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Modelling the impact of agri-environment scheme options on plants and soils

Bede R. F. West

2022

A thesis submitted to Bangor University in candidature for the degree Philosophiae Doctor

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Dedicated to my late father, without whom I would never have ended up here.
Jonathan West
01/10/1957 to 16/04/2018

Clancy of The Overflow

I had written him a letter which I had, for want of better
Knowledge, sent to where I met him down the Lachlan, years ago,
He was shearing when I knew him, so I sent the letter to him,
Just 'on spec', addressed as follows, 'Clancy, of The Overflow'

And an answer came directed in a writing unexpected,
(And I think the same was written with a thumb-nail dipped in tar)
'Twas his shearing mate who wrote it, and verbatim I will quote it:
'Clancy's gone to Queensland droving, and we don't know where he are.'

In my wild erratic fancy visions come to me of Clancy
Gone a-droving 'down the Cooper' where the Western drovers go;
As the stock are slowly stringing, Clancy rides behind them singing,
For the drover's life has pleasures that the townsfolk never know.

And the bush hath friends to meet him, and their kindly voices greet him
In the murmur of the breezes and the river on its bars,
And he sees the vision splendid of the sunlit plains extended,
And at night the wond'rous glory of the everlasting stars.

I am sitting in my dingy little office, where a stingy
Ray of sunlight struggles feebly down between the houses tall,
And the foetid air and gritty of the dusty, dirty city
Through the open window floating, spreads its foulness over all

And in place of lowing cattle, I can hear the fiendish rattle
Of the tramways and the 'buses making hurry down the street,
And the language uninviting of the gutter children fighting,
Comes fitfully and faintly through the ceaseless tramp of feet.

And the hurrying people daunt me, and their pallid faces haunt me
As they shoulder one another in their rush and nervous haste,
With their eager eyes and greedy, and their stunted forms and weedy,
For townsfolk have no time to grow, they have no time to waste.

And I somehow rather fancy that I'd like to change with Clancy,
Like to take a turn at droving where the seasons come and go,
While he faced the round eternal of the cash-book and the journal —
But I doubt he'd suit the office, Clancy, of 'The Overflow.'

by Banjo Paterson

Thesis summary

The premise that agri-environment schemes (AES) achieve their management goals and benefit biodiversity and landscape features as well as improve water and soil quality remain controversial. Their success is thought to be constrained by multiple factors such as target taxa, previous management and starting conditions. Modelling the responses of plants and soils and summarising these as indicators and metrics to determine the impacts of AES under global change, provides the basis of this thesis. The first chapter introduces global environmental

change and the place of AES in mitigating these and then moves on to explore predictive ecology and environmental modelling as useful sources of concepts, datasets and tools to support sustainable land management and policy in the in the UK. The objective is to use modelling to provide new evidence-based insights that help guide mitigation of global change impacts, principally agricultural intensification.

The second chapter explores the potential for grassland AES options in Wales (UK) to achieve expected impacts on plant diversity and soil condition. A 13-year time interval was modelled to estimate the response of plants and soils to AES options and climate change. Empirical models of soil response to extensifying grassland management were constructed from published experimental data and used to drive change in soil inputs to a small ensemble of ecological niche models for British plants. Outputs were summarised by grouping species by the ecosystem functions and services they support and by matching projected species composition to the National Vegetation Classification. Results indicated that at least 10 years of management under grassland AES options are needed to drive vegetation towards desirable plant assemblages more typical of lower fertility habitats while promoting desirable species groups and reducing undesirable ones. Also, management effects had a more marked effect on vegetation than climate variation within 13 years.

The third chapter focuses on tree planting as a commonly funded AES management prescription for afforestation, promotion of biodiversity and climate change mitigation. Using species niche modelling we explore how tree disease and climate change could limit achievement of these goals. In the temperate lowlands, succession takes 30 to 50 years to establish forest conditions, to explore establishment by planting, scenarios of broadleaved woodland development across Wales were modelled. This allowed estimation of the potential species composition of forests with, and without, climate change, and *Fraxinus excelsior* removal due to ash-dieback (*Hymenoscyphus fraxineus*). Results suggested some soil variables and woody species groups could achieve baseline forest values in less than 30 years. In contrast, other species groups failed to reach baseline equivalents within this time. Where *Fraxinus excelsior* was removed from the species pool it is expected that a scrub phase will persist or, if present, *Acer pseudoplatanus* will become dominant. The findings also indicated that given the UK's fragmented, habitats relying entirely on already degraded successional processes could lead to poor afforestation outcomes.

The fourth chapter concerns the effects of nitrogen (N) enrichment on UK grasslands and how indicators focused on this can or cannot be used to support assessment of AES success. Prolific use of N fertilisers and the exposure of natural and semi-natural ecosystems to surplus N has led to higher biomass production but has also created conditions that erode biodiversity. Also, gaseous N emissions from agriculture and fossil fuel burning lead to atmospheric deposition and accidental increases of N on land. These can be thought of as a 'hard rain' impacting vegetation positively or negatively by: stimulating higher crop yields or lowering diversity. The aims here are: to determine if N change will lead to a corresponding shift in grassland communities species composition; and to determine over what timescale changes in vegetation and soil can or cannot be measured. To explore this, modelling workflows were established consisting of: fertiliser-induced soil change using novel generalised linear mixed effect models; and, Bayesian models to estimate vegetation change caused by N deposition. This created scenarios reflecting change in N abundance inputs to the ecological niche model described in the previous two chapters. A novel result in the context of managing expectations from AES is that some changes in management are expected to take decadal timescales for measurable change to be observed. Thus, as indicators explored often showed little change

over the modelling duration, proof of management change as well measured indicators are advisable for results-based policy to determine AES outcomes.

The final synthesis chapter evaluates the magnitude and timescales of change expected under the AES prescriptions modelled and how this knowledge can be tied into current development and validation of future AES. Also, suggestions are made on methodological improvements to modelling AES outcomes as well as further research concerning long term ecological monitoring and big data use in ecology for large-scale restoration. The findings which concern the application of modelling to AES impacts can be summarised as a recommendation to fund longer and stronger AES prescriptions to ensure they achieve their goals. As ecological and environmental science to inform good AES design does exist, a novelty of the research is, that despite evidence of good practice being possible, the current approach is often insufficient. Therefore, the wider suggestion to improve AES delivery is regular monitoring and evaluation to inform ongoing adaptation-based design.

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Data Availability Statement

Summarised modelling data can be found within the appendices (including the DOI: http://dx.doi.org/10.13140/RG.2.2.10410.90560) and baseline datasets are within the following references:

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List of Abbreviations

AES – Agri-environment scheme

CAP – Common Agricultural Policy

CS – Countryside Survey

Eb/N/F/R – Ellenberg (Eb), nutrient (N), wetness (F), and reactivity (R) score

ERAMMP – Environment and Rural Affairs Monitoring and Modelling Programme

ENM – Ecological niche model

GMEP – Glastir Monitoring and Evaluation Program

SDM – Species Distribution Model

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Chapter one, introduction

1 | The power of foresight before hindsight: Predictive ecology applied to land-management and global change

1.1 | Land use and global change impacts on ecosystems

Climate change and habitat degradation are the two greatest threats to the biosphere and both are perpetuated by anthropogenic drivers (IPCC, 2018; Díaz *et al.*, 2020). As plants and soils form the trophic foundations of terrestrial ecosystems and play a major part in global biogeochemical cycling, maintaining them is crucial for natural resource production and at greater temporal and spatial scales for planetary function and life support (Millennium Ecosystem Assessment, 2005; Rockström *et al.*, 2009; Watson *et al.*, 2011).

Land management has a global impact on ecosystems and natural resource production, as described in the Millennium Ecosystem Assessment (Millennium Ecosystem Assessment, 2005) and the UK National Ecosystem Assessment (Watson *et al.*, 2011). Subsequent global reports have also raised similar concerns and have highlighted the need for the design of better land management regimes to mitigate or minimise the anthropogenic impacts on ecosystems (Simons and Weisser, 2017; Balmford *et al.*, 2018; WWF, 2018; Hayhow *et al.*, 2019).

1.1.1 | Agri-environment schemes and land management

Agri-environment schemes (AES) are designed to reverse the negative impact that agriculture (and land management) is having on ecosystem function by promoting more sustainable land management practices (Green *et al.*, 2005; Pe'Er *et al.*, 2019). Typically, AES incentivise land-managers to adopt or pursue practices or schemes mitigating deleterious environmental practices (Rose *et al.*, 2016) or, especially for higher tier AES interventions, to restore and create semi-natural habitat (Staley *et al.*, 2018). Until UK exit from the EU, the Common Agricultural Policy (CAP) has been the principle mechanism that has subsidised UK agriculture with a proportion of the EU budget for agricultural support being used to fund agri-environment

schemes with a view to making natural resource production more sustainable (Rose *et al.*, 2016; Pe'Er *et al.*, 2019). The reformation of AES is, however, now needed not only to improve the sustainability of land management (Pe'Er *et al.*, 2019) but also in light of Brexit to replace EU policies (Arnott *et al.*, 2019; Defra, 2020b). Examples of practices incentivised by AES include: leaving vegetation to grow at field margins or across grasslands to specific heights, reducing livestock numbers on land, reducing inputs onto land (typically fertiliser) and planting trees or seeding herbaceous plants (Rose, 2011; Defra, 2020b, 2020a); also looking to the future, UK AES are likely to focus more on promoting good soil management (Defra, 2018).

While AES refer to payments for alterations to agricultural practice this thesis considers land management subsidies beyond this, covering forestry as well (*see, Chapter 4*). While Rose (2011) defines AES as only being on agricultural land CAP does include woodland and scrub, e.g. Dadam and Siriwardena (2019). This provides a broader definition of AES inclusive of wider land management types covering forestry and conservation too. We use this holisitc definition of AES here. This also allows for parallel consideration of the holisitc AES definition with the UK government Environmental Land Management Scheme currently being developed (ELMS; Defra, 2020a)

The UK government and devolved administrations have commissioned reviews into the effectiveness of its agri-environment policy (Ormerod, no date; Oatway *et al.*, 2018) and are developing new environmental land management schemes (ELMS) currently (Defra, 2020b, 2020a). Therefore, research into the impacts of AES on plants and soils is timely and much needed.

Given the scale and time spans of AES, being national and up to 15 years in duration, with contracts typically lasting 5 years (Rose, 2011), monitoring their success remains important but challenging (Ormerod, no date) and has been a European reporting requirement (Oatway *et al.*, 2018). This is particularly crucial as not only do AES represent a large-scale tool to tackle global environmental issues but they also represent a major cost to the governments that fund them (Pe'Er *et al.*, 2019). Therefore, confirming success or determining the level of achievement is both environmentally and economically desirable.

Undertaking national scale environmental, farmer and economic AES monitoring is no small feat given the time span and area that has to be covered; this has only been attempted once within the UK, in Wales (Emmett, Alexander, *et al.*, 2016; Emmett *et al.*, 2017). Even within these projects, an assessment of the baseline data took several years of resurvey and determined that AES effects will take multiple years to become apparent (Alison *et al.*, 2020). Therefore to get the most out of, and add value to, the data that are produced from small to large scale AES monitoring (Ormerod, 2012a) it has been recommended that modelling is used to explore possible outcomes into the future to better inform policy and management (Ormerod, no date). Modelling using fine-resolution monitoring data is an attractive option for exploring future ecological responses to new packages of interventions over varying timescales and in the presences of additional external drivers such as climate change and pollutant deposition (De Chazal and Rounsevell, 2009; Mantyka-pringle, Martin and Rhodes, 2012; Titeux *et al.*, 2016).

1.2 | Introducing predictive ecology as key for the future

A comprehensive understanding is important for protecting and safely managing the ecosystems upon which we and other species depend, now and into the future (Rands *et al.*,

2010; Evans *et al.*, 2013; Mouquet *et al.*, 2015). This is why predictive ecology (as defined by, Evans *et al.,* 2013) is key for the future. Direct human activities and anthropogenic global changes are having major negative impacts on ecosystems (Green *et al.*, 2005; Millennium Ecosystem Assessment, 2005; IPCC *et al.*, 2014; Díaz *et al.*, 2020). Without attempts to predict the changes from these major factors it will not be possible to cope strategically and proactively with the impact they are likely to have (Evans *et al.*, 2013; Mouquet *et al.*, 2015). It would be a suboptimal and unpragmatic approach to engage in reactive management, that is waiting for an outcome and managing its consequences versus prior moderation of human activity to avert cost and build resilience to further driving forces. This requires forecasting outcomes and therefore requires predictive models. Even if they are wrong they are normally useful when constructed with good reasoning (Box, 1979). Predicting potential outcomes to inform: decision making, management, preparing for future change; to remove, reduce or mitigate negative impacts on ecosystems and natural resource production systems is vital for future planetary stewardship (Evans *et al.*, 2013; Guillera-Arroita *et al.*, 2015).

Ecological modelling is a well-established field and there are many examples where models have successfully informed decision-making (Schneider *et al.*, 2003; Harrison *et al.*, 2006; Sattler *et al.*, 2007; Venette *et al.*, 2010; Uden *et al.*, 2015).

1.2.1 | Modelling environmental variables for ecosystem change

Environmental change cannot be considered in the context of a single variable given the complexity of the interrelationships between environmental variables and nature e.g. climate models explore, temperature, precipitation, humidity, wind etc. (Lowe *et al.*, 2018; Sillero *et al.*, 2021). For this reason, predictive ecology considers the use of multiple variables from biotic to abiotic and this often leads to layered modelling work flows e.g. ecological niche models and

climate change models used in Harrison *et al.* (2006). However, as climatic-only ecological niche models (ENM, *see, 1.4*) often exclude local conditions a wider range of variables do need to be considered (Diekmann, Michaelis and Pannek, 2015; Sillero *et al.*, 2021), particularly here as land management intensity is often a good predictor of other biotic variables (Green *et al.*, 2005; Gossner *et al.*, 2016; Simons and Weisser, 2017). Even beyond local biotic conditions and climate change there are other global and local environmental variables that can effect ecosystems across scales, examples being: nitrogen deposition effects on vegetation (Stevens *et al.*, 2016) or successional stage and plant height traits (Brunet *et al.*, 2012). As detailed predictions beyond simple application of theory is needed, species niche models are used here to acquire estimates on future states. The reason niche models are applied is their ability to makes estimates with a given set of dimensions (environmental inputs) on how well a species is suited to conditions or how likely it is to occupy the site under the conditions observed or predicted.

Here four environmental factor types are considered given the relationships between land management; global change; plants and soils. These are detailed in sections *1.2.1.1* to *1.2.1.4* below.

1.2.1.1 | Climate change

Climate variables, mainly temperature and rainfall are known to affect species distributions, soil conditions, and are a major component of how we define biomes (Busby, 1991; Elith *et al.*, 2006; Alvarado-Serrano and Knowles, 2014; Urban *et al.*, 2016; Booth, 2017; Seaton *et al.*, 2020). Within the UK, the Met Office has been recording and modelling climate variables for decades. Its latest large dataset published, UKCP18 provides extensive past climate

observations and future climate predictions as key inputs for ecological modelling of climate impacts (Lowe *et al.*, 2018; Met Office Hadley Centre, 2018).

1.2.1.2 | Soil variables

Soil provides substrate for plants to grow in and represents a major loci of biogeochemical cycling (Gruber and Galloway, 2008). Given soil responses to management over time (Poulton *et al.*, 2003; Ashwood *et al.*, 2019; Xu *et al.*, 2020), soil variables are key for modelling ecological change especially at the local or finer scale (Diekmann, Michaelis and Pannek, 2015). Also soil variables, particularly macronutrients have been shown to give a linear response over time to management meaning that they can be simply modelled themselves (Poulton *et al.*, 2003; Thomaes *et al.*, 2012). Then these can be utilised as ENM inputs that may capture more nuanced species-environment relationships e.g. a unimodal habitat suitability response to macronutrient availability (Smart *et al.*, 2010).

1.2.1.3 | Plant and vegetation communities

Modelling species likely niche space or distributions is a common end point use of other environmental datasets (Elith and Leathwick, 2009; Peterson *et al.*, 2011; Sillero *et al.*, 2021) and these can be applied in modelling ecosystem services given relationships between species effect traits and service delivery (Lavorel *et al.*, 2011; Linney *et al.*, 2020). However, models covering sufficient species numbers to predict ecosystem change under differing scenarios are rare globally. In the UK the R (R Core Team, 2019) package MultiMOVE is an ensemble of ENM for all common and many rare plant species. This contains models for over 1000 plant taxa making it well suited to AES modelling (Smart *et al.*, 2010; Henrys, Butler, *et al.*, 2015).

1.2.1.4 | Biogeochemical cycling

The movement and change of major chemical elements; carbon (C), nitrogen (N), phosphorus (P) can link global change effects (Stevens *et al.*, 2004; Gruber and Galloway, 2008; Rockström *et al.*, 2009) and local management to the site level (Poulton *et al.*, 2003; Thomaes *et al.*, 2012; Ashwood *et al.*, 2019; Xu *et al.*, 2020). Modelling this or using published modelled data can tie the effects of local management change with global change (Stevens *et al.*, 2016; Levy *et al.*, 2020) resulting in improved model explanatory power and functionality (Diekmann, Michaelis and Pannek, 2015; Sillero *et al.*, 2021).

1.3 | Defining ecological niches and species models

To construct models for species, ecosystems, and management it is important to use clear terminology. Here I define a species realised niche as:
"The combinations of environmental and ecological factors that a species can exist in, that is within a given geographic region or biotic community, in combination with the impact that the species has on its surrounding resources, conditions and community." Adapted from Peterson *et al*. (2011).

The realised niche refers to where a species would actually be observed within an environment. If a species existing in isolation from constraining interactions with other species and suitable abiotic conditions for it, is considered, then this is the fundamental niche which a species can exist in. This is particularly useful when considering how changes in abiotic conditions may alter the geographic area where conditions are suitable for a species, thus possibly changing its distribution. Here a species fundamental niche is defined as the full range of conditions,

variables and interactions the species could exist in, this can be considered with or without species dispersal constraints (Colwell and Rangel, 2009; Peterson *et al.*, 2011).

A (species) ENM is any statistical or computational construct built to attempt to predict the suitability of a species to, or probability that a species could or will occur at a point within; an *n*th number of dimensions that the model can account for (Peterson *et al.*, 2011). These *n*th dimensions refer to any factor (spatial, temporal, trait based, abiotic or biotic) that can be considered to contribute to the realised niche (Colwell and Rangel, 2009; Alexander *et al.*, 2016). Models and metrics, however, cannot account for all the dimensions that make up a species niche due to the complexity of the natural world (Peterson *et al.*, 2011; Mouquet *et al.*, 2015). Ecological theory and research, with model construction considerations, limitations and parsimony, can help identify the minimum set of *n* dimensions that will define the niche sufficiently comprehensively to represent the space species occupy within them.

Here I use the term ENM (ecological niche model) rather than species distribution models (SDM) as the latter suggests the specific use of geographic spatial software datasets (Sillero *et al.*, 2021) where the goal is typically model occupancy at some grid square resolution. This differentiation is expressed in Colwell and Rangel (2009) where there is differentiation between niche space as ranges within *n* dimensions versus the real world geographic distributions (the biotope). This is important for context here as our focus is to predict change into the future with changing environmental conditions, not to explore current real-world distributions. Sillero *et al.* (2021) also provides a succinct differentiation of the two terms.

1.4 | Ecological niche model construction

Now a definition of an ENM has been established, the theory behind the construct of an ENM can be explored. To determine a species niche, the dimensions that define the ecological space in which the niche is embedded need to be considered (Elith and Leathwick, 2009; Boulangeat, Gravel and Thuiller, 2012). The dimensions in which a species exists are both spatial through, for example its dispersal from its point of origin and, also across environmental gradients or variables which may be less or more correlated spatially (Guisan and Thuiller, 2005; Boulangeat, Gravel and Thuiller, 2012). Environmental gradients are often abiotic, such as climatic variation which can be correlated with other variables such as altitude. Both maybe possible to map at varying resolutions hence a key consideration is the availability of datasets that can be used to quantify gradients in the niche dimensions across a geographical area. Many candidate variables that underpin a niche dimension can be correlated. Others may be less correlated but causally related to a mixture of other variables. For example current soil nutrient availability can be a complex function of existing soil type, related to climate and parent material, but interacting with legacy effects of land management history (Hawkins *et al.*, 2007; Sillero *et al.*, 2021). Biotic environmental variables refer to interactions with other species which fall into four types, predation, competition, parasitism, and mutualism which determine the species abundance and existence alongside other interacting species (Hirzel and Le Lay, 2008; Preston *et al.*, 2008; Alexander *et al.*, 2016).

1.4.1 | Biotic, abiotic and dispersal dimensions

The niche dimensions are conceptualised in the Biotic, Abiotic and Dispersal variables diagram (BAD diagram, **Fig. 1.1**) below. This allows niche dimensions to be considered conceptually with the location of realised species niche represented by the overlap of the different dimensions to create a space suitable for the species to exist. It is also important to remember that species are distributed through time (Elith and Leathwick, 2009) via their phenology and

their life span, particularly with the death of an individual creating a new opportunity for establishment by offspring of the same or different species.

