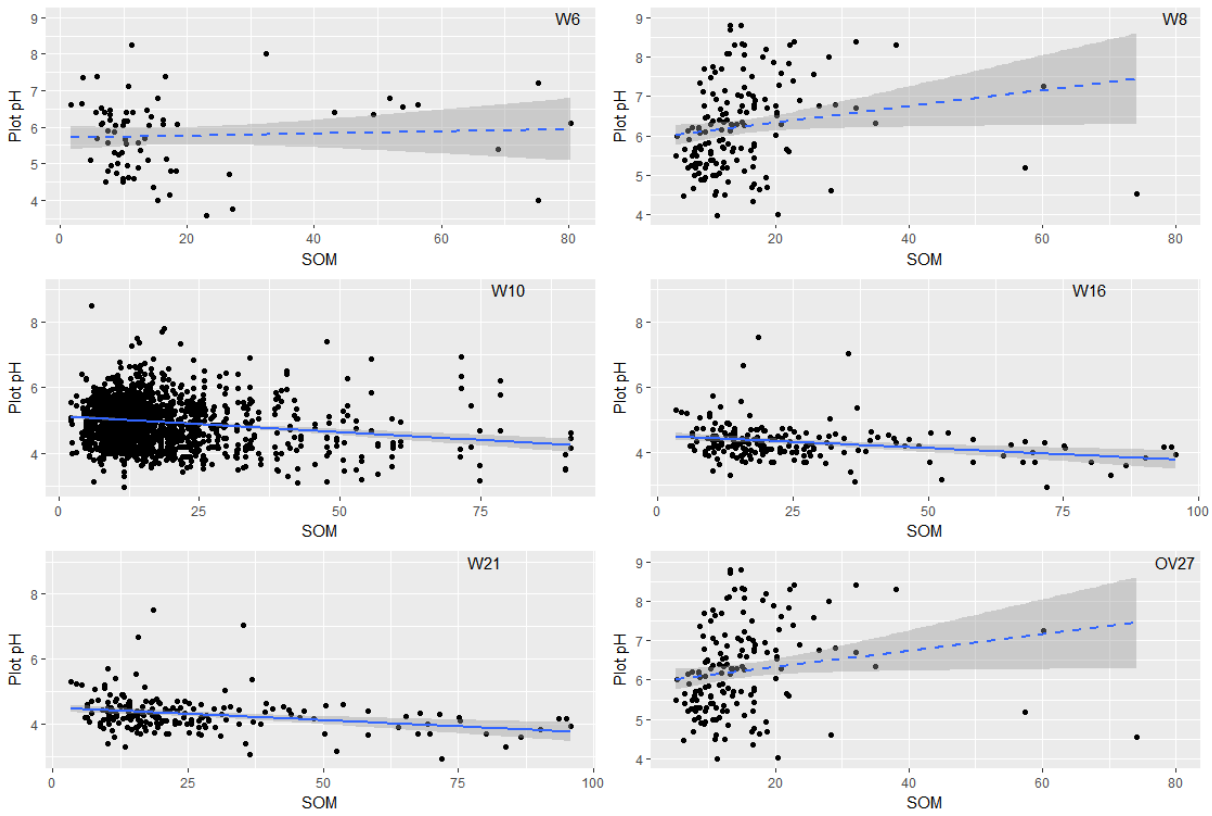

Figure 9. Change in plot pH with SOM content. For W10, W16 and W21 plots the pH reduces with increased SOM but this effect is not clear for other plot types