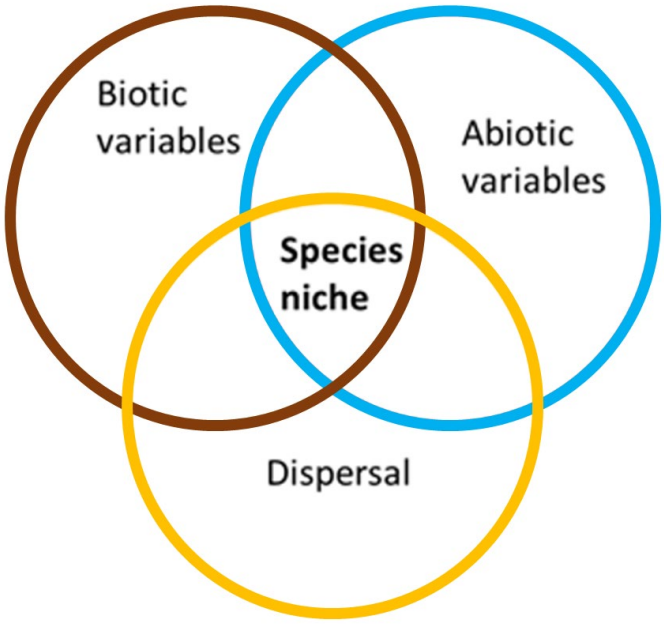

Figure 1.1. Biotic variables represented by the brown circle, Abiotic variables represented by the blue circle and Dispersal represented by the yellow circle to create the BAD diagram. Ideal conditions for the species are represented by the central space labelled **Species niche**. The yellow and brown bounded area in the bottom left represents where the plant species can disperse to with other plant species but where abiotic variables are unsuitable for establishment. The yellow and blue bounded area in the bottom right represents where the plant species can disperse to and grow under abiotic conditions but other plant species interactions fail to allow the species to establish. At the top, the brown and blue bounded area represents where biotic and abiotic conditions are suitable for the plant species but it cannot or has not dispersed there. Adapted from Peterson *et al.* (2011).

For model construction, it is not pragmatic to measure everything affecting the niche space shown in the centre of **Fig. 1.1** and it is likely to be impossible due to practical limitations in sampling. In order to be pragmatic and still create a model that considers niche space adequately, the right measures to represent the niche need to be selected (Elith and Leathwick, 2009; Sillero *et al.*, 2021). Spatial dimensions also need to be considered carefully in model construction as autocorrelation naturally occurs between space and environmental gradients (Guisan and Thuiller, 2005; Hawkins *et al.*, 2007), usually summed up as *nearer things are more similar*.

Ecologically relevant and suitable metrics must be chosen to represent the species niche for use in models as this allows for robust scientific explanation and insight through using

established theory also allowing for the construction of further theories (Guisan and Thuiller, 2005; Elith and Leathwick, 2009; Sillero *et al.*, 2021). Models that deliberately contain spatial components must be considered at the suitable scale so that model components are representative of the area and sites studied (Guisan and Thuiller, 2005; Sillero *et al.*, 2021). Difficulties can occur when the resolution of input data varies and when input and output spatial scales differ. A common disparity of scale is geographic climate data versus finer resolution sample data that record the occurrence of a species, this can cause several different problems in reliability (Guisan and Thuiller, 2005; Trivedi *et al.*, 2008; Mouquet *et al.*, 2015):

- Where input data scales vary (ideally, they should match), it can be simplest to use the coarse resolution to avoid error, averaging across cells to match resolutions.
- Alternatively, it may be possible to statistically split coarse cells to allow for combination with finer cells and increase precision.
- If output resolution is too coarse then finer variability in environmental mosaics will be unaccounted for.
- For overly fine output resolutions then variability may be predicted which does not exist.

For models without a spatial input requirement (e.g., those built non-spatially on data for species present in specific conditions) the above is less relevant (Sillero *et al.*, 2021). However, it still needs to be considered if for example a spatial climate dataset is taken apart to give seasonal temperature inputs. This is considered in Elith and Leathwick (2009) particularly under the heading “The Interplay of Geographic and Environmental Space”.

To further explore the **Fig. 1.1** BAD diagram abiotic and biotic inputs need consideration aside from the spatial model components discussed above (Hirzel and Le Lay, 2008; Sillero *et al.*, 2021). Abiotic inputs are used comprehensively in species ecological niche models (Elith and Leathwick, 2009; Bocsi *et al.*, 2016; Booth, 2017); especially climatic variables (Pearson and Dawson, 2005) as they are easy to obtain (Sillero *et al.*, 2021) and are directly suitable as

inputs. There is also a huge resource in terms of data and literature on species and climate relationships as temperature and precipitation are the major drivers of vegetation type at the biome scale (Urban *et al.*, 2016; Booth, 2017). Non-climatic abiotic inputs become more important when models are applied at local or site levels allowing for more heterogeneity to be accounted for (Hirzel and Le Lay, 2008; Elith and Leathwick, 2009; Diekmann, Michaelis and Pannek, 2015).

Biotic input components of models need careful consideration for incorporation (Pearson and Dawson, 2005; Boulangeat, Gravel and Thuiller, 2012) as biotic interactions are only easily expressed indirectly through correlative means unless experimental interactions are known or measured and appropriately modelled (Hirzel and Le Lay, 2008; Alexander *et al.*, 2016). However, through modelling species at separate localities and then modelling where they occupy the same space and comparing, this allows for information to be gained on how species interact or compete under the independent variables used for the modelling (Hirzel and Le Lay, 2008; Alexander *et al.*, 2016). An example of this is the approach of creating multiple models for a species niche to create a layered model structure like that applied in Boulangeat *et al.* (2012). Although good ecological theory and knowledge is vital to justify biotic components of models (Preston *et al.*, 2008), the simplest way correlative models can attempt to incorporate biotic interactions is to ensure inputs are from situations where species interactions are present and are thus expressed indirectly through effects on model inputs e.g. presence and absence data (Hirzel and Le Lay, 2008). However, this does not guarantee, and may prevent, robust capturing of true interactions as without data specifically expressing species interactions as they are likely to be under represented; this often requires dynamic modelling that is far more data intense than correlative modelling (Guisan and Thuiller, 2005).

The bottom and final component for the BAD diagram (**Fig. 1.1**) is dispersal. This is often unaccounted for or poorly captured in ENMs. This is because dispersal is difficult to measure and incorporate into models. Some models capture dispersal to some degree through sampling entire species ranges so allowing a coarse estimation to be made of where the species may colonise within or near its distribution (Elith and Leathwick, 2009; Boulangeat *et al.*, 2012). A common approach is to make assumptions about species dispersal, which should be biologically justified. This can be done by, predicting that species will colonise anywhere within their range that has suitable conditions, only applicable to widespread easily dispersing species (Peterson *et al.*, 2011) or using a dispersal predictor per species that can show distribution change over a given increment in time or environment (Boulangeat *et al.*, 2012). This usually centres on the use of traits such as seed number and seed size (e.g. Liu, Cossu and Dickie, 2019), which correlate with dispersibility. The constraint on this approach is that it relies on representative database measurements and is still only a proxy for the dynamic and probabilistic process of dispersal (Kimberley *et al.*, 2016). The post dispersal process of a species colonising a site refers to its establishment phase. Hence dispersal constraint leads to the conjecture that communities may not be saturated since favourable abiotic conditions and species packing theoretically provide unrealised or colonisable niche space. One approach is to treat vegetation patches as unsaturated and therefore include species from the local species pool as potential members of new assemblages but dependent on management intervention to overcome dispersal and establishment constraints (Mateo, Mokany and Guisan, 2017).

Additional theory behind the construction of an ENM, includes a number of conceptual assumptions that must be accounted for in the modelling process. The first consideration for correlative models throughout this work is that: environmental conditions making up niche dimensions adequately circumscribe the ecological space occupied by the species. (Elith and

Leathwick, 2009; Guillera-Arroita *et al.*, 2015). Another key component to correlative modelling is that species in the training data are at equilibrium with their environment under a reasonable number of conditions (sensu Sillero *et al*., 2021). If this is not the case then the model is likely to have poor or incomplete niche dimensions and may produce inaccurate predictive results (Hirzel and Le Lay, 2008; Elith and Leathwick, 2009). An exception to this, or more accurately a work around, is exemplified in Uden *et al*. (2015) where iterations of ENM constructions are demonstrated to be useful for estimating the spread of invasive species. An alternative to work around equilibrium assumptions to predict the suitability of a species to the environmental variables modelled, is favourability modelling in Chamorro *et al.* (2020).

Major considerations beyond input data types and abiotic, biotic and dispersal factors are statistical and computational model construction. As methods for this should be adequate both to compute the species niche space and be fit for end use (Elith *et al.*, 2006; Guillera-Arroita *et al.*, 2015), consideration of modelling methods and model testing are focused on in the next section.

1.4.2 | Ecological niche model components

The previous section can be thought of as considering aspects of robust design for ecological niche models. This section discusses the components of a workflow required to build a model. The modelling process can be broken down into three steps, building, running and applied use; as well as the construction of the model workflow, inputs (*see, 1.4.1 and 1.2.1*), modelling method and outputs. The thematic diagram in **Fig. 1.2**. provides a visual layout of this.

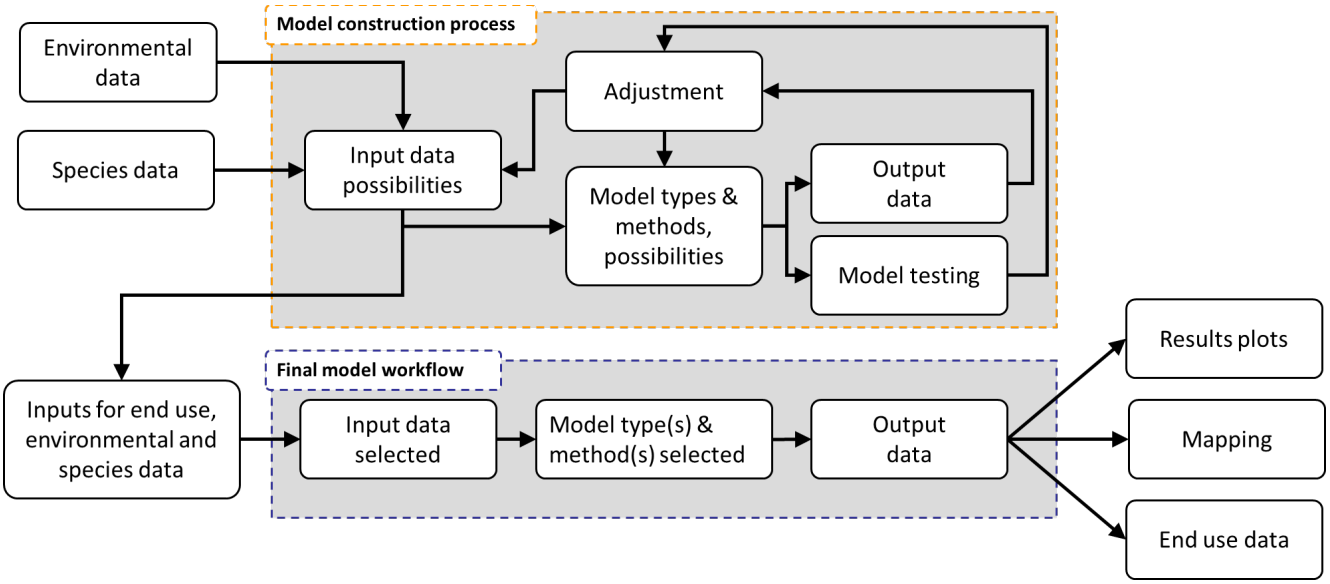

Figure 1.2. Thematic diagram showing inputs used for consideration in construction and final inputs. The orange box shows the process of constructing models via a testing process; providing input data and putting it through selected model types, then testing and adjusting until a final model construct is deemed suitable, as displayed in the blue box. Outputs can then be used for data visualisation, mapping or any suitable end use.

To start with the left-hand side of **Fig. 1.2**, the inputs must represent reality as closely as possible. This is relatively straight-forward with instrumentally measurable environmental variables (*see, 1.4.1*) like pH or temperature with clear methodologies (Hirzel and Le Lay, 2008; Peterson *et al.*, 2011). However, this is not the case with species records (Guillera-Arroita *et al.*, 2015). For example, the simplest form of species input data is presence data, a record of a species being at a site at a given time. Complications arise with imperfect detection, for example if a surveyor goes to a site and fails to record a species when it is present then this site data is omitted from model construction. Further complexity for detecting species and acquiring representative data is added when different types of species data are used, types increasing in information content include: presence, presence and absence (or pseudo-absence), occupancy detection (species surveying and detection probability accounting) and abundance (Sillero *et al.*, 2021). Each of these types of data has potential issues: imperfect detection (false-presence, false-absence); can prevalence/abundance be properly estimated; and environmental bias (Peterson *et al.*, 2011; Sillero *et al.*, 2021). These can lead to inclusion of incorrect data or

omission of correct data (Peterson *et al.*, 2011; Guillera-Arroita *et al.*, 2015). The issues raised here must be considered in the data being used to construct a model so that they can be either understood as limiting factors or better still (if possible) accounted for, this can be done getting a measure of species detectability and sampling effort or at the very least understanding limitations of the data (Guillera-Arroita *et al.*, 2015).

The inputs boxes in **Fig. 1.2** are divided into three to represent the staged use of inputs. The first two input boxes, Environmental & Species, are used in the construction phase and are divided as they are gathered and considered for use in model construction separately (the Environmental box is not further divided for simplicity). The grey 'Input data possibilities' box (**Fig. 1.2**) represents input selection and calibration which is often needed to ensure the data is suitable as an input and in a useable format for the model type(s) selected, this is often time consuming to carry out; (Sillero *et al.*, 2021). Calibration requirements will be described in model type methodologies e.g. SPECIES (Pear*son et al*., 2002); or determined in the modelling process (Elith *et al.*, 2006). The box 'Inputs for end use' does not divide environmental and species data, as typically at end use, the data inputs needed have been streamlined into one or very few data sets. A grey input box is still included in the final model construct as a calibration step is still very often a requirement at this stage (Elith *et al.*, 2006; Sillero *et al.*, 2021).

Sections *1.4.1* and the start of this section describe model input considerations to ensure models are given the best possible data to use. The next part of the modelling construct is the model type itself. Since the 1980s, a rapidly increasing number of modelling methods have become available (Booth, 2017) meaning there is a wide variety to choose from. **Table 1.1** below describes the modelling methods used in the core ENM (MultiMOVE, *see,* 1.6.4 for selection and use) and central to the thesis providing an example of the advantages and

disadvantages of different methods. The five model methods types below are considered due to their ability to work with presence and absence data allowing for robust predictions of probability of occurrence, suitability and detection issues (Guillera-Arroita *et al.*, 2015; Sillero *et al.*, 2021).

Table 1.1. A selection of five commonly used modelling methods ordered by increasing complexity. These are utilised in the central ecological niche model of the thesis, MultiMOVE (Smart *et al.*, 2010; Henrys, Smart, *et al.*, 2015) used for predicting plant species change and vegetation community shifts.

Model name (& references)	Inputs	Method/ Process	Outputs	Strengths and Weaknesses
Generalised linear models (GLMs). (McCullagh and Nelder, 1989; Ferrier *et al.*, 2002; Elith *et al.*, 2006; Hirzel and Le Lay, 2008; Alvarado-Serrano and Knowles, 2014; Sillero *et al.*, 2021)	Environmental input data must be selected to be ecologically realistic and computable, may need calibrating. Species presence or presence/absence data.	Fits formulas, typically quadratic or higher power curves to explain variable relationships to species.	Varied dependent on model construction.	GLMs are considered strong for their clear interpretable construction and outputs, which display strong statistical relationships. This is however often the criticism of them as they can oversimplify environmental relationships.
Generalized Additive Models (GAM). (Hastie and Tibshirani, 1986; Ferrier *et al.*, 2002; Guisan and Thuiller, 2005; Elith *et al.*, 2006; Alvarado-Serrano and Knowles, 2014; Sillero *et al.*, 2021)	Environmental input data must be selected to be ecologically realistic and computable thus may need calibrating. Species presence or presence absence data.	The same fitting functions as GLMs. However, a data derived smoother function is applied to allow for more complex relationships to be modelled.	Varied dependent on model construction.	GAMs provide strong correlative models striking a balance between clear interpretable models like the GLMs and more computationally heavy models like machine learning techniques. This also gives the technique the potential to be to simplified to be realistic or over fitting, limiting wider model application.
Multivariate adaptive regression splines (MARS). (Friedman, 1991; Elith *et al.*, 2006; Phillips, Anderson and Schapire, 2006; Sillero *et al.*, 2021)	Environmental input data must be selected to be ecologically realistic and computable, may need calibrating. Species presence or presence/absence data.	Fits sectioned linear regression to the data partitioning lines to fit to the data.	Varied dependent on model construction.	Faster computationally than other similar models (GAM). Less black box like than machine learning methods. As with GLM and GAM simpler model structure may not account for more complex ecological relationships but is more easily interpreted than more complex model structures.
Neural networks (NNet). (Ripley, 1994; Pearson *et al.*, 2002; Guisan and Thuiller, 2005; Elith *et al.*, 2006; Sillero *et al.*, 2021)	Presence absence species data along with any ecologically relevant data representing niche dimensions as the model method can utilise any input.	Neural networks are machine learning techniques recognising patters e.g. where species occur with environmental conditions. Networks of layered neurons whose function links from one layer to the next. Multiple iterations through the layers allow the model to adjust itself to have the best explanatory power.	Dependent on construction method and inputs.	NNets are very powerful model types able to take any inputs for the model process. Due to their ability to accommodate complexity and their power they are prone to overfitting data. Also as a machine learning technique, they are somewhat opaque making interpretation of the model difficult.

Model name (& references)	Inputs	Method/ Process	Outputs	Strengths and Weaknesses
Random forest (RF). (Breiman, 2001; Sillero *et al.*, 2021)	Any species data along with any ecologically relevant data representing niche dimensions as the model method can utilise any input although some calibration may be required to get good outputs.	Decision tree method similar to regression trees. The training data set is sampled randomly to feed trees, this sampling can be limited to prevent overfitting. This data is then used to construct trees which explain input relationships, each tree is selected randomly preventing relic correlations to be found and reducing overfitting.	Dependent on construction method and inputs.	Computationally complex, being a machine learning method means this model type can be difficult to interpret. However, its construction allows complex relationships to be modelled and overfitting is prevented by convergence and cross-validation being built into the method.

1.4.3 | Model complexity

It is possible to assume that a more complex model construction provides a better result. This, however, is not the case as species relationships with few or many environmental variables can be simple or complex. For example, species presence may be complex with variation in temperature due to other related or unrelated ecological factors uncounted for in a climate data only model. Alternatively, a species may be better represented by a model with multiple environmental variables as they provide more explanatory power. Thus, model creation requires careful consideration to be fit for purpose and have good explanatory power making good use of the data available, this does not mean complexity is needed.

An approach rather than applying single models as described above, is to provide multiple modelling methods in a single framework model (Stockwell and Peters, 1999; Thuiller *et al.*, 2009; Henrys, Smart, *et al.*, 2015). This type of model layering or model ensemble approach allows for multiple modelling techniques to be used to generate a robust average fit to the data with the variation within and among methods, providing robust uncertainty estimation around the average fit. Model weighting can then be applied to generate the optimal predictive capability for

each species. This involves generating and then applying a weight to the outputs of each method where the weight represents the ability of the modelling method to predict hold-out samples of the training data used to build the model. This is the approach used in MultiMOVE (Elith *et al.*, 2006; Thuiller *et al.*, 2009; Henrys, Smart, *et al.*, 2015). Another issue concerning complex models with multiple inputs is how data hungry they are, with machine learning models requiring more observations than others (Sillero *et al.*, 2021). Further, dynamic mechanistic models require a high level of detailed species biology knowledge (Kearney and Porter, 2009) which is hard to gain across multiple taxa.

1.4.3.1 | Dynamic and mechanistic process-based models

While calls for models that represent species biological responses dynamically are extremely well justified (Kearney and Porter, 2009; Purves *et al.*, 2013; Sillero *et al.*, 2021), they are not yet widely available at scales and high enough taxa numbers to be used in an applied ecological context. This is due to the level of data and species biological knowledge required to construct dynamic and/or mechanistic biological process based species ecological niche models (Kearney and Porter, 2009; Purves *et al.*, 2013).

As the focus here is modelling plant and soil responses to AES, the methodology utilises correlative models with environmental variable and species presence relationships rather than mechanistic or process-based models. This is because mechanistic and process-based models are presently unfeasible for the scales considered, as the right information to model processes and mechanisms does not yet exist in a sufficient quantity or form to cover entire species community relationships between multiple environmental dimensions (Evans *et al.*, 2013; Mouquet *et al.*, 2015; Urban *et al.*, 2016).

Another factor for consideration is that under no-analogue future conditions no model's performance is sure to be robust (Williams and Jackson, 2007; Fitzpatrick and Hargrove, 2009) and correlative models with clearly defined operating spaces provide a certainty of where they can and can't be relied on. This known entity factor of correlative models is also key in the context of the theory discussed above (*1.4.1 -1.4.3*). As this considers ideological construction that can lack pragmatic realism (Purves *et al.*, 2013; Urban *et al.*, 2016) or does not scale well as mentioned in Hirzel *et al.* (2008) e.g. few species interactions to whole community interactions.

Thus, the use of well-constructed correlative models, which can be immediately useful as tools to tackle current issues such as the environmental issues mentioned within *1.1-1.2* ; are the best services to offer for those trying to tackle these issues such as managers and policymakers (Ferrier *et al.*, 2002).

1.4.4 | Model testing and reality checking

In **Fig. 1.2** the building process of a model is shown by going through the process in the orange construction box to get to a final construct in the blue box. Traditional statistical tests using *p*-values can be used to assess if model results are significant via testing model outputs (Elith and Leathwick, 2009; Peterson *et al.*, 2011). An example of this would be testing model results from data withheld from model construction, or ideally independently gathered (Smart *et al.*, 2019; Sillero *et al.*, 2021). If the model predictions are shown to be significantly different from random then the model fits to independent data provide a degree of explanation of environmental variable & species relationships. This however, does not test how applicable the model is to the real world as a tool box of tests is required to gain any certainty of this (Elith and Leathwick, 2009). Beyond traditional statistics, the testing stages shown in the orange box of **Fig. 1.2**

represent dedicated model testing methods for predictive performance, a brief description of the two most established methods is provided here.

The first predictive performance statistic described is area under the receiver operating characteristic curve (AUC). This form of model testing determines if the model can discriminate between where a species should be predicted as present versus absent (Elith *et al.*, 2006). Values from conducting this give a score to predictive performance with a score of 0.5 or lower meaning the model is not better than random or worse; values with increasing proximity to one showing improving model performance (Elith *et al.*, 2006; Henrys,*et al.*, 2015). Similar to AUC is correlation between the data and model predictions, correlation can be determined using a traditional statistical test which gives an idea of how far the model deviates from the data and can also be tested for significance (Elith *et al.*, 2006; Peterson *et al.*, 2011; Sillero *et al.*, 2021).

Akaike's Information Criterion (AIC) evaluates a range of competing models based on fit of data to model given the number of parameters included in the model (Elith and Leathwick, 2009). AIC essentially scores models based on how close they are to the reality depicted by the training data (Burnham and Anderson, 2002) meaning a lower AIC shows a better model. These scores are, however, produced for comparisons of models constructed from the same data set only, and can be used for selection of the best model for the data (Burnham and Anderson, 2002). An example of AIC scores being used can be found in Preston *et al.* (2008).

To summarise the construction process (**Fig. 1.2**, orange box), a range of input variables are selected with good ecological justification to feed model building. Then either different versions of the same method or multiple model methods are constructed using these input variables. The model testing methods explained above can then be employed to select combinations of input

variables and modelling methods, as predictors of species occurrence or species suitability to inputs (Sillero *et al.*, 2021); the most robust model with the highest explanatory power can then be selected. This process forms the inputs and constructed model type that gives outputs, which can be employed for end use (**Fig. 1.2**, blue box). Outputs are also variable depending on the model construction that predictions represent (Guisan and Thuiller, 2005; Sillero *et al.*, 2021):

- Favourability or suitability score (representing how suitable environmental conditions within the data set are for species modelled, gained if the methodology can't account for detection of species in the training data);
- Relative likelihood of occurrence (probability that the species will occur under environmental conditions accounting for species detection not being perfect in the training data);
- Probability of occurrence (the actual probability that a species will occur under given environmental conditions given by the model and its assumptions, normally with well-informed species detection in training data).
- Further complexity in output types is seen across ecological niche modelling methods, but not described here. The close consideration of what each step in the construction process involves and consists off is well emphasised in this section (e.g. **Fig. 1.2**), for a more comprehensive guide to ecological niche model constructions Sillero *et al.* (2021) provides a step by step guide.

1.5 | Pragmatic application of ecological niche models

The approach here centres on the use of correlative niche models. These are selected for the availability of well established methods and data sets, as well as the fact that more processed based models are too data hungry and are not guaranteed to provide better predictions especially under global change (*see, 1.4.3.1*). Beyond this the possibility to clearly define niche space using the dimensions of environmental inputs to the species model provides a transparent definition of suitable habitat that can be managed toward or away from, e.g. Smart

et al. (2019). Over all three key reasons promote the use of correlative niche models: their established robust use; their ability to cover many species (with less data than process models*, 1.4.3.1*); and the simplicity of inputs allowing for setting of niche dimensions.

Many ENMs focus on making predictions from low resolution or sparse data which is commonly available over much of the world at a small scale grid square resolution (Ferrier *et al.*, 2002; Peterson *et al.*, 2011; Mouquet *et al.*, 2015) . Using species data like this along with low resolution climate datasets like “Worldclim” and environmental data from global data bases or herbarium records are the typical inputs for ENMs (Peterson *et al.*, 2011). While low-resolution models are useful ecological and conservation tools, when used at appropriate scales they only provide low resolution outputs. Finer resolution (large scale) approaches to modelling despite sufficient data being available in places appear to be less abundant despite calls for it (Evans *et al.*, 2013; Diekmann, Michaelis and Pannek, 2015; Mouquet *et al.*, 2015).

The scope of this project is to look at how AES prescribed management affects plant diversity and soil quality given interacting global change drivers. Given this applied focus in comparison with ENM as a wider subject many ENM methods are unsuitable for application within this project due to their low resolution. For this reason, many low resolution data examples and models are of limited application here, simply being examples of general ENM & SDM usage.

1.5.1 | Applying ecological niche modelling to land management and global change

The desired framing of the environmental modelling application described in *1.1.1 and 1.6* requires careful consideration of both the inputs used (*see, 1.2.1*) and the models to be built (*see, 1.4*). As does the time-frame and scale (also mentioned in *1.1.1*) to be used for modelling

as national or even global scale ENMs often look at 100 km^2 cells e.g. Hawkins *et al.*, (2007); to large for AES modelling. Incorporating the combination of land management and global change affecting environmental variables related to species realised niches requires revisiting the BAD diagram (**Fig. 1.1**, and *see, 1.5.1*). As typical land management operates at the field-scale and lower, environmental variables should be explored at this level (Diekmann, Michaelis and Pannek, 2015). For timescale, plant presence and abundance as well as land management practices tend to vary by season or annually. Thus, modelling over multiple decades or centuries as applied elsewhere in ENMs is less relevant (Fitzpatrick and Hargrove, 2009; Veloz *et al.*, 2012). Generally, land management is best monitored and modelled at a sub-decadal timescale (Ormerod, 2012a, no date; Oatway *et al.*, 2018); although it may take around 10 years for habitat changes to be observed (Critchley, Burke and Stevens, 2004; Maskell *et al.*, 2014a). Thus, annual monitoring and modelling is reasonable.

1.5.1.1 | Abiotic

Climate variables tend to be those first associated with the abiotic component of species niches and at a land management scale accuracy and precision of the climate data is key (Hawkins *et al.*, 2007; Diekmann, Michaelis and Pannek, 2015; Sillero *et al.*, 2021). While infield climatic data loggers are useful for site monitoring, publicly published climate datasets into the past and future are available down to the 1 km^2 e.g. UKCP18 (Lowe *et al.*, 2018).

In the context of climate change, novel (no-analogue) climates are those which do not exist at present, for this reason it is largely the case that models only considering environments currently seen across the planet cannot account for these future possible climates. This implies that ecological niche models only operating within currently observed environmental conditions will be inadequate to predict future compositions under no- analogue scenarios (Davis *et al.*,

1998; Williams and Jackson, 2007; Fitzpatrick and Hargrove, 2009). However, the appropriateness of the range of variation in the model training data is captured as the definition of correlative models operating space (for all variables in the training data). Thus, where this space is breached relative to future novel conditions there can be a loss of robustness and certainty in the prediction.

As the soil is a target for land management interventions (Rose, 2011; Oatway *et al.*, 2018), changes in management regime are guaranteed to affect soil variables and plant responses. This has led to the need to include edaphic data as an ENM input (Diekmann, Michaelis and Pannek, 2015). Soil variables measured related to ecosystem state and type tend to be chemical or physical properties (Seaton *et al.*, 2020) although these are also strongly influenced by soil organisms (microbial communities and mesofauna).

While climate change is the most commonly considered global change variable in ENMs other global issues are also worthy of consideration, such as the disruption of biogeochemical cycles (Rockström *et al.*, 2009; Steffen *et al.*, 2015). Datasets with modelled change of biogeochemical cycles are available, driven by change in drivers such as atmospheric N and S deposition (Tipping *et al.*, 2019; Levy *et al.*, 2020). Further, it is also critical to include changes in macronutrient availability (e.g. N, P, K) as this regulates soil fertility and thus plant species productivity and competition (Falkengren-Grerup, Brink and Brunet, 2006; Emmett, 2007).

1.5.1.2 | Biotic

Biotic interactions can be captured within models via deliberate inclusion of layered modelling (Boulangeat, Gravel and Thuiller, 2012; Sillero *et al.*, 2021). However, a convenience of presence-absence based ENMs e.g. MultiMOVE (Smart *et al.*, 2010; Henrys, Smart, *et al.*,

2015), is that they capture species realised niches inclusive of biological interactions (Guillera-Arroita *et al.*, 2015) although the interactive process are not explicitly modelled.

Ecological interactions that require consideration in ENMs management can affect species diversity directly and indirectly (Gossner *et al.*, 2016). The manipulation for ecological restoration of species diversity need consideration (Pywell *et al.*, 2007; Wagner *et al.*, 2014) as does the manipulation for production purposes. This is particularly pertinent where trade-offs are likely (Smart *et al.*, 2006; Simons and Weisser, 2017). Plant health (pathogen and disease risk) is another factor that may lead to deliberate removal of species from ecosystems to reduce infection or pathogen spread also, actual loss due to mortality from infection, global change is worsening this (Pautasso *et al.*, 2010).

Also, global change such as habitat loss, N deposition and climate change may have long-term effects on species diversity that should be captured within abiotic model components but may already have had an effect on baseline conditions within model construction data. This needs consideration through wider species pool modelling to prevent shifting baseline syndrome (Soga and Gaston, 2018); for example referencing back to established national vegetation classifications (Rodwell, 1998).

1.5.1.3 | Modelling with dispersal versus dark diversity

An ecologically robust way to capture species dispersal is to consider species functional traits relating to dispersal e.g. Brunet *et al*., (2012), or to construct a dispersal dedicated model component as part of a model or layered set of models (Boulangeat, Gravel and Thuiller, 2012). However, as this requires further data for construction, other more parsimonious options are available although these are traded off with robustness and may move predictions away from a

certain realised reality. If the community is considered to be saturated and is not expected to gain empty niche space over the modelled time period, then the site recorded species pool may capture enough diversity that dispersal constraints are negligible. This is however an unlikely situation and unsaturated communities and the opening of niche spaces are thought to be the norm (Mateo, Mokany and Guisan, 2017). A way to account for possible colonisers and capture the variation of species that may establish in the plot into the future is to use the local area species pool to determine which species to model and those with highest suitability or probability of occurrence predicted as those likely to establish. This is equivalent to modelling dark diversity, described in Pärtel *et al*., (2011). Dark diversity can be considered as all the species within a local area of a site that could grow under the environmental conditions at the site. Within this thesis modelling predicts potential colonising species by habitat suitability, observed or unobserved (but in the local pool) at baseline, forming a dark diversity pool.

As land management for resource production is often based around the cultivating or planting of specific species (Smart *et al.*, 2006; Bathgate *et al.*, 2011; Simons and Weisser, 2017; Vanguelova *et al.*, 2019) this can negate the need to consider dispersal and establishment in ENMs. This is because management deliberately seeding, or planting species may guarantee their presence but not their prosperity; this is where modelling suitability rather than probability of occurrence can give a more useful insight into vegetation community composition and ecosystem state. Hence in what follows, I interpret ENM outputs as estimating the suitability of a given configuration of abiotic conditions for a species *if it could reach the patch and establish* rather than a probability of occurrence.

1.5.2 | Land management and ecological niche modelling

The previous section introduces some applied theory to modelling land management effects of species; this section looks at relevant approaches for data gathering monitoring AES and modelling approaches. Given global change and land management's role in its perpetuation (Green *et al.*, 2005; IPCC *et al.*, 2014; Díaz *et al.*, 2020) AES have been set up a tools to mitigate this and move towards sustainable land management practices (Rose, 2011; Pe'Er *et al.*, 2019). While AES design is thought to be robust and monitoring regularly carried out the level of success is thought to be low and calls are often made to monitor and model AES schemes (Ormerod, 2012a, no date). This work attempts to further these efforts.

As the creation of ecological models for applied use is most worthwhile when providing greater insight than applying ecological theory (Sinclair, White and Newell, 2010) the need for the integration of models becomes more desirable to explore interactions. This however leads to the question; how can greater insight be gained from modelling rather than the simple application of ecological theory?

A trade-off of parsimony and model complexity arises when trying to robustly capture species at equilibrium with their environment; the training data often does not capture combined and interacting environmental factors e.g. climate change and land use/management (De Chazal and Rounsevell, 2009; Titeux *et al.*, 2016). This is usually because time-series dynamic data is needed to quantify the random, directional, and cyclic patterns in the way species populations change interdependently in mixed species assemblages. The impacts of land management combined with global change provides additional novel impetus that can deflect these dynamics in ways that are potentially not readily predictable even where existing training data allows for dynamic interactions to be modelled (Benito Garzón, Robson and Hampe, 2019; Radchuk,

Kramer-Schadt and Grimm, 2019). This follows if the training data do not capture the future novel interactions between no-analogue configurations of driving variables. As the planet moves into an uncertain future this is more likely to be the rule than the exception posing major challenges for ecological forecasting (Chazal and Rounsevell, 2009; Mantyka-pringle, Martin and Rhodes, 2012; Mantyka-Pringle, Martin and Rhodes, 2013). Also, wide scale models looking at fewer or simplified national to global trends are acknowledged not to capture local conditions as well e.g. Purves *et al.* (2013). While integration of land use or management models with ecological niche models can be complex due to differing data types, this must be tackled for the sake of exploring interactions that will otherwise be neglected (Mantyka-pringle, Martin and Rhodes, 2012; Mantyka-Pringle, Martin and Rhodes, 2013; Titeux *et al.*, 2016).

While models applied to specific ecosystems and management have been built and utilised e.g. the Hurley Pasture Model (Johnson and Thornley, 1985), when they are applied outside of the ecosystems or management conditions in which they were built there are many performance issues (Arah *et al.*, 1997; Thornley and Cannell, 1997). This is also reflective of the mechanistic modelling issues discussed in *1.4.3.1*. More recent research has explored layered modelling techniques (dynamic and correlative) to gain wider application (De Vries *et al.*, 2010) and this has led to policy-relevant findings of pollution impacts for specific ecosystems management (Rowe *et al.*, 2014; Rowe *et al.*, 2016). The applicability of a modelling methodology to research aims in the sections below highlights the difficulties of ecological niche modelling and forecasting land management effects.

In the context of determining AES success, multiple factors have to be considered for representation within modelling. The timeframe from a response in taxa modelled (both for construction data and model predictions) has to be sufficient e.g. Taylor *et al.* (2009) with plant

species and insect taxa responding to over a decade of AES grassland management. In addition, to capture ecosystem variation at a national scale requires many sampling sites for regional comparison of taxa, diversity and habitat response, to management (Socher *et al.*, 2013). This also requires a local level sampling that is scaled up to sufficiently capture local processes at national scales (Weiss *et al.*, 2014). Another factor affecting species pools in the context of modelling is plant health, as pathogens (e.g. fungal and insect diseases) can remove species e.g. crops and trees from ecosystems (Pautasso *et al.*, 2010); incorporating this into ecological niche models provides yet another complexity for construction.

The multiple factors discussed above has led the approach taken here to be largely correlative for a parsimonious approach applicable to many species by; reducing the computational resource needed; ensuring data and knowledge construction inputs are already available; and allowing scalability from fine resolution plant and soil data to national policy relevant outputs. A layered modelling approach is taken here using predicted climate data to capture climate change plus soil and vegetation input variables are modelled or manipulated to represent management change and deposition (*see, 1.6.6*). However, this approach does propagate many sources of uncertainty through the modelling workflow, (*see,* **Fig. 5.1**, for a graphical representation); *1.6.1*, shows input data use.

The considerations throughout *1.5*, requires a high specificity of data that is surprisingly lacking in ecology (Chazal and Rounsevell, 2009) but have been sourced as far as possible as described below.

1.6 | Environmental data sources for ecological modelling in Great Britain

The environmental and ecological data requirement for constructing a robust modelling workflow at a national scale is significant; fortuitously the UK is renowned for its environmental data (Lowe *et al.*, 2018; Henniges *et al.*, 2022). National assessments of UK habitats have been conducted since the 70s (Barr *et al.*, 2014) with climatic data available back to the 1860s (Lowe *et al.*, 2018; Met Office Hadley Centre, 2018) and some botanical records date back much further (Clarke, 1897). More recently, comprehensive national reports have developed a greater understanding of trends and specific drivers and benefits from UK ecosystems (Watson *et al.*, 2011; Hayhow *et al.*, 2019). This has provided an extensive amount of data covering the UK environment much of which is freely available. This means construction and input data for ecological modelling from high resolution “on the ground” species and local environmental data is abundant in the UK (Rodwell, 1998; Morecroft *et al.*, 2009; Brown *et al.*, 2014; Lawley, Emmett and Robinson, 2014; Emmett *et al.*, 2017; Tipping *et al.*, 2017; BSBI, 2018; Lowe *et al.*, 2018; Alison *et al.*, 2020; Levy *et al.*, 2020). These all provide ideal training data for fine scale or multi-scale ecological models as described below.

1.6.1 | Ecosystem data

As ecosystems are complex and varied, datasets covering multiple taxa and environmental variables are more unusual but data and research from specific contexts are available. These range from dedicated national studies e.g. national grassland soil carbon stock predictions (Manning *et al.*, 2015), to free national soil classification maps and associated soil quality indicator databases (Lawley, Emmett and Robinson, 2014). There are however, some national

surveys with fine resolution data across taxa and environmental variables that capture a wide geographic distribution that can provide suitable ecological modelling inputs (Brown *et al.*, 2014; Emmett, Alexander, *et al.*, 2016; Emmett *et al.*, 2017). These surveys provide the abiotic variables and some of the biotic variables described in *1.4.1 and 1.5.1*. The two national surveys used to provide data for this thesis are described below.

1.6.1.1 | Glastir Monitoring and Evaluation Program

The Glastir Monitoring and Evaluation Program (GMEP) provides a survey of farms, farmers, landscape features, water and soil (Emmett *et al.*, 2017). GMEP is used as a baseline to inform the Welsh Government how well their Glastir AES (Rose, 2011) will achieve its 6 goals into the future:

1. Combating climate change
2. Improving water quality and managing water resources
3. Improving soil quality and management
4. Maintaining and enhancing biodiversity
5. Managing landscapes and historic environment and improving public access to the countryside
6. Woodland creation and management

The GMEP program ran from 2012 to 2016 and the relevant inputs for constructing fine resolution correlative modelling of UK ecosystems cover vegetation and soils. The methodologies for recording and surveying these are described in the vegetation and soil field handbook (Smart *et al.*, 2016), here: https://nora.nerc.ac.uk/id/eprint/506219/13/N506219CR.pdf. While the data utilised throughout this work is from GMEP a follow up program, the Environment and Rural Affairs Monitoring & Modelling Programme (ERAMMP) continues to track the progress towards Glastir's goals.

1.6.1.11 | Environment and Rural Affairs Monitoring & Modelling Programme (ERAMMP)

The ERAMMP followed on from GMEP and had the same aims set by Welsh Government. However, additional outputs are included: modelling scenarios for the EU exit process, and being a source of data to report on the state of Wales' natural resources (Emmett, Alexander, *et al.*, 2016).

1.6.1.2 | Countryside Survey's

The Countryside Survey (CS) is a national monitoring program for the habitats of Great Britain that has been running since 1978 (Bunce *et al.*, 2012). The CS monitors plants and soils with its methodologies providing the foundation to GMEP and ERAMMP. CS underpins a lot of the monitoring of the UK countryside and natural resources (Carey, Wallis, Emmett, *et al.*, 2008) including the UK National Ecosystem Assessment (Watson *et al.*, 2011). The plant and soil data recorded by CS has allowed for the construction of ENMs (Smart *et al.*, 2010; Henrys, Smart, *et al.*, 2015) and ecological change models throughout this work. The plant and soil data collection was conducted using methodologies detailed in their respective handbooks, the soils manual (Emmett *et al.*, 2008) and the vegetation manual (Maskell *et al.*, 2008). The last full scale CS survey was conducted in 2007 but a rolling 5 year program is continuing under the project UKSCAPE (Rennie *et al.*, 2020).

1.6.2 | Botanical diversity

The UK's comprehensive botanical recording history (Henniges *et al.*, 2022) means that vegetation community data (Rodwell, 1998) and plant species records (Walker *et al.*, 2010) are rich. When this is combined with data from GMEP and the Countryside Survey this provides a comprehensive set of inputs for AES monitoring and modelling as called for in Ormerod's (2012a, no date) work.

1.6.2.1 | Botanical Society of Britain and Ireland distribution database

The Botanical Society of Britain and Ireland (BSBI) distribution database (Db) is the repository for the recording, and surveillance of British and Irish flowering plants and stoneworts (vascular plants and charophytes); this provides data for conservation, monitoring and modelling (Walker *et al.*, 2010; BSBI, 2018). Methodologies for BSBI Db recording are laid out in Walker *et al*. (2010). In this thesis it is used as the source for constructing local species pools around each high-resolution modelled location.

1.6.2.2 | National vegetation Classification

The British National Vegetation Classification was developed to be a common standard developed for plant conservation by describing plant communities (Rodwell, 1998, 2006), This provides standardised community compositions that can be referenced into the future for conservation and research efforts.

1.6.2.3 | Combining botanical and environmental datasets

When the BSBI distribution database and British National Vegetation Classification are combined with the environmental data from GMEP and the Countryside Survey it provides a rich data set that captures local environmental conditions as is required in local ecological niche modelling (Diekmann, Michaelis and Pannek, 2015). This means the datasets described (*1.6.1* and*1.6.2*) cover all the input requirements detailed in *1.4.1* and *1.5.1* other than abiotic climatic data and global change data described in the following section *1.6.3* .

1.6.3 | Global change

The global environmental issues introduced in *1.1* and *1.2.1* have their own modelling communities which provide comprehensive predictions (Lowe *et al.*, 2018; Levy *et al.*, 2020) from a variety of modelling techniques (often dynamic and mechanistic process-based). These are published both, to allow for change and trends into the future to be understood and, to provide data for other modelling communities. The datasets described below complete the modelling data requirements detailed in *1.4.1* and *1.5.1*.

1.6.3.1 | UKCP18

The Met Office UKCP18 climate data projections include past observed as well as future predicted climatic variables that have been made available through downscaling to the 1 km scale (Robinson *et al.*, 2022), these also align to the IPCC standard scenarios (Lowe *et al.*, 2018). The data is produced within a dedicated program to both track climatic change, predict climate change and provide inputs for other models.

1.6.3.2 | National deposition data

The disruption of global biogeochemical cycles is a by-product of global change that leads to the deposition of chemical species that affect ecosystem process and habitats (Rockström *et al.*, 2009; Stevens *et al.*, 2016; Tipping *et al.*, 2019). Modelling concentration-based estimated deposition values allow for the monitoring of these potential pollutants and estimating their trends. This also provides data for further modelling as utilised here (Tipping *et al.*, 2019; Levy *et al.*, 2020).