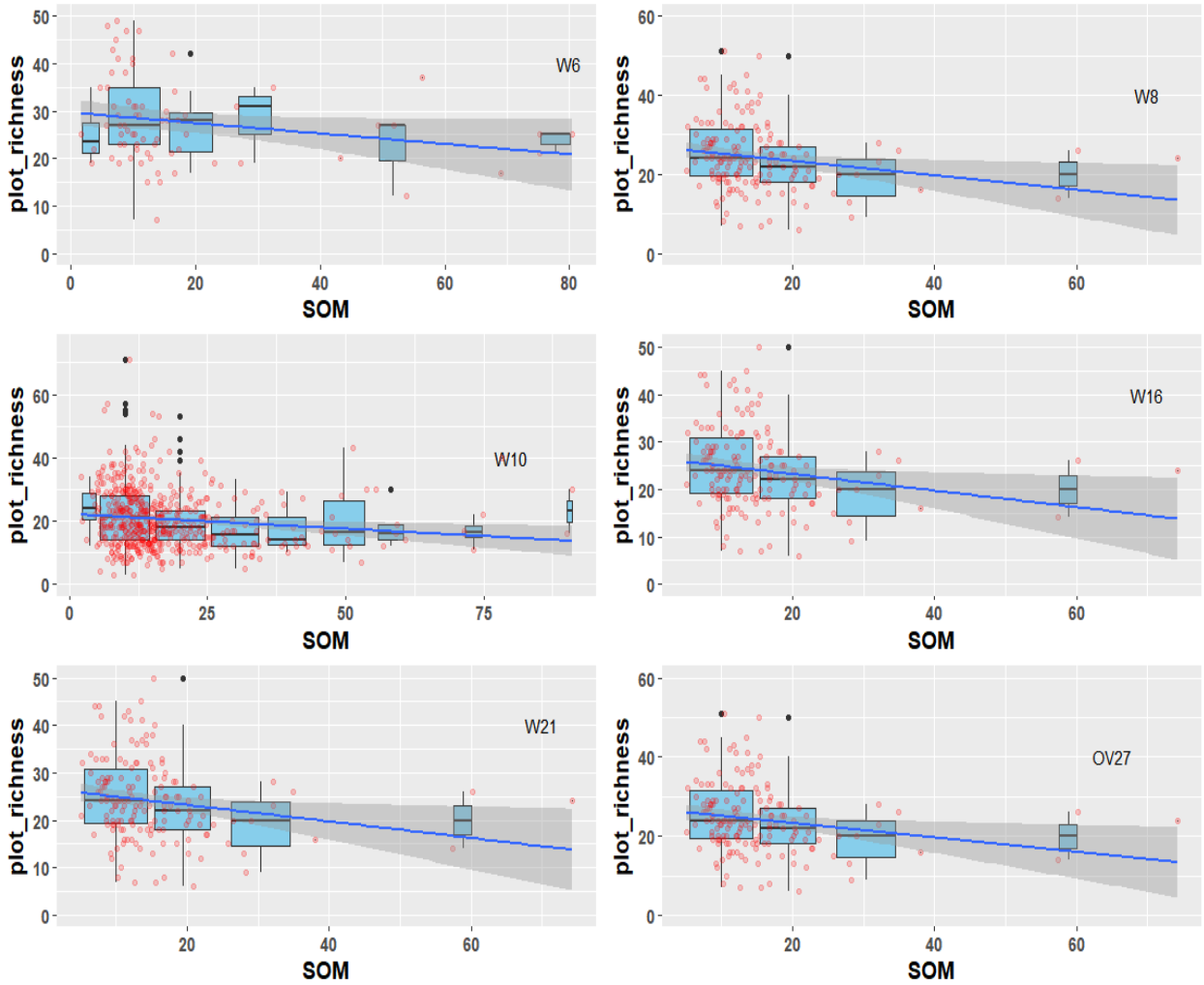

Figure 10. Plot richness with SOM for the six most common NVC communities in this data. The blue boxplots show the range in richness when grouped, the red dots are the raw ungrouped data. The variation in richness is high when SOM is low and vice versa.

Increased nitrogen deposition can both increase SOM [Fang et al., 2014; Zak et al., 2016] and reduce richness [Bobbink et al., 1998; Pitcairn et al., 2002; Simkin et al., 2016; Stevens et al., 2016]. A smaller buffer could allow increased nitrogen deposition, [Draaijers et al., 1988; Kennedy & Pitman, 2004], which might be reflected in the Ellenberg N values [Maskell et al., 2010]. Therefore, if woodlands with smaller buffers showed both increased Ellenberg N values and increased SOM, nitrogen deposition might be the mechanism behind the change in SOM and the reduced richness. In support of this figure 11 shows that while buffer is negatively correlated with Ellenberg N values, but, in

contradiction, it is positively correlated with SOM content. The latter association may be confused by the location of plots within the woodland.