1.6.4 | MultiMOVE

The combination of the datasets described above has led to the creation of an ecological niche modelling package constructed in the R environment (R Core Team, 2019); MultiMOVE (MM) which has undergone several years of development (Smart *et al.*, 2010, 2019; Henrys, Butler, *et al.*, 2015).

Given the national coverage of MM and its ongoing development, see Henrys *et al.* (Henrys, Butler, *et al.*, 2015) for the latest version, it is probably the most suitable currently available ENM for exploring AES via the approach described here. Also, given the number of taxa within MM and the scale of the construction datasets covering Great Britain; to the best of my knowledge, there is no more comprehensive software package to use for exploring land management and global change effects on UK plant taxa.

The more recent MM updates (Henrys, Butler, *et al.*, 2015) have led to a weighted model average function to better incorporate the varying strengths of each method applied to each species in the model ensemble (**Table 1.1**). Also within this work the link between soil variables and vegetation in the modelling (a layered modelling approach) has been improved on from the GLMs created to express the relationships for GBMOVE (Smart *et al.*, 2010). These take the form of newly constructed Neural networks that outperform the GLMs and provide a more robust link from soil variables to the mean Ellenberg scores driving the model (*see, Appendix A.3)*.

1.6.5 | Long-term ecological data

Despite the rich history of biological and environmental recording within the UK (> 200 years) datasets monitoring long term change in response to managed and natural processes are surprisingly rare when reviewing literature for this work, this has been observed by others

(Chazal and Rounsevell, 2009). The projects described in *1.6.1* are changing this view, however; but the fundamental need for data representing management change is still required to construct models predicting how variables will change. While chronosequences and space-for-time differences in habitats and management can provide proxy data for soil responses to management over time, they are of limited applicability for disentangling the effects of multiple global change impacts on ecosystems (Walker *et al.*, 2010; Damgaard, 2019). To explore management change and find data suitable for modelling, literature and data searches are necessary for management change model training. The Ecological Continuity Trust website's "sites" page (https://www.ecologicalcontinuitytrust.org/sites) was a valuable starting resource for finding long-term land management based ecological monitoring datasets within this work (Ecological Continuity Trust, 2020). The exact method for the literature reviews and models constructed for the land management scenarios created are described in each of analysis chapter.

This work takes advantage of long-term ecological datasets or chronosequences to model land management effects on ecosystems. Synergistically utilising this with the UK national datasets described throughout *1.6* to provide the required inputs for ecologically modelling AES impacts on plants and soils successfully.

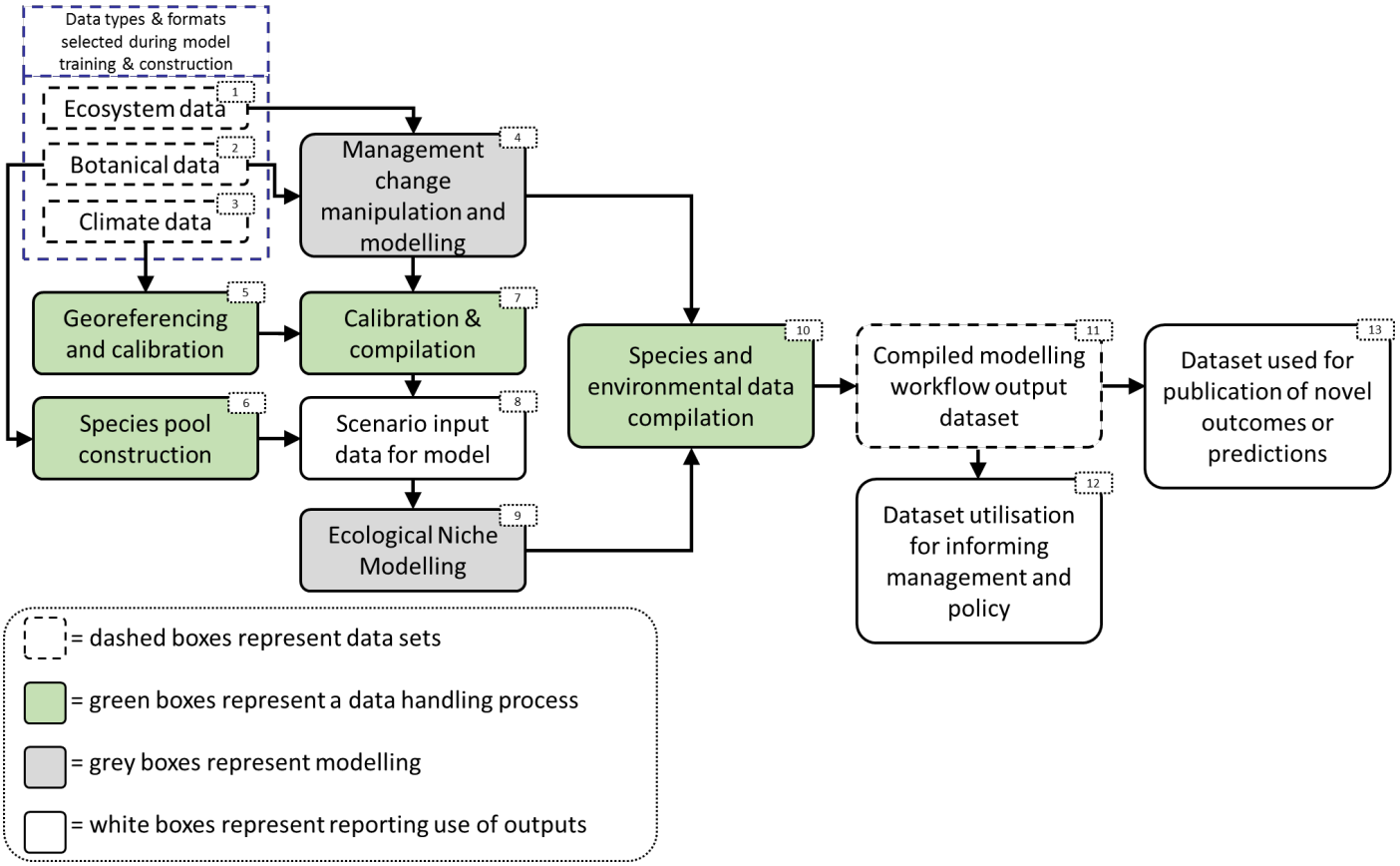

Figure 1.3. Example ecological modelling workflow for predicting management change effects on plant species and environmental variables. Numbering details: 1. Refers to datasets capturing non-climatic environmental variables often abiotic but can be biotic too (e.g. vegetation height or habitat type), non-climatic global change data would be inputted here; 2. Botanical species data for the species pool that the ecological niche model will run, this data can be linked to the ecosystem data; 3. Climactic data, can local to the site within the ecosystem data or taken from observation or prediction datasets; 4. Utilisation of the data in 1-3 through modelling or manipulation to represent management (these models are constructed prior to workflow assembly); 5. Georeferencing and calibrating climatic data to the location modelled; 6. Utilisation of the botanical data to determine which species to modelled at location; 7. Finalisation of inputs to the ecological niche model; 8. The compiled dataset representing the modelled scenario; 9. The species ecological niche model (ENM) run; 10. Compiling the management affected environmental data with the species ENM output data; 11. The full output dataset of the modelling workflow representing the modelled management scenario; 12. Reporting of the results that best inform management and policy to achieve pre-determine goals, the key objective of modelling land management; 13. Reporting of results for novel findings or methodologies for academic literature. Boxes 1-3 are within a blue dashed box as the exact formats and data types will have been determined at the modelling workflow construction stage (*see, section 1.4, Fig.1.1*).

1.6.6 | Modelling workflow

Furthering the development of a model construction workflow (**Fig. 1.2**) utilising the data input described in the previous sections (*see, 1.6.1-5*); **Fig. 1.3** demonstrates a conceptual approach to modelling land management effects on species and environmental variables. This is a representation of the overarching modelling approach used throughout this thesis. The **Fig.1.3**

boxes are numbered corresponding to the different dataset described in *1.6*, the numbering being:

1. **Ecosystem data**: environmental survey data such as GMEP (*see, 1.6.1.1*) and CS (*see, 1.6.1.2*).
2. **Botanical data**: BSBI (*1.6.2.1*) and the plant species date from species GMEP (*see,* 1.6.1.1) and CS (*see, 1.6.1.2*).
3. **Climatic data:** while this can be observed locally through data loggers it typically refers to predicted data, UKCP18 here (*see,* 1.6.3.1).
4. **Management modelling**: Constructing management driven models of environmental inputs from ecological data (*see, 1.6.5*), these are then used to predict changes in **Fig. 1.3, 1**. Manipulation of data e.g. canopy height, can also be conducted to represent a habitat transition e.g. grassland to forest. Non-climatic global change data can also be incorporated into the workflow here, such as deposition (*see, 1.6.3.2*).
5. **Georeferencing**: A data handling process to locate the climatic data (**Fig. 1.3, 3**) with the sites in **Fig. 1.3, 1**.
6. **Species pool**: Using species record to create a species pool for modelling appropriate for the locations from **Fig. 1.3, 1**.
7. **Calibration & complication**: Compiling the input datasets and ensuring they are fit for the ENM run e.g. MultiMOVE (Henrys, *et al.*, 2015) requires soil variables to be converted to Ellenberg scores (Ellenberg, Dull and Weber, 1992; Hill, Preston and Roy, 2004).
8. **Input data**: A compiled dataset representing the management scenario to be modelled in the ENM **Fig. 1.3, 9**.
9. **ENM**: The central ecological niche model, MultiMOVE (Smart *et al.*, 2010; Henrys, *et al.*, 2015) being the established model utilised in this work.
10. **Data compilation**: Combining and compiling the outputs of **Fig. 1.3, 4&9.**
11. **Workflow output**: The full modelled management scenario dataset from**.**
12. **Dataset utilisation, management and policy**: The relevant data that has been requested or can be used as evidence for calls (Ormerod, 2012a, no date; Emmett, Alexander, *et al.*, 2016; Oatway *et al.*, 2018) for better environmental monitoring of AES and providing data for evidence based policy.
13. **Publication of novel outcomes**: The dataset produced by or the methodology used within the workflow that represents novel insight for publication in academic journals.

Separated from **Fig. 1.3, 12**, as the data utilised there is often only purposed for reporting of current state or predicting future states of the environment.

1.7 | Thesis brief and research objectives

The premise that AES achieve their management goals and benefit biodiversity and landscape features, and improve the quality of water and soil (Rose *et al.*, 2016) remains controversial, with success thought to be constrained by factors such as target taxa, their availability in local species pools and legacy effects of previous management, including residual soil fertility (Kleijn and Sutherland, 2003; Critchley, Burke and Stevens, 2004; Norton, Henrys and Crowe, 2014). Using plants and soils as indicators and metrics to determine the impacts of AES, and if they achieve their goals into the future under global change, forms the basis of this thesis. The objective is to use modelling to provide new evidence-based insights that help guide mitigation of global change impacts, principally agricultural intensification. As environmental modelling is well established (Mouquet *et al.*, 2015), I utilise it here as a tool to inform how current action may reduce or mitigate negative change and improve or maintain positive ones.

The five chapters are described as follows; the first chapter introduces the concepts of predictive ecology and environmental modelling as useful tools to inform on sustainable land management and policy (this chapter). In chapter two, I use modelling to assess the impact of AES impact on grasslands and the timeliness of their success. The third chapter looks at tree planting and succession and how aligned AES interventions can contribute to biodiversity and national carbon storage goals. Within the fourth chapter, I look at the effects of nitrogen enrichment on grasslands (deposition and fertiliser use), and how indicators and metrics focused on this can or cannot be used to support assessment of AES success. In the final and fifth chapter, I synthesise the findings to summarise what level of change at what timescale can be expected of AES and how this knowledge can be tied into current development and validation of future AES.

1.7.1 | Research objectives

Three overarching research questions have been formulated to guide a model-based exploration of AES impacts in the presence of global change (climate change and nitrogen deposition). These represent an attempt to provide answers to calls (*see, 1.1.1 &1.5.2*) for more comprehensive monitoring and modelling of AES (Rose, 2011; Ormerod, 2012a, no date; Alexander, *et al.*, 2016; Emmett *et al.*, 2017; Oatway *et al.*, 2018).

Thesis research questions:

1. Will target plant communities successfully reassemble toward desirable compositions or reference habitats in response to agri-environment scheme prescribed management?
2. How long will reassembly take within modelled habitats?
3. How do soil conditions and species groups related to ecosystem services and functions change in response to prescribed agri-environment scheme management?

The following section introduces the data and model-based exploration of AES laying out a workflow.

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Chapter two, analysis chapter one

2 | Working hard or hardly working? Modelling botanical dark diversity to compare agri-environment scheme options in temperate grasslands

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BW and SS conceived the initial ideas and aims, BW then constructed the model workflow and soil change review with the neural networks contributed by SS and the climate data by ER, all other data is sourced as referenced in or within the acknowledgements. BW led the writing of the manuscript with contributions from all other authors to the drafts and final approval for submission.

2 | Abstract

1. Agri-environment schemes (AES) incentivise land-management practices aimed at mitigating environmental impacts. However, their effectiveness depends on the duration and type of management. We explored the potential for grassland AES options in Wales (UK) to achieve expected impacts on plant diversity and soil condition.
2. We modelled the response of plants and soils to AES options over a 13-year time interval. We applied scenarios of change in soil conditions based on three grassland management types, to high resolution baseline soil and vegetation data collected in grasslands across Wales, UK. We also applied scenarios of climate change to determine the extent to which this might modify the impact of AES intervention on plant species compositional turnover.
3. Empirical models of soil response to extensification were constructed from published experimental data and used to drive change in soil inputs to a small ensemble of ecological niche models for British plants. These models were applied to the species in each baseline plot plus a wider 10×10 km species pool, thus estimating dark diversity (species that can potentially colonise) at each location. Outputs were summarised by grouping species by the ecosystem functions and services they support and by matching projected species composition to the National Vegetation Classification.
4. Scenario modelling indicated that at least 10 years of management under grassland AES options was needed to drive vegetation towards desirable plant assemblages more typical of lower fertility habitats while promoting desirable species groups and reducing undesirable ones.
5. **Synthesis and applications**: Management effects had a more marked effect on vegetation than climate variation up to 2029. Realising modelled changes in possible future plant assemblages is likely to require additional measures to assist plant dispersal and establishment.

2.1 | Chapter introduction

Since the mid-nineteen-eighties, agri-environment schemes (AES) have provided a mechanism whereby land-managers are paid to reduce the intensity of agricultural management and its negative impacts on ecosystems while restoring and maintaining biodiversity (we term this

extensification). However, doubt has been cast on the effectiveness of AES success in delivering desired outcomes (Kleijn and Sutherland, 2003; Norton, Henrys and Crowe, 2014). Evidence of AES success is mixed, and dependent on factors such as starting conditions, focal organism(s), focal habitat, desired public-good and the length and intensity of management duration and monitoring (Critchley, Burke and Stevens, 2004; MacDonald *et al.*, 2019). While positive outcomes have been found in differing taxa and habitats (Keenleyside *et al.*, 2011; Bright *et al.*, 2015; Dadam and Siriwardena, 2019; MacDonald *et al.*, 2019), others have reported (a) low success (i.e., maintaining the status quo; (b) inconclusive effects, or (c) lack of sufficient monitoring (Kleijn and Sutherland, 2003; Critchley, Burke and Stevens, 2004; Davey *et al.*, 2010; Mountford and Smart, 2014; Norton, Henrys and Crowe, 2014; Arnott *et al.*, 2018; Staley *et al.*, 2018). Estimating the impact of future AES remains critical if they are to help address climate change and the biodiversity crisis cost-effectively (Keenleyside *et al.*, 2011; Rose, 2011; European Commission, 2013; Pe'Er *et al.*, 2019). Previous evidence has shown that positive effects may take longer to observe than the typical length of AES monitoring (Maskell *et al.*, 2014b; Norton, Henrys and Crowe, 2014).

Determining AES success for plants and soils is of particular interest within the study area (Wales, UK) as the Welsh AES Glastir, specifies goals targeted at vegetation and soil conditions (Rose, 2011; Welsh Government, 2016). Recent research in UK has often focused on AES effects on more mobile taxonomic groups with findings ranging across positive, negative or non-significant change (Taylor and Morecroft, 2009; Bright *et al.*, 2015; Colhoun *et al.*, 2017; Dadam and Siriwardena, 2019; MacDonald *et al.*, 2019). This varied by taxa and habitat although more targeted AES interventions appear to have more positive outcomes (Bright *et al.*, 2015; Colhoun *et al.*, 2017). Plants and soils however have been less recently studied with past research finding mixed success even over time periods beyond standard AES agreement times

(Critchley, Burke and Stevens, 2004; Feehan, Gillmor and Culleton, 2005; Taylor and Morecroft, 2009). Determining the success of AES in achieving ecological goals depends on defining ecological change in terms of appropriate indicators and measuring progress toward or away from desirable end-points (Horrocks *et al.*, 2014). We use this approach coupled with simple plant species ecological niche models (ENM) to forecast impacts on plants and soils in the presence of climate change. We focus on grasslands and estimate impacts at fine resolution but at national scale across Wales, UK (Emmett *et al.*, 2017).

Temperate grasslands are a major focus for both food production and conservation of biodiversity, they are also ecosystems where there is a pressing need to identify management regimes that can optimise food production and biodiversity recovery achieving impactful and economically viable levels of both (Simons and Weisser, 2017). The effects of extensifying management in grasslands vary in detectability and magnitude from short-term; 3-5 years (Maskell *et al.*, 2014b; Defra, 2015) to long-term; 10-30 years (Pywell, Webb and Putwain, 1994; Critchley, Burke and Stevens, 2004; Smith *et al.*, 2014) with greater levels of restoration achieved over longer timescales. Thus, understanding the timescale of soil and plant community response to management is important to manage expectations among practitioners and policymakers. If restoration goals are likely to take longer to achieve than typical AES agreements then both monitoring and management require continuity over a longer period. Over more distant time horizons, it becomes important to know if ecosystem management outcomes could be altered by climate change (IPCC, 2018; Díaz *et al.*, 2020). Here we explore if climate change is likely to risk delivery of benefits from future AES. This is key because plant species that might be expected to thrive under extensifying management prescribed by AES could experience reduced habitat suitability because the local climate becomes increasingly unfavourable. The evidence for climate change impacts on plant species is somewhat species-

specific, scale dependent (time and space) and mixed on whether positive or negative impacts are likely. Europe-wide assessment suggests that the UK will see lower (c. 10%) species compositional turnover than the Mediterranean zone (Alkemade, Bakkenes and Eickhout, 2011) up to 2100 and overall net positive impacts on habitat suitability for a representative range of plant species by 2050 (Wamelink *et al.*, 2020). A UK-centred assessment also estimated that around 40% of vascular plants had medium to high opportunity for expansion reflecting the northern range edge of many species in southern Britain while montane and northerly distributed species would retract (Pearce-Higgins *et al.*, 2017) . These studies assess distributional change in suitability at grid square scale. These patterns are inevitably the outcome of the success or failure of dispersal and population growth in the presence of other species at the scale of the vegetation patch (Huston, 1999) . Evidence for annual and longer-term effects of weather at this scale suggest that warmer, wetter conditions favour perennial grass species at the expense of smaller forbs (Silvertown *et al.*, 1994; Dunnett *et al.*, 1998). However, in a study of the drivers of vegetation change across low productivity, semi-natural habitats across Scotland from the 1970s to 2005, Britton *et al.* (2017) detected positive climate impacts on patch-scale diversity of several plants species groups. If warmer but wetter future conditions interact with high residual fertility and filter against dispersal and establishment of species typical of less intensively managed grasslands then any broadly positive effects of a warming climate are unlikely to be realised without field and landscape-scale intervention (Grass, Batáry and Tscharntke, 2021). In this respect longer term outcomes are likely to be critically dependent on interactions with socio-economically driven changes in land-use (for example AES) and hence any managed changes in productivity of the habitat matrix (Di Marco *et al.*, 2019; Grass, Batáry and Tscharntke, 2021).

We use plant species ecological niche models (ENM) to explore the separate and combined effects of AES interventions and climate change on the plant species composition observed in a large, nationally representative series of locations recorded across Wales, UK. We model dark diversity, which we define as all species that have the potential to colonise a site under environmental conditions that suit them (Pärtel, Szava-Kovats and Zobel, 2011). This comprises species observed in each baseline location as well as species drawn from a wider pool (within 10 km). These additional species may end up more suited to the conditions at each modelled location as the environmental filter changes in response to each management scenario. Modelled dark diversity therefore provides an indication of ecological restoration potential expressed in terms of the number and identity of species known to have occurred in and around each location that could potentially persist given successful dispersal and establishment. We forecast impacts on plants and soils using the MultiMOVE R package (Smart *et al.*, 2010; Henrys, Smart, *et al.*, 2015). Inputs to the model are vegetation height, soil conditions and climate variables. We change the baseline values of these inputs over the relatively short interval, 2016 to 2029, to explore near-term impacts of AES management with and without predicted climate change. The result is a suite of forecasts that estimate the impact of scenarios of climate change and management impact on plant species composition over time.

In summary, we address the following research questions: (1) Does extensified management increase the suitability of conditions for species that support ecosystem functions and services as well as promoting beneficial change in soil conditions? (2) Will climate change drive down modelled plant species diversity potentially offsetting of any gains linked to AES intervention? (3) How much does predicted plant diversity and soil condition change after 5 years of AES management?

2.2 | Materials and Methods

2.2.1 | Data sources

Soil and vegetation data were recorded from 2×2 m square quadrats (n=828) located across Wales as part of the Glastir Monitoring and Evaluation Programme (GMEP) survey carried out between 2013-2016 with each site surveyed once over that time (**Fig. 2.1**). See Emmett *et al.* (2017) and Seaton *et al.* (2020) for detailed soil and vegetation sampling methods. Soil samples were taken from one corner of each 2×2 m quadrat to determine gravimetric % soil moisture; fresh pH in distilled water, total C % and total N%. The soil variables from each plot were transformed into mean abiotic (Ellenberg) indicator scores and the resulting indicators scores used as the inputs to the ENM (Ellenberg, Dull and Weber, 1992; Hill, Preston and Roy, 2004). The GMEP soil and vegetation data were collected using a random design stratified by a physiographic classification of all 1 km squares across Wales. We focus on three grassland habitat types targeted for extensification within AES; improved (IG), neutral (NG) and acid grassland (AG) as defined in Jackson (2000), *see, Appendix A.1*.

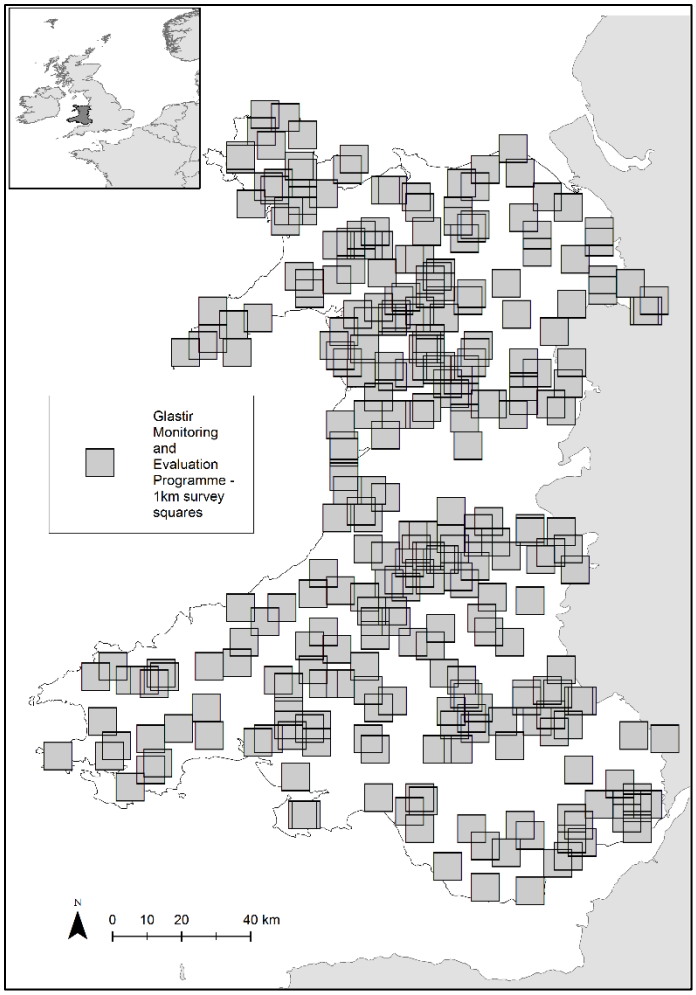

Figure 2.1. Map of the Glastir Monitoring and Evaluation Programme (GMEP) 1 km squares surveyed between 2013-2016, survey squares are not shown to scale to preserve data confidentiality.

2.2.2 | Species ecological niche modelling

We used the MultiMOVE R package (Henrys et al 2015) as the source of ENMs for higher and lower plants in the British flora. The package has been tested and applied in a number of studies under a range of contrasting scenarios (De Vries *et al.*, 2010; Henrys, Smart, *et al.*, 2015; Rowe *et al.*, 2015; Emmett *et al.*, 2017; Smart *et al.*, 2019). In summary, it uses a small ensemble of five statistical methods to model the realised niche of 1262 taxa covering the most common and many less common plants and bryophytes (Henrys *et al.*, 2015; Smart *et al.*, 2019 for full description) in the British flora. Since the majority of dominant and frequent species in the

flora are included, the models are able to account for plants that contribute the most to supporting ecosystem functions and services across British ecosystems. There are seven inputs to each model for each species; the three mean Ellenberg indicator values that equate with pH (Ellenberg R), soil moisture (F) and fertility (N), cover-weighted vegetation height and three climate variables. The derivation of these inputs is described below.

The mean Ellenberg values represent plant species preferences along environmental axes (Ellenberg, Dull and Weber, 1992). Along with cover-weighted vegetation height and the three climate variables, these indices quantify the realised niche of each species as represented in the national-scale, fine resolution presence-absence data used to train the models (Smart et al 2010; Henrys et al 2015). When used in predictive mode the habitat suitability of a species is projected into the ecological space defined by the model inputs at baseline and then given a scenario of climate and management change that drives change in the model inputs. Thus, the predicted position of a species can change in this suitability space as its model inputs change.

2.2.3 | Deriving Ellenberg scores from soils data

Only a subset (5%) of the training data used to build MultiMOVE had measured soil variables (Henrys, Smart, *et al.*, 2015; Smart *et al.*, 2019). Utilising mean Ellenberg scores calculated from the species composition of each training plot as model inputs allowed every plot to contribute to model building, with the proviso that the species being modelled was removed from calculation of each mean Ellenberg score so as to avoid circularity. In a second modelling step relationships were derived between these scores and the measured soil variables in the 5% subset. This provided transfer functions that could then be used to convert measured or modelled soil variables into the required Ellenberg scores used as model inputs. The transfer functions were generated using neural network models (*see, A.3*). This method was selected

because of the need to optimise accuracy based on a small set of predictors with strong prior ecological justification for their inclusion. Model construction was achieved using the Neural network R package (Venables and Ripley, 2002) and is described in Appendix *A.3* . This step allows soil changes to be translated into MultiMOVE inputs.

2.2.4 | Soil change models

An additional suite of models were used to quantify how soil conditions would be likely to change in response to AES management options in grassland. A literature search was conducted to assemble data on how soil carbon, nitrogen and pH changed over-time with management applied to British grassland habitats. Studies were only included where soil analysis methods matched those used in GMEP and where the treatment effect was a reasonable match to AES options (**Table 2.1**). This search resulted in datasets of varying size for each variable. Requests were made to study authors to provide full datasets, including relevant open access data. *See, appendix A.4* , for contributing datasets and selection methodology.

Generalized linear mixed-effect (GLMM) models (lmer4 R package; Bate*s et al*., 2014) were constructed to estimate change in each soil variable over time given each extensification scenario (**Table 2.1**). Details for the categories for each scenario are in *appendix A.4*.

Soils across Britain are recovering gradually from historically-high sulphur deposition (Emmett *et al.*, 2010; Kirk, Bellamy and Lark, 2010). We accounted for this by adding a pH annual increment calculated from 29 years of data for each grassland habitat type (Emmett *et al.*, 2010).

2.2.5 | Calculating cover-weighted vegetation height

Cover-weighted canopy height is another model input variable. It expresses the successional stage of the vegetation (Smart *et al.*, 2010; Henrys, Smart, *et al.*, 2015) and is calculated as follows across the *i* = 1 to *n* species in each sample plot:

$$\text{Cover weighted canopy height} = \frac{\sum_{i=1}^{n}(\text{vegetative canopy height} \times cover)}{\sum_{i=1}^{n}(cover)}$$

The species % cover was recorded in each plot while vegetative (non-flowering) canopy height data were obtained from published sources (Stace, 1997; Hill, Preston and Roy, 2004).

2.2.6 | Climatic data

Three climatic variables (minimum January & maximum July temperature, and total annual precipitation) are also used as inputs to MultiMOVE. Long-term annual average values of these variables were originally used to train the MultiMOVE models and are used as inputs in predictive mode (Smart *et al.*, 2010; Henrys, Smart, *et al.*, 2015). The UKCP18 database (Lowe *et al.*, 2018; Met Office *et al.*, 2019) was used as the source of all climate data and surveyed sites were geo-referenced to the 1 km resolution of the cells. The historical climate was derived from UK land surface observations (HadUK-Grid) interpolated from meteorological station data onto a uniform 1 km grid (Lowe *et al.*, 2018; Met Office *et al.*, 2019). The observed data was averaged from 1981 to 2016 to give a baseline representative of conditions in 2016. For future high emissions (RCP8.5), climate projected from UKCP18 was selected and downscaled to 1 km matching the baseline resolution, this represents a worst-case scenario projected climate (Robinson *et al.*, 2022). This approach interpolates variables to a finer resolution while adjusting for local topography (*see, Appendix A.2* and Robinson *et al.* (2022)).

2.2.7 | Defining the plant species pool and modelling dark diversity

We modelled a species pool that combined the list of species observed in each baseline GMEP plot with additional species recorded in the wider 10 km square grid cell in the last 20 years (Walker *et al.*, 2010; BSBI, 2018). In so doing we allow the estimated species composition of each plot location to change because the modelling can draw on this wider pool. That is, given a scenario of management and climate change the plant species with the highest modelled habitat suitability values could all have been absent from the baseline species composition in each plot. This amounts to modelling dark diversity (Pärtel, Szava-Kovats and Zobel, 2011) change where we include species that are estimated to find conditions suitable at a location even when absent at baseline. This is possible to do with high spatial realism because of the high quality of both regional species pool data available for Britain (Walker *et al.*, 2010; BSBI, 2018), and the availability of high-resolution soil and plant observations at each modelled location (*see, 2.2.1*).

2.2.8 | Model testing

To build confidence in model application, we tested whether predicted habitat suitability scores for each baseline GMEP plot correlated with observed species' presence. We used logistic regression with modelled habitat suitability as the sole explanatory variable. A two-tailed Wilcoxon rank test was also applied to test whether species absent in the observed baseline data had significantly different statistical ranks to species that were present. All statistical work was conducted in the R environment (R Core Team, 2019).

2.2.9 | Summarising ENM outputs

The predictions at baseline and in response to each scenario were summarised in two ways: First, by treating the output habitat suitability scores for each species in each plot as a % frequency, this profile of modelled outputs for each plot were matched to the British National Vegetation Classification (NVC) (Rodwell, 1998) using the MAVIS software (Smart, 2000). Second, the modelled suitability scores for species classified by particular ecosystem-service supporting groups were summed to give an estimated species count per group per 2×2 m quadrat for that functional group (Calabrese *et al.*, 2014). The species groups used were as follows: nitrogen-fixers (nutrient cycling); nectar plants (pollinator food source; Baude *et al.*, 2016); forage grasses (livestock production), and injurious weeds (Maskell *et al.*, 2020) of which increased abundance of the latter can be viewed as a disservice to agricultural production (Smart *et al.*, 2017). *See, Appendix A.5,* **Table A.5** for species lists.

2.2.10 | Scenario modelling

The modelled baseline represents the observed environmental and climatic conditions in 2016. We then defined scenarios of change in the model inputs (soil conditions and vegetation height) representing the impact of AES interventions over 5, 10 and 13 years. The interventions were all based on extensifying options in the Welsh Glastir AES that reduce fertiliser inputs and reduce stocking rate to achieve a target vegetation height. *See, Appendix A.4.2,* ***Table A.1***.

Three scenarios were defined – Reduced Stocking (RS), Low soil nutrient inputs (LI) and No inputs (NI); (**Table 1.1**). The soil models generated above from the experimental literature estimate change in soil variables given the assumed impact of the Glastir AES options (*see, Appendix A.4.2,* ***Table A.1***). This means we can use the soil models to predict the amount of change in the soil variables expected over the different time periods and then use these as

inputs to the ENM after first converting them into mean Ellenberg scores using the neural network models (*see, 2.2.3*). No non-AES or “business as usual” management scenario was constructed as insufficient time-series nor chronosequence data could be found to represent this.

The scenarios were created by using empirical models of management-induced change in soils variables to represent the impact of relevant AES options, details in **Table 2.1**. The process is fully described in *Appendix A.4*.

Table 2.1. Scenario descriptions for the agri-environment scheme management prescriptions modelled. Two climate states were applied: High emissions (RCP 8.5 UKCP18 downscale modelled 1 km); and Baseline average climate (1981 to 2016). Full scenario details and soil variable modelling details can be found in *Appendix A.4, Table A.1*.

Scenario	Management description	Recovery from acidification applied
Baseline	Observations from the GMEP survey.	No
Low inputs (LU)	Management using a reduced amount of fertilizer application, with sward height managed to promote plant diversity. Medium intensity, minimal fertilizer inputs & intermittent grazing.	Yes
Reduced stocking	Grassland with a reduced number of livestock, with sward height managed to promote plant diversity. Medium intensity management with intermittent grazing and cutting	Yes
No inputs	No chemical inputs applied. Extensification management with intermittent grazing and cutting with minimal to no fertiliser applications	Yes

2.3 | Results

2.3.1 | Testing the model against baseline observations

Greater modelled suitability scores were associated with a greater chance of the modelled species being present in a quadrat and species observed in each quadrat also had a significantly higher rank suitability score ($P < 0.001$; two tailed Wilcoxon rank test, *see, Appendix A.5.1,* **Fig. A.2**). Note that this is a strong test since the baseline data are wholly independent of the model training data. Also see Smart *et al.* (2019) for further testing of MultiMOVE.

2.3.2 | Modelling change as a function of AES intervention and climate

2.3.2.1| Baseline and projected climate

The observed baseline (1981-2016 averages) and the high emissions (RCP8.5) predictions are notably different, although there is overlap in value ranges (*Appendix A.5.2,* **Fig. A.6**). Annual rainfall values are all within the range of MultiMOVE's training data (*Appendix A.5.2,* **Fig. A.6*, A***) however, for temperature (especially minimum Jan temperature, *Appendix A.5.2,* **Fig. A.6*, B***) a spike in projected values in 2026 moves outside the range of the GB-wide training data resulting in a lack of robustness in model performance for these locations.

2.3.2.2 | Projected change in soil conditions

Across the three scenarios, the modelled direction of change in soil variables was similar with differences between habitat types (*Appendix A.4.4,* **Fig. A.1**). Overall, improved and neutral grasslands tended to increase in %C and decrease in %N but changes were small over the time period. Predicted change was more marked in acid grasslands where both %C and %N were expected to decrease. Modelled changes in pH varied the most, increasing in the low input and reduced stocking scenarios and decreasing under no fertiliser inputs (*Appendix A.4.4,* **Fig. A.1**).

Scenarios	Scenario setting	Improved grassland species groups				Neutral grassland species groups				Acid grassland species groups			
		Nitrogen fixing	Nectar plants	Forage grasses	Injurious weeds	Nitrogen fixing	Nectar plants	Forage grasses	Injurious weeds	Nitrogen fixing	Nectar plants	Forage grasses	Injurious weeds
Low inputs	Baseline climate & vegetation < 7 cm	+	+	+	-	+	+	+	0	0	+	0	0
	Baseline climate & vegetation > 7 cm	+	+	+	-	0	+	+	0	0	+(-)	0	0
	Projected climate & vegetation < 7 cm	+	+	+	-	0	+	+	0	+	+(~)	+	0
	Projected climate & vegetation > 7 cm	0(-)	+(-)	+	0	0	+	+	0	0	+(-)	+(~)	0
No Inputs	Baseline climate & baseline vegetation	0	+	+	-	0	+	+	0	0	+(~)	0	0
	Projected climate & baseline vegetation	0(-)	+(-)	+	-	0	+(-)	+	0	0	+(-)	0	0
Reduced stocking	Baseline climate & vegetation < 7 cm	+	+	+	0(-)	+	+	+	0(-)	0	+(-)	0(-)	0
	Baseline climate & vegetation > 7 cm	0(-)	+	+	0(-)	+(-)	+	+	0(-)	0(-)	+(-)	+(-)	0
	Projected climate & vegetation < 7 cm	+	+	+	0(-)	0	+	+	0(-)	0(-)	+(-)	0(-)	0
	Projected climate & vegetation > 7 cm	0(-)	+(-)	+	0(-)	0(-)	+(-)	+	0(-)	0(-)	+(-)	0(-)	0

Figure 2.2. Modelled dark diversity trends across years (2016, 2021, 2029) of species supporting ecological functions, disservices or services (Smart *et al.* 2017). Symbols: **+** = 2021 & 2029 medians above the 2016 3rd quartile; **0** = 2021 & 2029 medians not outside the 2016, 1st & 3rd quartile; **-** = 2021 & 2029 medians below the 2016, 1st quartile; **(-)** = 2029 median >10% lower than 2021 median; **(~)** returns to within baseline 1st & 3rd quartile after 2021 but by less than 10% change from the 2021 median; *see, Appendix A.5.2, Fig. A.4 & Fig. A.5* for boxplot trends. Scenarios represent three groups of grassland management options representative of agri-environmental schemes (*see, Appendix A.4, Table A.2*). Scenarios were created by using baseline (2016) and predicted climate data (UKCP18) combined with management-driven predictions of soil change as inputs to the plant species ENMs available in MultiMOVE.

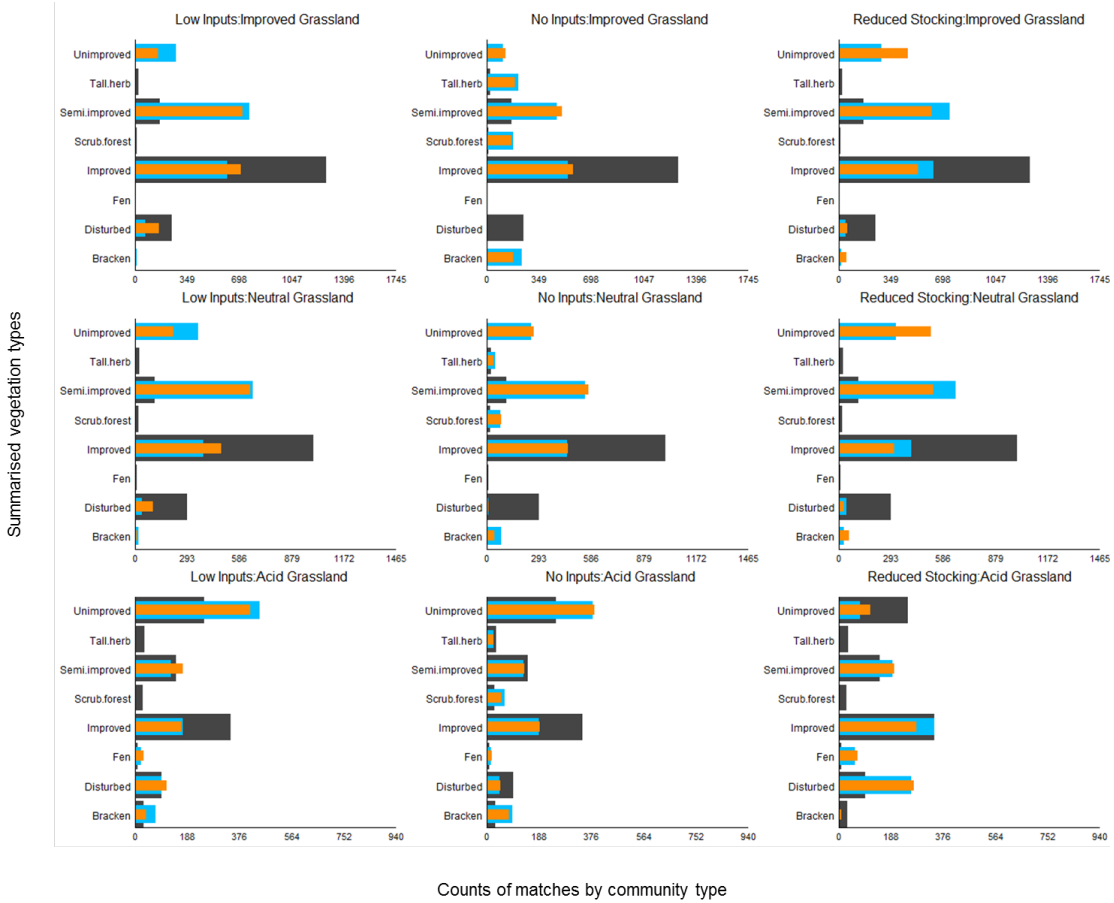

Figure 2.3. Plant community profiles of modelled baseline (2016) versus scenario-driven species composition (2029). Each graph shows the counts of matches by community type where each type featured in the top five matching coefficients when the modelled species' suitabilities in each quadrat were compared to the species compositional profiles of the UK National Vegetation Classification (NVC). Modelled baseline (**dark grey**); scenarios, no climate change (**blue**) & predicted climate change (**orange**, 2029). Broad-habitat types (rows): **IG** = Improved grassland (348 plots); **NG** = Neutral grassland (292 plots); **AG** = Acid Grassland (188 plots). For **Low Inputs & Reduced stocking**, vegetation height is as stipulated as 100 mm (**Table 2.1**). **Summarised vegetation types** were derived by grouping (*Appendix A.5.1,* "**Table A.4**) NVC unit matches for the baseline and modelled GMEP plots. Matches are from MAVIS processing of the habitat suitability outputs from ecological niche modelling.

2.3.3 | Modelled habitat suitability and vegetation change over 13 years

2.3.3.1 | Plant species and dark diversity changes grouped by link to function and service

The suitability of conditions for injurious weeds remained stable (acid grasslands) or declined (improved and neutral grasslands) in all scenarios seeing a more gradual decline up to 2029 under the Reduced Stocking scenario. Nitrogen-fixers were also largely stable but their suitability was predicted to increase under Low Inputs and Reduced stocking in improved and neutral grassland (**Fig. 2.2**). Stability and decline in the later part of the interval were projected in Acid grassland for nitrogen-fixers (**Fig. 2.2**).

Modelled dark diversity of both nectar plants and forage grasses were predicted to increase in the majority of grassland and management scenario combinations but with a decline in the suitability of conditions for these groups of species in acid grassland under Reduced Stocking up to 2029. Within the acid grassland broad-habitat increases in forage grasses are only predicted given management for taller vegetation (>100 mm) or under predicted climate change (**Fig. 2.2**).

Including predicted climate change made little overall difference to forecast changes in dark diversity between 2016 and 2021. However, between 2021 and 2029 predicted climate values were estimated to drive declines in the suitability of conditions for a number of functional groups including nectar plants and nitrogen-fixers in improved grasslands under Low and No Inputs (**Fig. 2.2**).