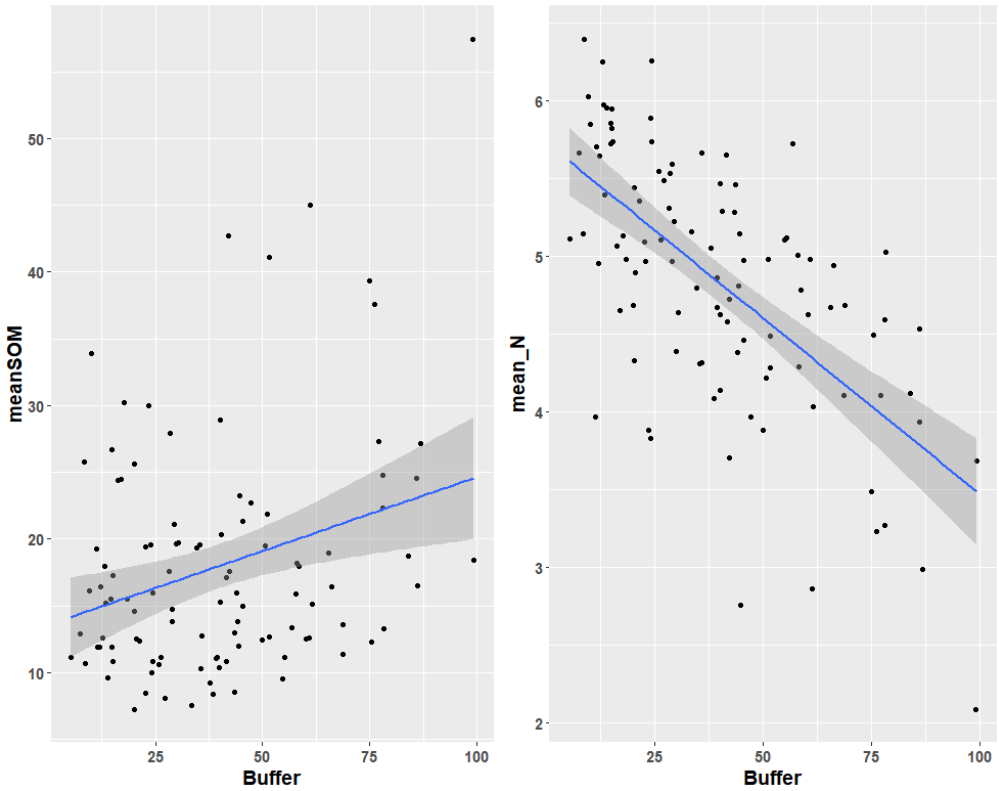

Figure 11. Change in mean SOM and Ellenberg N values with Buffer size. If nitrogen deposition was leading to increased SOM, then woodlands with smaller buffers would have greater SOM and larger Ellenberg N. The graph on the right shows that smaller buffers correlates with higher Ellenberg N, but not to greater mean SOM.

In summary, whilst SOM is negatively correlated with species richness, the causal mechanism is not evident. However, other authors, using modelled estimates of nitrogen deposition rather than Ellenberg N values with this dataset have shown positive correlation between SOM and modelled nitrogen deposition, [Kirby, 2005]. It is also interesting to note that nitrogen deposition values were on average lower in Scotland [RoTaP, 2012], which may be another factor contributing to the increased richness of the more Northern woodlands.

SOIL pH

The GBM selected mean pH as important for predicting species richness. Figure 12 demonstrates that in this data plot richness does have a unimodal response to plot pH, in agreement with Cornwell & Grubb, [2003]

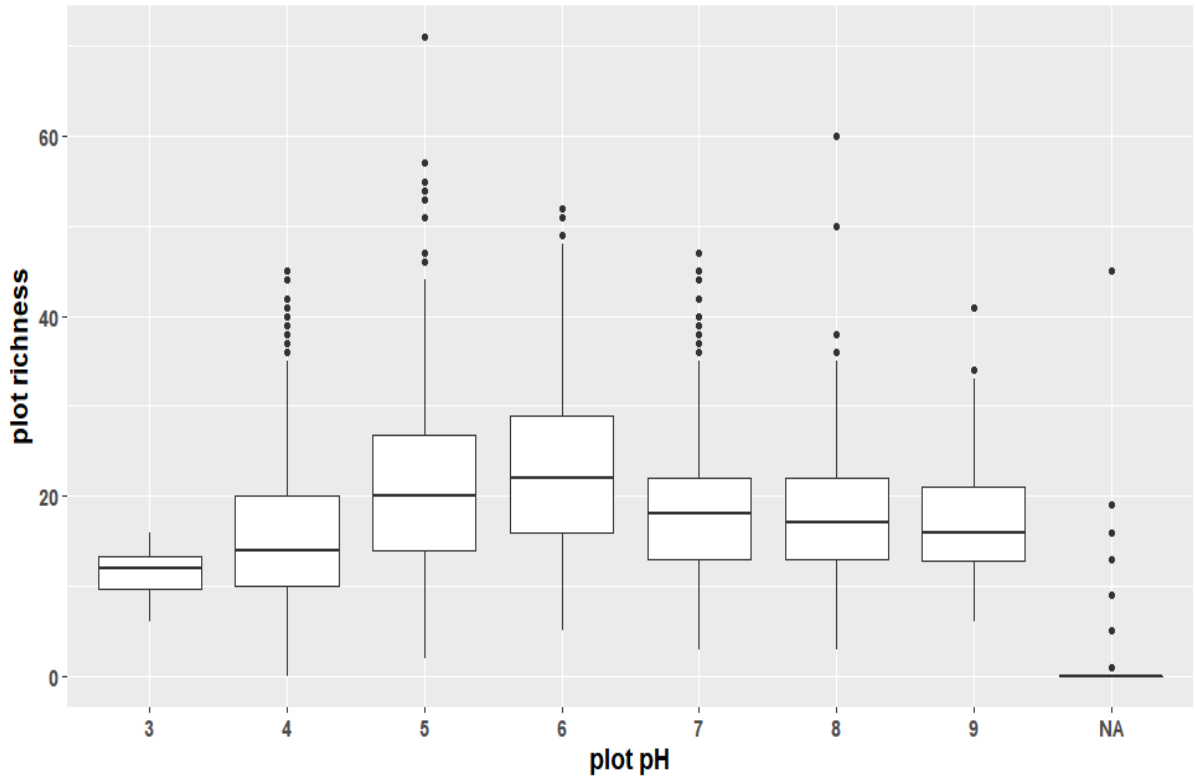

Figure 12. Plot richness response to pH can be seen to be unimodal with a peak around pH6.