Modelled changes in responses of functionally important species were consistent with the longer-term aim of reducing management intensity. For example, suitability increased for less-productive forage grasses such as *Anthoxanthum odoratum* (*Appendix A.5.2,* **Fig. A.7**),

and decreased for injurious weeds e.g. *Rumex obtusifolius* (*Appendix A.5.2,* **Fig. . A.8**). We emphasise that change in suitability of conditions may not correlate positively with short-term changes in abundance within sampled plots. For example, reduced nutrient inputs and grazing reduces the vigour of perennial grass cover providing gaps which can be rapidly exploited by injurious weeds even though suitability of abiotic conditions is expected to decline over the longer term (Maskell *et al.*, 2020). Consistent with a reduction in management intensity a net increase in habitat suitability is projected for a range of common nectar plants (associated with lower agricultural intensity). Examples include *Cirsium palustre* and *Lotus corniculatus*, both showing small but consistent increases in median suitability score for all scenarios (*Appendix A.5.2,* **Fig. A.9** & **Fig. A.10**). Within the Nitrogen-fixing species group a consistent pattern was only seen in Acid grasslands (**Fig. 2.2**); where across the extensification scenarios, nitrogen-fixer diversity was typically maintained or declined somewhat by 2029 (*Appendix A.5.2,* **Fig. A.4***, top row*).

2.3.3.2 | Vegetation community change

Modelled outcomes of all three extensifying scenarios were similar with or without climate change (**Fig. 2.3**). Over the 13-year interval conditions became more suitable for semi-improved and unimproved grassland communities at the expense of improved grassland communities (**Fig. 2.3**, losses from MG11&MG11a and gains to the semi-improved MG6&MG6a). Introducing climate change had minor effects on change in the distribution of best fitting community units. The effect of the Reduced Stocking scenario in acid grassland was less consistent with expectation. Here unimproved communities decreased in favourability with small net gains to semi-improved grassland, fen and assemblages typical of more disturbed conditions.

By 2029 (**Fig. 2.3**), the greatest impact of the extensifying scenarios was predicted to be in the more productive neutral and improved grasslands with more occurrences of later

successional community types including OV21, scrub and forest units W17 and W25 and Bracken U20. The greater variation in vegetation types expected to arise following AES intervention suggests a degree of dependence on variable starting conditions. Overall, then, modelling suggests that a desirable shift in conditions favouring plant community types more typical of lower fertility could be achieved in 13 years. Only the results for 2029 are shown in **Fig. 2.3**. After 5 years (typical AES agreement length, presented in *Appendix A.5.2,* **Fig. A.3**) little change in plant community type was predicted.

By 2029 modelled assemblages within Improved grassland, showed greatest matches with community units dominated by the forage grasses *Lolium perenne, Anthoxanthum odoratum, Poa trivialis, Cynosurus cristatus* and *Dactylis glomerata* (NVC units include MG11, 6 and 7 communities). Modelled assemblages were also a frequently higher match with wetter, yet still productive grasslands, dominated by the common and abundant rush *Juncus effusus* and the common grass *Agrostis stolonifera* (NVC communities MG10 and 11). Modelled species compositions within Neutral grasslands were similar to the widespread, U4 NVC community, typically less fertile and with low pH and dominated by the fine-leaved grasses *Festuca ovina* and *Agrostis capillaris* but often joined by species more indicative of agricultural improvement such as *Holcus lanatus* and *Trifolium repens*. Consequently, the modelled impact of extensifying interventions appeared to drive a shift toward assemblages typical of less productive, yet lower pH conditions, resulting in increased fit to less productive grassland but not to the characteristically more species-rich lowland unimproved neutral grasslands (MG4, 5 & 8 NVC communities). This is despite the fact that species typical of these assemblages will have been present in most species pools and therefore potential contributors to the modelled dark diversity of each patch. In none of the random sample of grassland plots did the neutral, unimproved hay meadow assemblages feature in the top 5 best fits. This is perhaps not surprising given the rarity of these traditionally-managed hay meadows in Wales (Stevens, 2010; Alison *et al.*, 2020). The implication from our modelling

is that in most places, changes in soil conditions and possibly canopy height, are not expected to be sufficient to favour the rarest neutral grassland communities. Even where such conditions do arise, assisted dispersal and establishment may be required. Modelled changes applied to low soil pH acid grassland starting points may have been expected to result in increasing fits to heathland assemblages. However, we only applied a minor change in canopy height consistent with the interventions modelled. A taller canopy height filter will have increased the possibility of admitting taller heathland ericoids into the estimated dark diversity for each location conditional on the soil regime (cf. Medina-Roldán, Paz-Ferreiro and Bardgett, 2012).

2.4 | Discussion

The benefits of our approach are simplicity plus high realism and generality. This is because we modelled at fine-resolution but across a representative national sample of locations. Using an AES survey as a baseline for modelling also derives more value for money from these often costly field campaigns while also addressing repeated calls for better use of modelling to understand the ecological impacts of interventions (Kleijn and Sutherland, 2003; Lavorel *et al.*, 2011; Horrocks *et al.*, 2014; Staley *et al.*, 2018; MacDonald *et al.*, 2019).

2.4.1 | Modelling the management scenarios

We conclude that given sufficient time (>10 years), the three extensifying management scenarios appear able to drive desirable changes in soil carbon and nitrogen which in turn increase the likelihood of achieving maintenance and restoration outcomes for plant communities and species groups. Hence 13 years of low to no inputs, creates conditions more suitable for plant community types associated with lower fertility. This is consistent with Critchley *et al.* (2004) who also showed that plant community restoration could occur in a

range of grasslands types in Britain in parallel with reductions in soil fertility within 4 to 8 years.

In the modelled scenarios, the low fertility acid grassland showed the greatest increase in range of vegetation community types but not necessarily to markedly lower fertility assemblages (**Fig. 2.3**). In contrast the higher fertility improved & neutral grasslands showed greater shifts from their baseline with significant gains to unimproved grassland vegetation types. Less fertile starting conditions (acid grassland) have less productivity to lose but also appear to show the greatest diversification in community type in response to 13 years of extensifying management. These patterns are consistent with the dependence of response on starting conditions (Critchley *et al.*, 1996).

Our results predict the changing habitat suitability of species that arise when we filter the species pool by adjusting grazing regime via impact on vegetation height, nutrient inputs via impact on soil conditions and climate. We do not model dispersal, plant establishment and population processes that result in the formation of dominance hierarchies and realised alpha diversity (Gavish *et al.*, 2017). Hence, when observations are compared with model predictions, species compositional turnover is likely to lag behind abiotic change (Boulangeat, Gravel and Thuiller, 2012) or not occur unless further intervention assists dispersal and establishment (e.g. Wagner *et al.*, 2014). This is consistent with our treating patches as unsaturated (Mateo, Mokany and Guisan, 2017); meaning that our outputs should be interpreted as an estimation of the dark diversity of species that will itself be filtered as a result of local and regional processes (Pärtel, Szava-Kovats and Zobel, 2011).

We adopted a simple data-driven approach to modelling soil change over a relatively short time interval, deliberately chosen to reflect the duration of scheme agreements (5-13 years). The trends we projected have indeed been observed under extensification (Marriott *et al.*,

2010; Medina-Roldán, Paz-Ferreiro and Bardgett, 2012) including increasing soil C, decreasing fertility and small biodiversity gains (Medina-Roldán, Paz-Ferreiro and Bardgett, 2012). This is most consistent in our modelling of neutral grassland (*Appendix A.4.4,* **Fig. A.1**; and *Appendix A.5.2,* **Fig. A.4**).

We believe that there was sufficient consistency in the available soil observations to produce robust models; but only just as long-term experimental data that can be used to represent extensification AES options reliably appears to be rare (*see, 2.2.4 and Appendix A.4*). Despite a number of long-term experiments existing across the UK, we found a surprising lack of long-term datasets that could represent changes in soil variables driven by fundamental processes of succession, disturbance and changes in macro-nutrient availability in response to management. We are not alone in noticing this (Chazal & Rounsevell 2009).

We show that all three AES scenarios were predicted to diversify the range of plant communities relative to baseline. However, much more limited change was estimated to occur over 5 years; the typical duration of Glastir scheme agreements (*Appendix A.5.2,* **Fig. A.3***).* Our results, suggest that consumers of evidence from monitoring programs should expect little major change after 5 years when newly applying AES prescriptions, but continuing management is capable of creating conditions suitable for target communities and plant species. Stevens *et al.* (2010) also described the lower impact of such interventions expected in the shorter term on Welsh grasslands. Modest impacts over similarly short-timescales have been seen elsewhere in temperate grasslands (Marriott *et al.*, 2010; Medina-Roldán, Paz-Ferreiro and Bardgett, 2012; Norton, Henrys and Crowe, 2014).

2.4.2 | Climate change and plant diversity

Given the short time interval across which we modelled, we applied a worst-case-scenario future climate projection to explore the potential strength of the modelled responses on an annual basis (e.g. Morecroft *et al.*, 2016). Inspecting the time series of annual projections showed considerable variation with a peak in maximum July temperature in 2026 that moved outside of the training space of our ENM ensemble (Lowe *et al.*, 2018; Met Office Hadley Centre, 2018), *see, Appendix A.5.2,* **Fig. A.6**. This exemplifies the challenge of any model to reliably project species niche dynamics into novel climate space (Williams and Jackson, 2007; Fitzpatrick and Hargrove, 2009; Veloz *et al.*, 2012). Even though the 2021 and 2029 projected climate variables were within the model's training space, no-analogue climate configurations become much more likely in future (Mouquet *et al.*, 2015; Alexander *et al.*, 2016). This challenges the impacts modelling community to achieve useful prediction by modelling genotypic and phenotypic adaptive capacity at the species level and thereby freeing ENM from the constraints imposed by the range of their historical training data (Benito Garzón, Robson and Hampe, 2019). This is an active research frontier and approaches vary in data demand (Catullo, Ferrier and Hoffmann, 2015; Benito Garzón, Robson and Hampe, 2019; Mokany, Bush and Ferrier, 2019). For our purposes, species' adaptive capacity is arguably less relevant to our results as we consider an interval ending relatively soon in 2029 and defined to explore AES performance under realistic agreement lengths (Rose, 2011).

We estimate that the effect of the extensifying interventions will substantially outweigh modelled climate change effects in the time period modelled (**Fig. 2.2**; **Fig. 2.3**; *Appendix A.5.2,* **Fig. A.4**). The strong effect of management relative to other drivers clearly depends upon the severity of the driver (Guiden *et al.*, 2021) and future directional change in climate accompanied by acute effects of extreme events is increasingly likely (Dodd *et al.*, 2021). Because we were interested in modelled impacts over a relatively short near-term interval

and interested in the potentially acute filtering effects of the weather in any one year, we applied annual predicted climate variables. A longer term average would have been a safe, but less responsive, and we believe a less informative option (cf. Morecroft *et al.*, 2016; Rose *et al.*, 2016).

Based on our model investigation we estimate that under climate change predicted diversity change varies between functionally-important species groups. While climate impacts are more noticeable up to 13 years, climate change does not consistently drive diversity through this interval.

2.4.3 | Management effect timescales

Over the modelled time period, changes in soil variables were predicted to be modest and consistent with observed responses in the time series used to build the soil models (e.g. Defra, 2015; Pywell *et al.*, 2007). The change over time drove shifts toward conditions more suitable for unimproved grassland communities by 2021, although the greater change is seen at 2029 (*Appendix A.5.2,* **Fig. A.3** versus **Fig. 2.3**). Therefore, longer durations should bring about more desirable change (Horrocks *et al.*, 2014). This is congruent with other research suggesting that either management must carry on for longer to see a change or that the interventions are increasingly impactful per unit of time under agreement (Marriott *et al.*, 2010; McSherry & Ritchie, 2013; Medina-Roldán *et al.*, 2012). This is consistent with other studies where extensification time periods in excess of 10 years show greater change (Pywell, Webb and Putwain, 1994; Kirkham *et al.*, 2011; Hayes and Lowther, 2014; Wagner *et al.*, 2014). Thus, we estimate that just 5 years of AES management intervention is likely to result in limited benefit to the plant species groups explored here.

2.5 | Conclusions

The common AES prescription scenarios represented in our results are all a form of broad-shallow extensification of management. Lighter touch AES prescriptions are more acceptable to grassland agricultural managers because they require fewer changes in practice (Arnott *et al.*, 2018). Our modelling suggests that these interventions can produce positive effects if given enough time (at least 10 years). Another option would be to engage in greater targeting and more active management but taking much more account of local opportunities and constraints (Firbank, 2005). Thus from the perspective of the policy maker, considering funding longer and stronger interventions such as those applied in restoration ecology (e.g. Pywell *et al.*, 2007; Staley *et al.*, 2018 & Wagner *et al.*, 2014) is worthwhile if major change to plant diversity, species composition and soil health is desired (Stevens, 2010; Török *et al.*, 2021).

2 | References

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Chapter three, analysis chapter two

3 | Make like a tree and leave: How will tree species loss and climate change alter future temperate broadleaved forests?

This chapter has undergone review by co-authors and been submitted to the journal of Forest Ecology and Management.

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Contribution statement:
BW and SS conceived the initial ideas, BW constructed most of the modelling workflow with the calibration neural networks created by SS. AK, RM, SK and ER contributed data or helped with data acquisition. BW created the original manuscript with subsequent editing and comment from all authors.

3 | Abstract

Forest creation (planting or natural colonisation) has the potential to reduce biodiversity loss and mitigate climate change but, tree disease emergence may counteract this. Further, given decadal timescales required for forest establishment, climate change is increasingly likely to act as a filter on plant community assembly. In the temperate lowlands succession takes 30 to 50 years for non-forest land to establish woodland plant assemblages, while the timescales required for new forest to sequester carbon suggest unassisted succession will be too slow for net zero 2050 targets. However, if plantations can establish faster than succession it would be beneficial to recommend planting native species as soon as possible. We explore scenarios of broadleaved woodland development across Wales, UK, as a case study area. We use a suite of empirical Species Niche Models for British plants to estimate the potential species composition of forests with, and without, projected climate change. Additionally, we examine how tree canopy composition alters if *Fraxinus excelsior* is widely impacted by ash-dieback (*Hymenoscyphus fraxineus*). The results suggest soil total carbon and nitrogen could achieve baseline broadleaved forest values in less than 30 years. However only timber and woody flora species groups showed diversity scores that surpass baseline broadleaved forest diversity, with nectar plants and ancient woodland indicator species failing to reach baseline equivalents within 30 years; although complete congruence is unlikely given baseline forests could be hundreds of years old. Where *Fraxinus excelsior* was removed from the species pool we predicted that a scrub phase will persist or, if present, *Acer pseudoplatanus* will become the canopy dominant. The heavier shade cast by this species is likely to result in differences in species composition of the understory and ground flora diversity is likely to decrease. Reliance on unassisted succession will also depend critically on (a) dispersal from local source populations and (b) on establishment filters that could be severe in landscapes with high management intensity history. These findings indicate that given the UK's fragmented habitats relying on already degraded successional processes would lead to poor afforestation outcomes.

3.1 | Chapter introduction

3.1.1 | Environmental crises and tree disease

Forest creation has potential to slow, or reverse, global biodiversity loss and climate change (Read *et al.*, 2009; Di Sacco & Hardwick *et al.*, 2020; Stafford *et al.*, 2021). Active (planting) and passive (natural colonisation via succession/rewilding, e.g. Broughton *et al.*, (2021)) afforestation represent two key approaches to achieve this, often described as nature-based solutions (Seddon *et al.*, 2019; Helm *et al.*, 2020; IUCN, 2020). However, climate change will impact forests development (Alexander *et al.*, 2016; Wessely *et al.*, 2017; Di Sacco A & Hardwick K *et al.*, 2020), so species suitable for afforestation need careful selection (Read *et al.*, 2009).

Exotic diseases are likely to pose threats to afforestation through novel interactions with factors such as pollution and extreme weather (Kirk, Bellamy and Lark, 2010; Skovsgaard *et al.*, 2017; Carroll, 2020; Dodd *et al.*, 2021). An example is ash-dieback (*Hymenoscyphus fraxineus* (T.Kowalski) Baral, Queloz & Hosoya) which is infecting and killing European ash (*Fraxinus excelsior* L.); this has been a concern in Western-Europe for around a decade (Kjær *et al.*, 2012; Pautasso *et al.*, 2013; Baral, Queloz and Hosoya, 2014). With *F. excelsior* being the dominant in many UK woodlands (Mitchell *et al.*, 2016) the future's uncertain for these habitats. Evidence is needed urgently to guide tree-planting and rewilding given uncertainty in future driver interactions. This is particularly the case for the design of effective agri-environment schemes options, for example woodland creation and tree planting within the Glastir scheme in Wales (Rose, 2011; Welsh Government, 2017); or non-governmental afforestation plans (for example: The Bonn Challenge; Woodland Trust free trees; Rewilding Britain).

In temperate biomes evidence suggests it takes at least 30 years for distinctive forest plant communities to assemble (Falkengren-Grerup, ten Brink and Brunet, 2006; Brunet *et al.*, 2012); with research in Britain suggesting 30 to 50 years for at least partial woodland plant community assembly (Walker, Sparks and Swetnam, 2000; Harmer *et al.*, 2001; Poulton *et al.*, 2003; Ashwood *et al.*, 2019). This duration means climate change is increasingly likely to act as a novel filter on species composition of the canopy and understorey potentially giving rise to either vacant niche space or no-analogue assemblages (Read *et al.*, 2009; Alexander *et al.*, 2016). Therefore, timely and credible assessments of effects of these novel filters are needed if ecologists and foresters are to answer the call for “the right trees planted in the right place” (Di Sacco, & Hardwick, *et al.*, 2020).

In this study we investigate the combined effects of climate change and *F. excelsior* loss due to ash-dieback on forest communities. Climate change in the context of ash-dieback (*H. fraxineus*) will mean canopy gaps emerging in previously *F. excelsior* dominated forests (Skovsgaard *et al.*, 2017). Species that will benefit from vacated niche space are uncertain although likely replacements have been highlighted (Mitchell, 2014; Skovsgaard *et al.*, 2017).

3.1.2 | Forest carbon sequestration

Afforestation sequesters carbon in both above- (Di Sacco& Hardwick, *et al.*, 2020) and below-ground carbon pools (Minasny *et al.*, 2017; Mayer *et al.*, 2020), whilst also being profitable and mitigating biodiversity loss (Di Sacco& Hardwick, *et al.*, 2020; Read *et al.*, 2009); therefore speeding up afforestation seems desirable. The UK 2050 net-zero carbon strategy describes how excess carbon emissions can be absorbed by natural carbon sinks like forests (HM Government, 2021). However, Read *et al.*, (2009) highlighted, over 10 years ago, that benefits from forest establishment may take 50 to 100 years to come to full fruition; too slow for UK 2050 targets (HM Government, 2021).

Considering forest carbon (C) storage for climate change mitigation there are two key factors that are important to ensure net C gain in forests. The first, high organic C soils when planted with trees, often fail to show a net C gain, even decades after planting, and sometimes suffer C loss (Friggens *et al.*, 2020; Mayer *et al.*, 2020; Casado *et al.*, 2022). For this reason, high C content soils should not be planted, ruling out habitats including C-rich acid grasslands and heathlands, most being upland in the study area Wales, UK (see: Emmett *et al.*, 2017 & Seaton *et al.*, 2020); *see, Appendix B.1* , for Welsh broad habitat details. The second, directly relating to net C flux in forests is C priming, where C introduced into the soil under increased CO_2 and higher temperatures causes greater microbial activity, respiration and loss of soil organic matter. This has been observed under experimental conditions for temperate soils (Smith *et al.*, 2013). An increase in soil C especially in the upper layers (e.g. top 15 cm considered here) may not be representative of an overall increase in soil C sequestration, certainly if soil fertility is low (De Graff *et al.*, 2006; Hungate *et al.*, 2009). This is because labile C can prime lower layers (microbial activation) giving rise to C loss throughout the soil profile (Smith *et al.*, 2013; Guenet *et al.*, 2018). However, in the longer term (at least 3 years but more likely >25 years for more stable C pool gains) increases in the C pool provides net C sequestration; although it is only an increase in the labile fraction (De Graff *et al.*, 2006; Guenet *et al.*, 2018; Mayer *et al.*, 2020), but this C can be fixed to be more recalcitrant as described in Cotrufo *et al.*, (2013).

3.1.3 | Biodiversity and carbon

As benefits to biodiversity and C sequestration may not be achievable in the same ecosystem and land use area, strategies are required to optimally allocate management interventions, given the: ecological potential of the starting landscape, and trade-offs within ecosystem and land use types (Read *et al.*, 2009; Di Sacco & Hardwick, *et al.*, 2020; Linney *et al.*, 2020). But there are differences in definitions, forest establishment does not have a

consistent end point across the studies. We consider establishment by progress towards established (baseline) forest conditions, via modelled changes in plant communities and key soil variables (pH, carbon, and nitrogen) which have been highlighted as important for soil health in Seaton *et al.*, (2020). The 30-50 year UK forest establishment timeframe might be overly long as some studies suggest shorter timescales from 20 to 30 years (Falkengren-Grerup, Brink and Brunet, 2006; Vesterdal *et al.*, 2008; Brunet *et al.*, 2012; Thomaes *et al.*, 2012). However, there is evidence that many forest plants can establish within 15 years when adjacent to older forest (Brunet *et al.*, 2012). If faster forest establishment is achievable this should also lead to faster acquisition of benefits.

A constraint to assembly of characteristic woodland plant communities is the depletion of plant species pools due to the degraded nature of UK landscapes with only 13% forest cover, one of the lowest in Europe (Hayhow *et al.*, 2019; Forest Research, 2020). Natural migration of understory forest species may occur at <3 to 12 m per year depending on species (Brunet *et al.*, 2012). Progression of succession is very pertinently highlighted in the uplands in Wales by McGovern *et al.*, (2013) and in England by Marrs *et al.* (2018) with no tree cover established even after 50-60 years in grazing exclusion experiments. Even when wider upland species diversity has been seen to increase in that time (Alday *et al.*, 2022) it is clear that the way a forest is established, and the age it is allowed to reach before it is altered is a major factor in the carbon sequestered, its biodiversity, and therefore health (Brunet *et al.*, 2012; Kröel-Dulay *et al.*, 2015; Ashwood *et al.*, 2019; Berdeni, Williams and Dowers, 2021). If plantation broadleaved forest can establish faster than successional timeframes (< 30 years), it appears best to recommend planting native species using minimum soil disturbance techniques (*sensu* Berdeni *et al.*, 2021) as soon as possible to mitigate climate change and biodiversity loss.

Considering other key factors of importance to this study, broadleaved forests have been seen to sequester carbon slower than conifers (Mayer *et al.*, 2020) but plantation coniferous forests tend to have lower biodiversity. Also many coniferous species are not native (Carey, Wallis, Chamberlain, *et al.*, 2008), and therefore not considered for obtaining desirable outcomes in this study (Stafford *et al.*, 2021).

3.1.4 | Research aims

The combined effects of climate change and disease-induced tree mortality are explored by modelling scenarios of soil and climate change (**Fig. 3.1**). We generated habitat suitability scores for woodland plants across a range of habitats in Wales, UK and summed these to estimate dark diversity (Pärtel, Szava-Kovats and Zobel, 2011) at high resolution sample points. Dark diversity refers to the species within the local pool that can inhabit a patch given its observed or modelled conditions (Pärtel, Szava-Kovats and Zobel, 2011). This means we model potential colonising species into future scenarios that are observed and unobserved at baseline as dark diversity predictions. We applied “worst-case-scenario” (RCP 8.5) climate projections (Lowe *et al.*, 2018; Met Office Hadley Centre, 2018) and model over longer time-periods than achieved to date (Mitchell *et al.*, 2016).

Thus, we aim to contribute evidence that will aid ecological restoration accounting for place-based pool of possible colonists (Pärtel, Szava-Kovats and Zobel, 2011) including: ancient woodland indicator (AWI) species (Glaves *et al.*, 2009); woody flora (Kallow, 2014; Trivedi and Kallow, 2017); timber species (Pyatt, Ray and Fletcher, 2001; Bathgate *et al.*, 2011); and nectar producing species (Smart *et al.*, 2017; Alison *et al.*, 2021). We attempted to answer the following research questions:

i. Which trees and shrubs could replace *F. excelsior* with and without alteration of climate?

ii. Do modelled changes in soil conditions and increasing shade from a growing tree canopy filter forest plant assemblages over a 30-year period approximate to reference baseline conditions in established broadleaved forest?

iii. To what extent are these modelled assemblages changed in their species composition by projected climate change?

3.2 | Methods

The following sections follow the numbering in **Fig. 3.1**, detailed in the parentheses. All modelling, statistical analysis and data plotting was conducted in R statistical software version 4.0.3 (R Core Team, 2019). The R package MutliMOVE (**Fig. 3.1**, 5.0) forms the ecological niche modelling core of the workflow (Henrys, Butler, *et al.*, 2015).

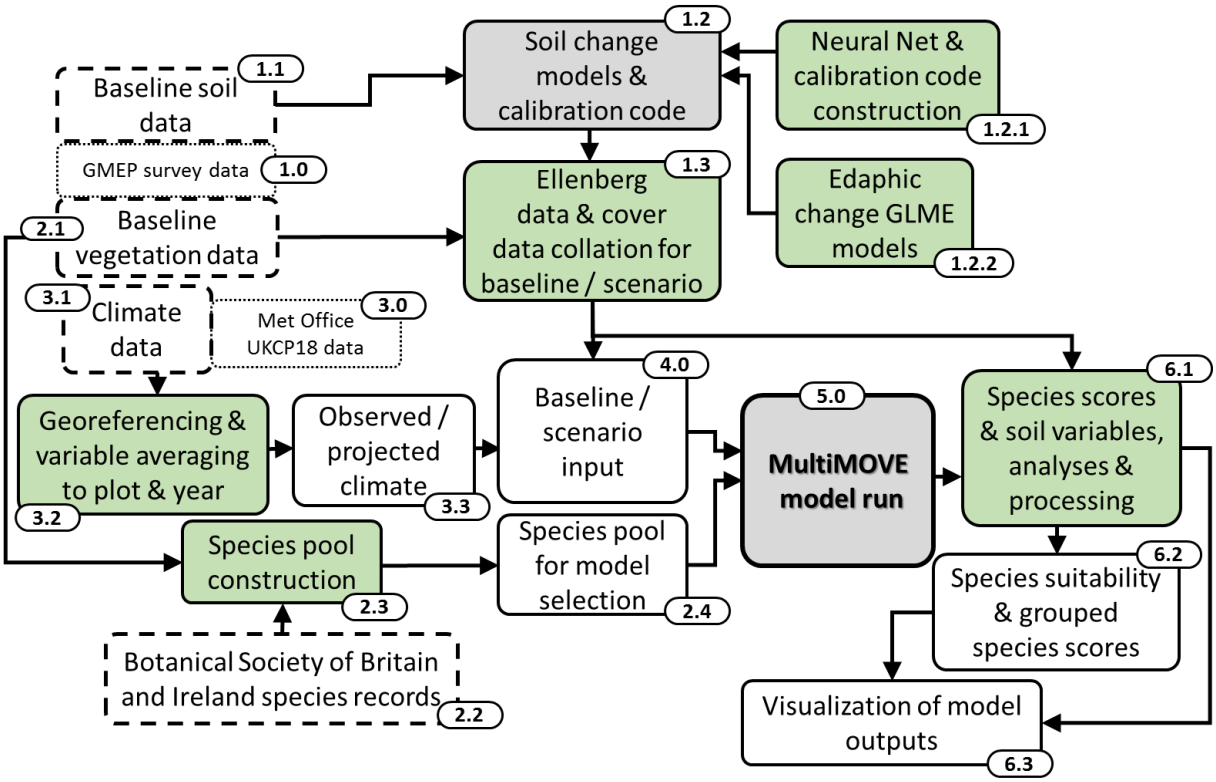


Figure 3.1. Schematic representation of the modelling workflow. Numbered boxes refer to sections in main text. Green boxes represent a coded process; grey boxes represent model runs; white boxes are datasets; white boxes with dashed outlines represent input data.

3.2.11 | GMEP Survey data (1.0)

Co-located soil and plant species compositional data were recorded as part of the Glastir Monitoring and Evaluation Program (GMEP). Within the study 732 plots surveyed once between 2013 and 2016 are used; detailed survey methodologies are described in Emmett *et al.* (2017) and Seaton *et al.* (2020).

3.2.12 | Baseline soil sampling (1.1)

A set of five soil cores (5 cm diameter x 15 cm depth) were taken from the edge of each (200 m^2) quadrat's central 2×2 m square. Measurements of pH in water, carbon (%), nitrogen(%) and gravimetric moisture content (%) from each plot define baseline model inputs and are the starting values that are adjusted over time to reflect the impact of tree planting for subsequent woodland development .

3.2.13 | Soil response models and calibration (1.2)

A suite of transfer functions were used to estimate values of vegetation indicator variables (mean Ellenberg values) for each quadrat given measured soil variables (Ellenberg, Dull and Weber, 1992). This step was necessary because the plant ecological niche models (ENM) were originally built using mean Ellenberg values plus vegetation height and climate as inputs (De Vries *et al.*, 2010; Smart *et al.*, 2010; Henrys, Smart, *et al.*, 2015). Ellenberg values represent the position of a plant species along ecological gradients of wetness (Ellenberg F), fertility (Ellenberg N) and reactivity (Ellenberg R) created by Ellenberg *et al.* (1992) and modified for Britain by Hill *et al.* (2004). To avoid circularity in building plant species niche models we excluded the focal species from the calculation of the mean Ellenberg scores when modelling its niche (*see, Appendix A.3*).

3.2.13.1 | Neural network calibration code (1.2.1)

Neural networks were used to model the three Ellenberg scores using soil variables in 2.1.2 as inputs (*sensu, 2 ,* West *et al.* (no date)). Details of the creation of the Neural networks can be found in *Appendix A.3*.

3.2.13.2 | Edaphic change models (1.2.2)

Our approach to modelling change in the soil variables over time in response to planting and woodland development was empirical data driven as dynamic biogeochemical modelling would be too coarse and not applicable (*see, 3.4.1*). Soil change under woodland development was modelled as follows; a literature search was conducted to find empirical soils data from time-series or chronosequences that measured change under afforestation by UK native broadleaved species. Care was taken to ensure the soil variables were measured in the same way as GMEP soil measurements. This process yielded nine data sets which were either sourced from the published literature or provided by the original authors (*see, Appendix B.2,* **Table B.1.**). As many datasets did not record all four soil variables, they were modelled separately using generalised linear mixed effect (GLME) models. These GLME models were based on the following covariates: starting value of the variable modelled, time (years of woodland development) and afforestation type. All models used a random effect for study or data source. Here, we assume that the modelled change is reasonably correlated with other soil variables whereas in reality we know they interact in varied ways. GLME models differed in terms of the final set of covariates included (*see, Appendix B2.3*). The best performing model for soil moisture change (lowest AIC, highest R^2) consisted of forest type and starting Ellenberg wetness value, this led to a uniform response across modelled years. *See,* Appendix *B.2,* for GLME construction and training data. An annual incremental addition to soil pH was added following *2* , West *et al.* (no date) and Emmett *et al.* (2010) for each broad habitat type to represent a recovery from deposition

based acidification. This reflects the expected response to ongoing recovery from historically-high levels of sulphur deposition (Kirk, Bellamy and Lark, 2010).

3.2.14 | Ellenberg and cover data collation (1.3)

The soil measurements for each GMEP plot were inputted to the neutral network models (directly for baseline or through the GLME plantation models), these are translated into predicted mean Ellenberg values, which are required inputs for the MultiMOVE species niche models. Alongside this for the baseline cover-weighted canopy height was calculated using vegetation species data from 2.1 and average vegetative height (Hill, Preston and Roy, 2004) as for *2*, West *et al.* (no date). This derived variable expresses the successional stage of the habitat and, by proxy, the light availability at plot ground level (Depauw *et al.*, 2020).

To represent forest growth, we incrementally increased cover-weighted canopy height (CWCH) by the years modelled in the workflow (**Table 3.1**). To do this a literature review was conducted to find growth rates for *F. excelsior* and other broadleaves grown in and native to the UK. Where the papers found did not contain *F. excelsior* an average across the native broadleaved species included was taken (see the following for data: Claessens *et al.*, 1999; Hein, 2003; Harmer, Boswell and Robertson, 2005; Dobrowolska *et al.*, 2011; Harmer, Kiewitt and Morgan, 2012). The CWCH year increments shown in **Table 3.1** are created by taking an average height reached over the given number of years in meters from the litrature catergorised as CWCH values. The catergorisation of meters to CWCH was as for the MultiMOVE manual (Hernys *et al.,* 2015): CWCH 5 as 1.0-3.0 m; CWCH 6 as 3.1-6.0 m; CWCH 7 as 6.1-15.0m; CWCH 8 as >15m. Half units were used in 2026 & 2036 as grows rates weren't always sufficiently different to move between catergories but growth still had to be represented.. Model testing showed that this approach to filtering species by their canopy

height and by soil conditions is able to reproduce the observed woodland community type satisfactorily, given succession (see figure 11.4 in Rowe *et al.* (2015)).

3.2.15 | Baseline vegetation (2.1)

Baseline vegetation data was equivalent to that used in *2*, West *et al.* (no date), species and their percentage cover for broad habitats: Arable and Horticulture (A&H); Improved Grassland (IG); Neutral Grassland (NG); and Bracken (Br). *See, B.1 ,* for broad habitat type descriptions.

3.2.16 | Defining the wider species pool (2.2 & 2.3)

The Botanical Society of Britain and Ireland distribution database provided the local 10 km species pool (BSBI, 2018) as defined in *2*, West *et al.* (no date). The species pool modelled at each plot location comprised the unique list of plant species observed in the baseline quadrat (**Fig. 3.1**, 1.0 & 2.1), those recorded in other quadrats in the GMEP 1 km square (**Fig. 3.1**, 2.1) and additional species present in the wider 10 km square pool.

3.2.21 | Observed and predicted climate data (3.0 & 3.1)

Here, we used the same climate data as *2*, West *et al.* (no date), this being observed historic data averaged from 1981 to 2016 as a baseline; and 'worst case scenario' future high emissions (RCP8.5), both at the 1 km cell resolution (Lowe *et al.*, 2018; Met Office *et al.*, 2019; Robinson *et al.*, 2022). The RCP8.5 1 km data source is the same as *2*, West *et al.* (no date).

3.2.22 | Georeferencing and variable averaging (3.2)

Climate data were geo-referenced to each plot location via the 1 km climate data cell they occurred within, as for *2*, West *et al.* (no date).

3.2.23 | Observed or projected climate application (3.3)

The climate data was utilised in the three scenarios, with all modelling done for 2016 using baseline climate data, the planted scenarios applied baseline and projected climate so that results for each, across years, could be compared.

3.2.31 | Model inputs (4.0)

Lastly, the MultiMOVE model was run for all species in the pool attached to each quadrat location using the seven input variables (the three mean Ellenberg values; cover weighted canopy height; minimum January & maximum July temperature, and total annual precipitation). MultiMOVE then uses theses inputs to give habitat suitability scores to the species in each plots pool with the generated scores allowing species to be ranked. This ranking provides a prediction of which species will be filtered in (or out) of plots under the differing scenario inputs (**Table 3.1**).

Table 3.1. Details of woodland development scenarios modelled with and without *Fraxinus excelsior*. Scenarios are: *Baseline* = Modelled forests from observed environmental data in GMEP survey; *Baseline CC* = as for Baseline but with the predicted climate change data as inputs; *Plantation broadleaved* = Broad habitat types, Arable and Horticulture, Improved Grassland, Neutral grassland and Bracken with soils modelled as having been planted with broadleaved trees under a baseline climate; *Plantation broadleaved CC* = As for *Plantation broadleaved* but with the predicted climate change data as inputs. Baseline climate = Baseline average climate (1981 to 2016); Predicted climate = High emissions. AES = agri-environment scheme; Glastir option codes: WC4 = Enhanced Mixed woodland creation; WC2 = Native woodland biodiversity creation; 611 = Trees & Shrubs transplants for planting (Woodland + Advanced scheme area); 101 = Trees and scrub establishment by planting.

Scenario	Management	Species pool	Soil models categorical setting	Related Glastir AES options	Recovery from acidification applied	*Scenario versions*. [years modelled]
Baseline	Observed forests in GMEP survey.	Dark diversity; No *F. excelsior*	None	None	No	*2*, Observed climate averaged (1981 to 2016) with/without *F. excelsior*. [2016]
Baseline CC	Observed forests in GMEP survey.	Dark diversity; No *F. excelsior*	None	None	Yes	*18*, Predicted climate, with/without *F. excelsior*. [2021,2026,2029,2036,2043,2046,2050,2056]
Plantation broadleaved	Planting UK native broadleaves	Dark diversity; No *F. excelsior*	***pH*** & ***N%***: planted broadleaved ***C%***: broadleaved	WC4; WC2; 611; 101.	Yes	*18*, Observed climate, with/without *F. excelsior*. [2021,2026,2029,2036,2043,2046,2050,2056]
Plantation broadleaved CC	Planting UK native broadleaves	Dark diversity; No *F. excelsior*	***pH*** & ***N%***: planted broadleaved ***C%***: broadleaved	WC4; WC2 ; 611; 101.	Yes	*18*, Predicted climate, with/without *F. excelsior*. [2021,2026,2029,2036,2043,2046,2050,2056]

Years from Baseline (2016)	Time interval description	Cover weighted canopy height setting	Year modelled
5	AES agreement time 1	5	2021
10	AES agreement time 2 and first decade	6.5	2026
13	AES agreement time 3	7	2029
20	Second decade of change	7.5	2036
27	The 25-year environment plan end	8	2043
30	Third decade	8	2046
34	Net zero emissions goal year	8	2050
40	Fourth decade	8	2056

3.2.32 | MultiMOVE (5.0)

The MultiMOVE ENM consists of an ensemble of five modelling methods whose outputs are combined to produce a weighted model average habitat suitability score (**Fig. 3.1**, 4.0). This covers the realised niche of 1262 taxa within Great Britain covering the most common and many less common plants and bryophytes (see Henrys *et al.*, 2015; Smart *et al.*, 2019 for full description). The ENM package has been utilised by many studies under multiple scenarios and is subject to a process of ongoing validation and testing (West *et al.*, no date; De Vries *et al.*, 2010; Henrys, Smart, *et al.*, 2015; Rowe *et al.*, 2015; Emmett *et al.*, 2017; Smart *et al.*, 2019).

3.2.33 | Summarising model outputs (6.1)

The outputs from **Fig. 3.1**, 1.3 & 5.0 were summarised by habitat type and scenario for the modelled interval 2016 to 2056. For comparison of soil variables modelled with the baseline broadleaved woodland values we used an unpaired t-test on log transformed data to achieve normality. This allowed determination of how modelled planted soil for a given year differs from observed forest soils.

As for *2* , West *et al.* (no date) logistic regression was used to build credibility by testing whether species' presence and absence in the baseline was correlated positively with the modelled habitat suitability scores for each plot location (*see, Appendix A.5-A.5.1*).

3.2.34 | Habitat suitabilities and species groups (6.2)

Habitat suitability scores were used in two ways for analysis. First, we summed suitability scores for specific subsets of ecosystem service-supporting species producing dark diversity (**Fig. 3.2**) estimates for each year, habitat and species group (Calabrese *et al.*, 2014). Dark diversity (Pärtel, Szava-Kovats and Zobel, 2011) refers to all the species within a local area of a site that could grow under the environmental conditions at the site, here this includes

species pools in **Fig. 3.1**, 2.1 & 2.2; with higher habitat suitability scored species being ranked as those best suited. We used four species lists as follows: UK woody flora (a woody tissued flora list provided by the UK National Tree Seed Project (Kallow, 2014; Trivedi and Kallow, 2017)); ancient woodland indicators for Wales (Glaves *et al.*, 2009); timber species being a timber producing subset of the woody flora (Pyatt, Ray and Fletcher, 2001; Bathgate *et al.*, 2011); and nectar producing species (Smart *et al.*, 2017; Alison *et al.*, 2021) – *see, Appendix B.3.1,* **Table B.3**. Secondly, the habitat suitability scores per plant species were treated as a frequency table and matched to the British National Vegetation Community (NVC) units (Rodwell, 1998) via the software MAVIS (Smart, 2000), using methods as for 2, West *et al.* (no date).

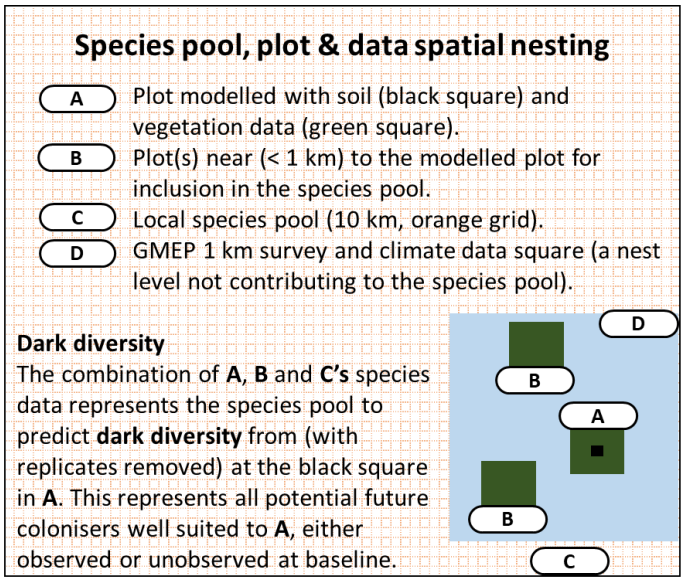


Figure 3.2. Species pool, plot and spatial data nesting. The spatial nesting of the squares provides a visual as well as descriptive explanation of dark diversity. The survey square within C refers to the Glastir Monitoring and Evaluation Program 1 km squares proportionally representing land use across Wales.

A key component of the workflow for considering *H. fraxinus* impacts is the inclusion or removal of *F. excelsior* from the model outputs. The removal of *F. excelsior* from the outputs allows for species and vegetation types ranked below *F. excelsior* vegetation to be identified as likely replacements of the species and how this may change future vegetation.

3.3 | Results

3.3.1 | Soil variables modelled

Outputs of the soil variables models (**Fig. 3.3**), show all habitats are expected to increase in pH given alterations applied due to expected recovery from historically high S deposition. Moreover, every habitat (**Fig. 3.3**) other than Bracken starts at higher pH than the broadleaved woodland reference (**Fig. 3.3, A**). Nitrogen and carbon in some planted broad habitats appears to respond with predicted change becoming congruent with (not significantly different from) the reference baseline broadleaved habitat by the 2040s.

Planting is predicted to increase topsoil C concentrations (**Fig. 3.3, A**), habitats either exceed or reach equivalent baseline broadleaved reference values. This depends on starting soil C as it is an input parameter, and the change is modelled linearly. Bracken is similar to the baseline at the start but exceeds broadleaved woodland values by 2046. Arable, improved and neutral grassland start with significantly lower values at baseline but are then predicted to accumulate carbon becoming no different (arable) or exceeding (grasslands) the baseline by 2056.

Little soil N% change is predicted, other than increasing in arable where values start lower than the broadleaved reference and end significantly higher (**Fig. 3.3**). Overall, the results predict increasing pH and C:N ratio. The higher pH starting points and predicted changes suggest that developing woodland plant communities will reflect appreciably higher pH than the average Welsh woodland (**Fig. 3.3, A**).