EFFECT OF DRIVERS OF SPECIES RICHNESS ON GRADIENT OF SPECIES AREA CURVE AT TWO SCALES.

The fitted nest *z* values were distributed around 0.25. This agrees with the value of z predicted by other authors [Preston, 1962, Connor et al., 1983; Sugihara, 1976]. At the larger scale, plot z was found to be distributed around 0.5. These two values correspond to those found by Crawley & Harral [2001] for vascular plants in the county of Berkshire, South East England.

At smaller scales, PHI has a significant positive effect on nest z while SOM has a negative effect. This model suggests that biological variables appear to be influencing the slope of the species area curves, in contradiction to the remarks of other authors [Connor et al., 1983; Sugihara, 1976; Tjorve & Tjorve, 2017], but this is not necessarily the case. Both Sugihara [1979] and Tjørve & Tjørve [2017] point to the role of community structure and aggregation in shaping the species area curve. PHI, by introducing elements into the woodland that increase plant species richness, is likely, on average, to be increasing the richness of each plot. This will imply a more diverse community over which the curve is constructed. Similarly, SOM can have a homogenizing effect on the plots due to loss of species richness, either directly [Kooijmann & Cammeraat, 2010] or because increased SOM indicates increased nitrogen deposition and eutrophication that favours the abundance of competitive species potentially suppressing species diversity in the understorey, [Maskell et al, 2010, Pallet et al 2016]. Both PHI and SOM can be seen therefore, as influencing community structure either positively or negatively and so effecting nest z. It should also be noted that model-averaged R^2 for nest z was only 0.31, and that of the full model 0.33 so neither of the variables explained substantial variance in nest z.

At larger scales ζ_r has a significant positive effect on plot z, and mean SOM and mean TD have a significant negative effect. ζ_r is significant at the larger scale because it represents species turnover across the woodlands. The greater the species turnover, the greater the expected slope. Similarly, increasing mean TD and mean SOM are likely to have a homogenising effect on the woodland and therefore, to reduce plot z. At the larger scale, it is species turnover and heterogeneity that has been shown to influence the exponent of the species accumulation curves rather than biological factors. At this scale the model was more successful at explaining the variance in plot z, having R^2 of 0.44 for the model-averaged model and 0.47 for the full model.

VARIABLES OMITTED

The species richness model explained 47% of the variance in plant richness. Since we chose only those variables that we both knew were likely to affect richness and that were available within the dataset, several important potential variables were omitted which may improve the explanatory power of the model. Woodland age and past land use have been shown to affect species composition [Hermy, 1994] and richness [Dzwonko & Loster, 1989; Peterken & Game 1984]. Ancient woodlands are more likely to contain long-lived, poorly dispersing perennials whose migration to new woodland sites is limited [Kimberley, Blackburn & Whyatt, 2015]. This constrains the potential richness of new woodlands, particularly if they are isolated. Ancient cultivation has also been shown to induce a species compositional gradient and thereby increase richness [Dupouey et al., 2002].

Plant available phosphorus has been shown to reduce species richness of native plants in alder forests [Hrivnak et al., 2015]. Phosphorus eutrophication favours competitive species particularly at higher light levels and this can result in the exclusion of other species [Keersmaeker et al., 2004].

The amount of light reaching the woodland floor influences richness, with greater richness at higher light levels, [Kenedy & Pitman, 2004]. However, eutrophication together with high light levels encourages shade-intolerant, competitive species which tend to reduce richness, [Cornwell & Grubb, 2003, Keersmaeker et al., 2004]. Conversely, low pH in conjunction with low light levels can result in very little ground cover, [Cornwell & Grubb, 2003]

USE OF ζ_r AS HETEROGENEITY METRIC

Results presented here suggest that ζr is a useful way to quantify species turnover. This variable was selected as the most influential by the GBM and was significant when used in model-averaging. The fact that ζ_r was a significant parameter when modelling the slope of species accumulation curves across the wood, but not when modelling the slope of species area curves across plots, demonstrates

that it quantifies species turnover. This metric could be easily generated from species lists as an indicator to woodland managers of the number of different habitats within the woodlands.

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