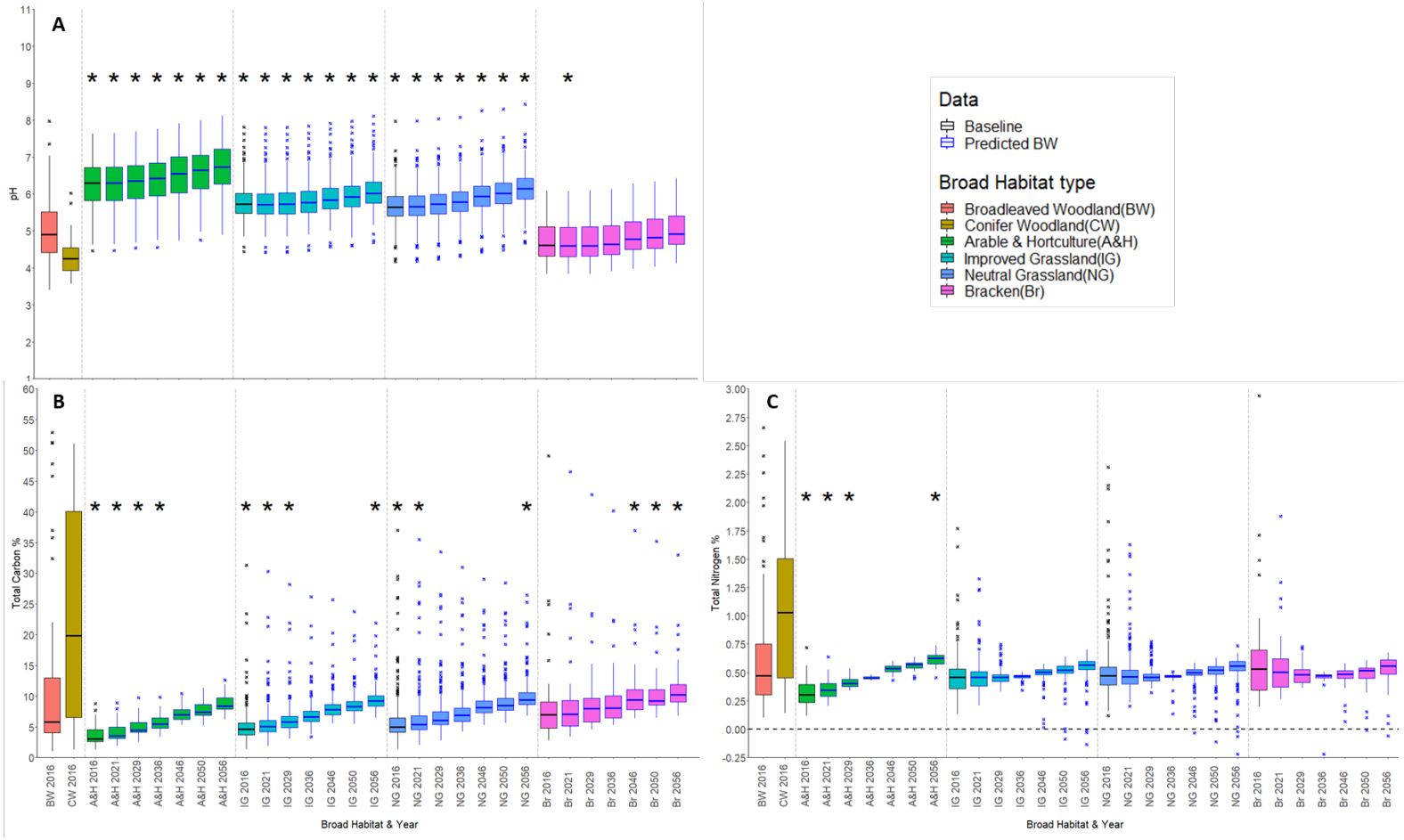


Figure 3.3. Modelled change in soil variables under tree planting per Broad Habitat (BH) type and year, for pH (A), total soil carbon percentage (B) & total soil nitrogen percentage (C). The year 2016 for each BH type represents the observed data (black boxes), subsequent years data were predicted by using 2016 data as inputs to generalised linear mixed effect models of broadleaved woodland plantation on respective soil variables (blue boxes). Asterisks (*) at Y=9 for pH; Y=40 for Carbon & Y=2 for Nitrogen, represent significant differences (p-value=0.05) of logged variables of the 2016 Broadleaved Woodland baseline compared to the modelled values for the Broad Habitat type and year below each asterisk. Where asterisks are not shown planted habitat values were not significantly different from the target Broadleaved Woodland baseline.

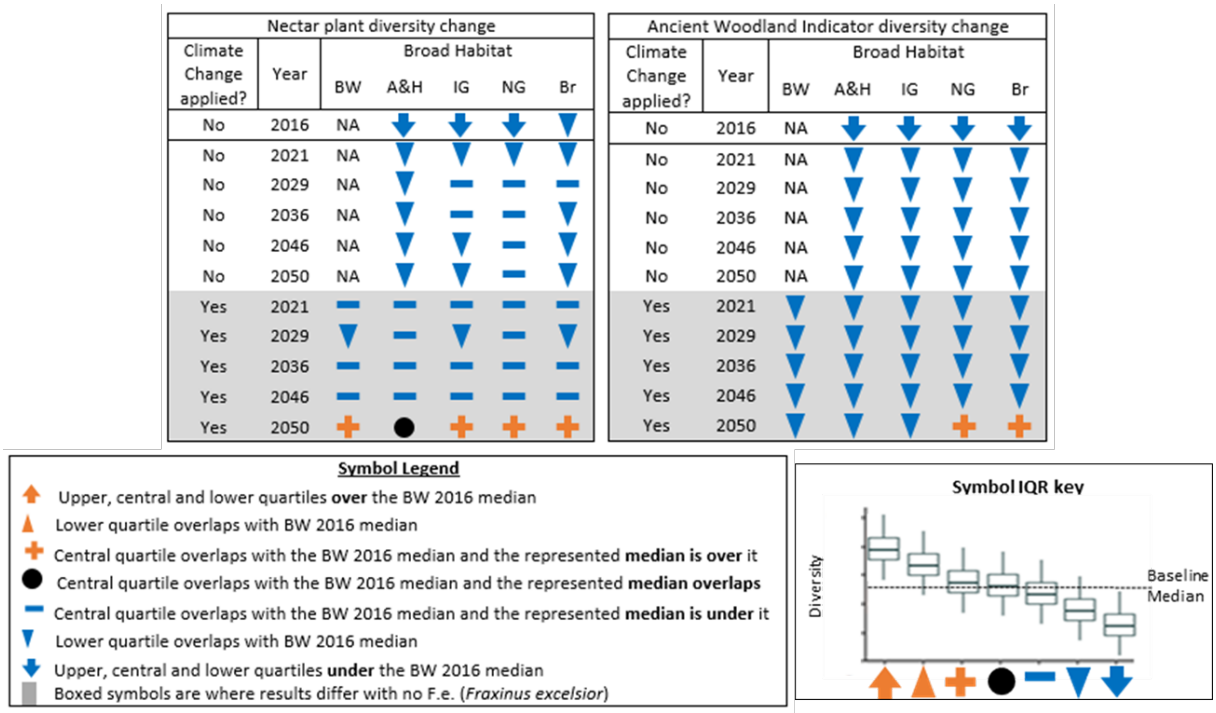


Figure 3.4. Species group diversity change. Symbols define how the species group's diversity score (interquartile range (IQR) and median) for a given year and broad habitat type compares with the Broadleaved Woodland baseline median (2016) given accumulation of woodland dark diversity, either with or without climate change. Thus relative to the baseline, blue symbols indicate a decrease, black, no change and orange an increase. Broad Habitat types: **BW** = Broadleaved woodland (2016 baseline); **A&H** = Arable and horticulture; **IG** = Improved grassland; **NG** = Neutral grassland; **Br** = Bracken. The data used to create these boxplots was generated using an ecological niche model MultiMOVE, inputs were altered to represent baseline (1981-2016) and future climates using downscale UKCP18 climate data, incremental increase of cover weighted canopy height representing tree growth and generalised linear mixed effect models of soil variable change under broadleaved plantation. All diversity scores are representative of modelled dark diversity, thus the baseline score will be higher than the 2016 observed diversity. *See, Appendix B.3.2, Fig. B.7* for boxplots showing the IQRs of each species groups diversity scores per habitat and scenario.

3.3.2 | Model validation against baseline observations

Logistic regression showed that a greater habitat suitability score (weighted model average) increased the probability of the species being observed in baseline quadrats (*P* <0.001, *see, Appendix A.5.1,* **Fig. A.2**). The mean rank of species observed as present also had a significantly greater habitat suitability scores than the mean rank of the species not observed (*P* <0.001; two tailed Wilcoxon rank test, *see, Appendix A.5.1,* **Fig. A.2**).

3.3.3 | Species groups and predicted dark diversity

Predicted dark diversity for two groups of ecosystem service-supporting plants both showed deviations from the baseline broadleaved woodland across the time interval.

3.3.3.01 | Nectar plants and ancient woodland indicators

When climate change is included as a filter on the plant species pool, predicted diversity of both groups matches the broadleaved baseline by 2050 for Neutral Grassland and Bracken starting points (**Fig. 3.4**). This also occurs for nectar plant diversity in the two agriculturally-intensive habitats, Arable & Horticulture and Improved Grassland, but woodland specialist diversity still lags behind the broadleaved reference for these two habitats with climate change included (**Fig. 3.4**). Without climate change, predicted diversity shows a persistent lag behind the baseline reference even by 2050 for both plant groups. This applies across all starting habitats except Neutral Grassland where nectar plant diversity moves appreciably toward but does not match baseline values by 2050.

Nectar-producing, plant diversity scores in broadleaved woodland drop below the baseline median in **Fig. 3.4**, from 2021 to 2046; this appears to be a reshuffling of the community rather than a pan-taxa climate response. This is reflected in habitat suitability scores of *Hedera helix* and *Rubus fruticosus* (*Appendix B.3,* **Fig. B.4***, B&C*) in 2021, 2036 and 2046 being below the 2016 baseline; and *Crataegus monogyna* (*Appendix B.3,* **Fig. B.4***, A*) and *Hyacinthoides non-scripta* (*Appendix B.3,* **Fig. B.3***, C*) rising above the baseline until 2029 then remaining above or near the 2016 baseline until 2050.

Under climate change ancient woodland indicator species (AWI) in baseline broadleaved woodland showed a drop in diversity, alongside a drop in all the climate variable values in 2029 (**Fig. 3.4** & *Appendix B.4,* **Fig. B.10**). This climate response is confirmed by habitat suitability scores of *Arum maculatum, Circaea lutetiana*, *Hyacinthoides non-scripta* and *Oxalis acetosella* all having the lowest or near lowest scores across the modelling in 2029, then rising from the 2040s onwards (*Appendix B.3.2,* **Fig. B.3**). However, no modelled planted habitat reaches the AWI median prior to 2050.

3.3.3.02 | Timber Species and Woody Flora

Dark diversity scores of both groups in **Fig. 3.4** are predicted to have exceeded the baseline reference by 2050 with and without climate change. Different levels of response were observed among habitats: Bracken was predicted to show the largest positive response over the shortest period. Increasing canopy height in this habitat results in both species groups dark diversity exceeding the modelled baseline by 2029 (**Fig. 3.4**). In broadleaved woodland filtered by climate change similar suitability changes occur for the predicted dominants. These are *Acer pseudoplatanus*, *Fagus sylvatica*, *Fraxinus excelsior* and *Quercus* Sp. all showing similar trends from year to year (*Appendix B.3.2,* **Fig. B.5**).

Woody flora (*Appendix B.3.2,* **Fig. B.9**) showed a drop in diversity scores with *F. excelsior* removed as does the timber species scores (*Appendix B.3.2,* **Fig. B.8**). However, this is reduced as *F. excelsior* makes a smaller relative contribution to the woody flora group as it is larger than the timber group.

For both planting scenarios, under baseline and predicted climate (**Fig. 3.5**), there is less variation in the woody flora scores (*Appendix B.3.2,* **Fig. B.9***,C&D*) than the timber species scores (*Appendix B.3.2,* **Fig. B.8***,C&D*). However, individual species results under climate change in baseline broadleaved woodland shown changes in the rank order of their habitat suitabilities. For example *Corylus avellana* shows its lowest scores in 2029 & 2050 (*Appendix B.3.2,* **Fig. B.6**); but *R. fruticosus* shows its highest (*Appendix B.3.2,* **Fig. B.4***, C*) in 2029 & 2050; indicating a reshuffling of the woody flora community.

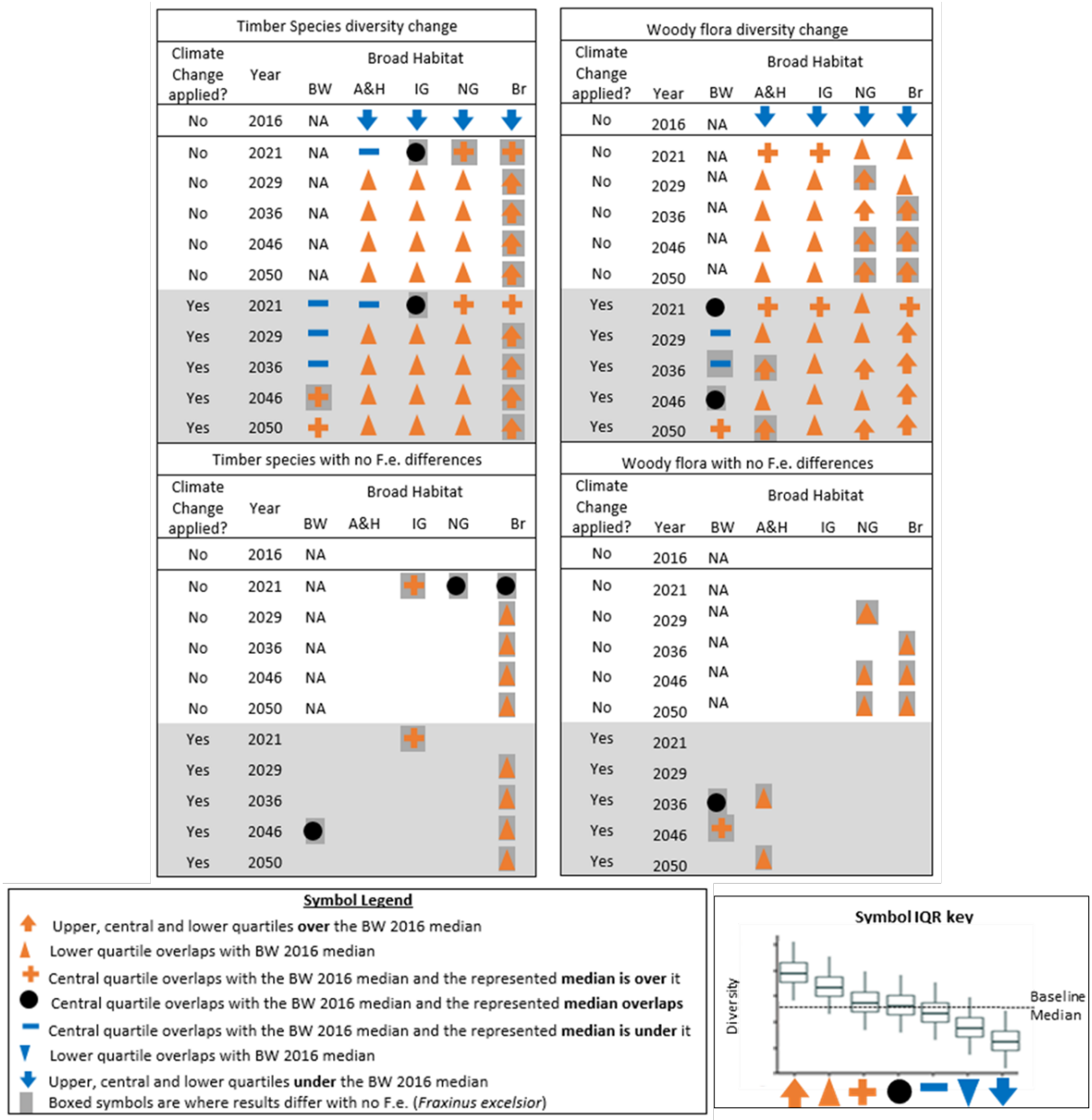


Figure 3.5. Timber and woody species group diversity change. Symbols define how the species group's diversity score (interquartile range (IQR) and median) for a given year and broad habitat type compares with the Broadleaved Woodland baseline median (2016) given accumulation of woodland dark diversity, either with or without climate change. Thus, relative to the baseline, blue symbols indicate a decrease, black, no change and orange an increase. Broad Habitat types: **BW** = Broadleaved woodland (2016 baseline); **A&H** = Arable and horticulture; **IG** = Improved grassland; **NG** = Neutral grassland; **Br** = Bracken. The data used to create these boxplots was generated using an ecological niche model MultiMOVE, inputs were altered to represent baseline (1981-2016) and future climates using downscale UKCP18 climate data, incremental increase of cover weighted canopy height representing tree growth and generalised linear mixed effect models of soil variable change under broadleaved plantation. *See, Appendix B.3.2,* Fig. B.8 & Fig. B.9 for boxplots showing the IQRs of each species groups diversity scores per habitat and scenario.

3.3.3.1 | Vegetation and Fraxinus excelsior modelling

Results within **Fig. 3.6 & Fig. 3.7** are a subset of data, only including sites where *Fraxinus excelsior* habitat suitability scores suggest the species is likely to be present according to logistic regression conducted on baseline scores (*see, A.5.1*). Thus, these figures specifically focus on ash woodland. The species results (**Fig. 3.5**) build confidence in the modelling as a plausible range of common woodland trees, shrubs and herbs are predicted to have the highest modelled suitabilities. Overall there is little difference in the top species' identity with, or without, climate change, and also little turnover through time.

The modelled results for the *F. excelsior* plots (**Fig. 3.6**) provide an estimation of suitable species to plot conditions representing the dark diversity pool (see more species in, *Appendix B.3.1,* **Table B.2**). The years included are: the baseline, 2016; 20 years from baseline, 2036; 30 years from baseline (research question ii), 2046; and net-zero target year, 2050.

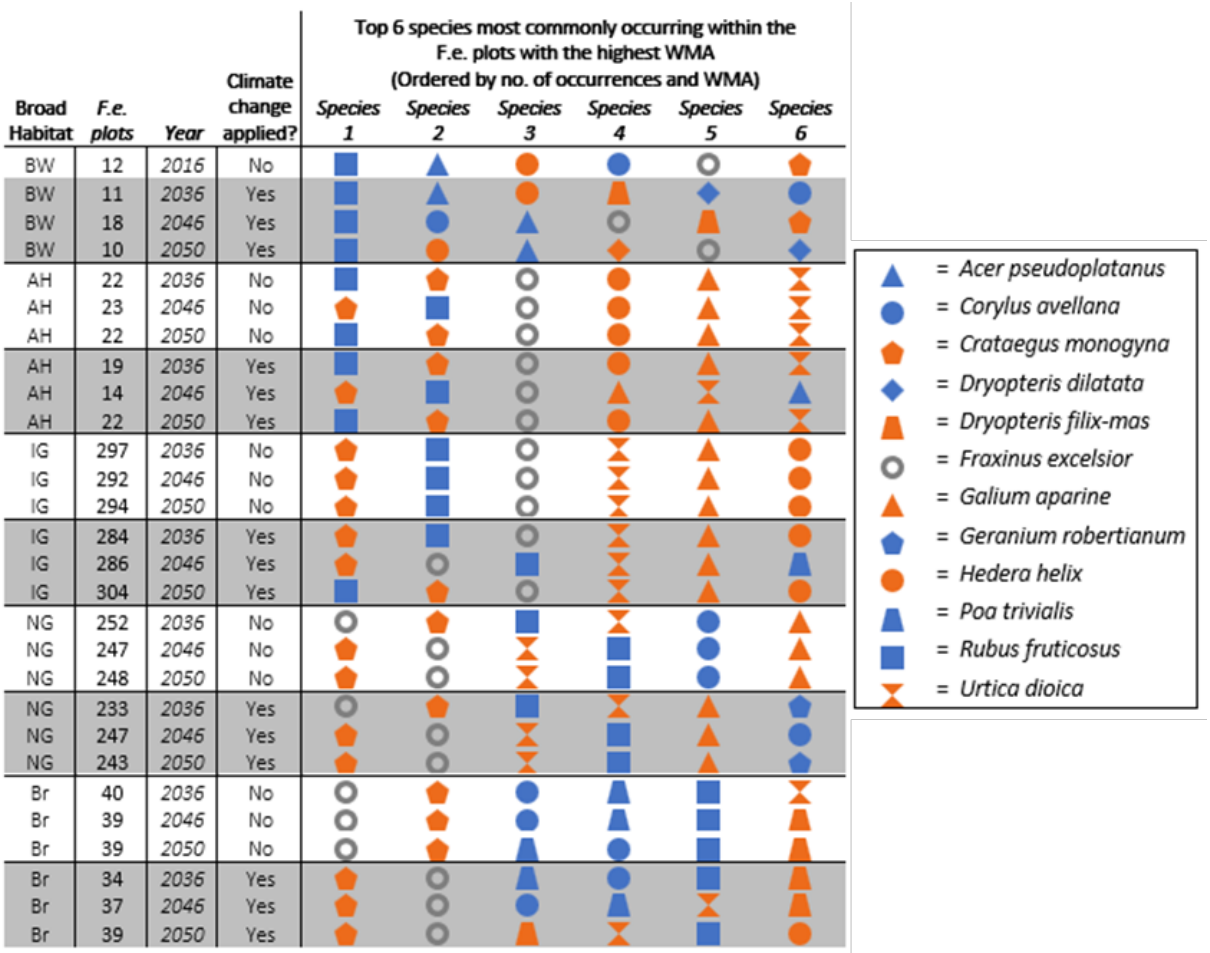
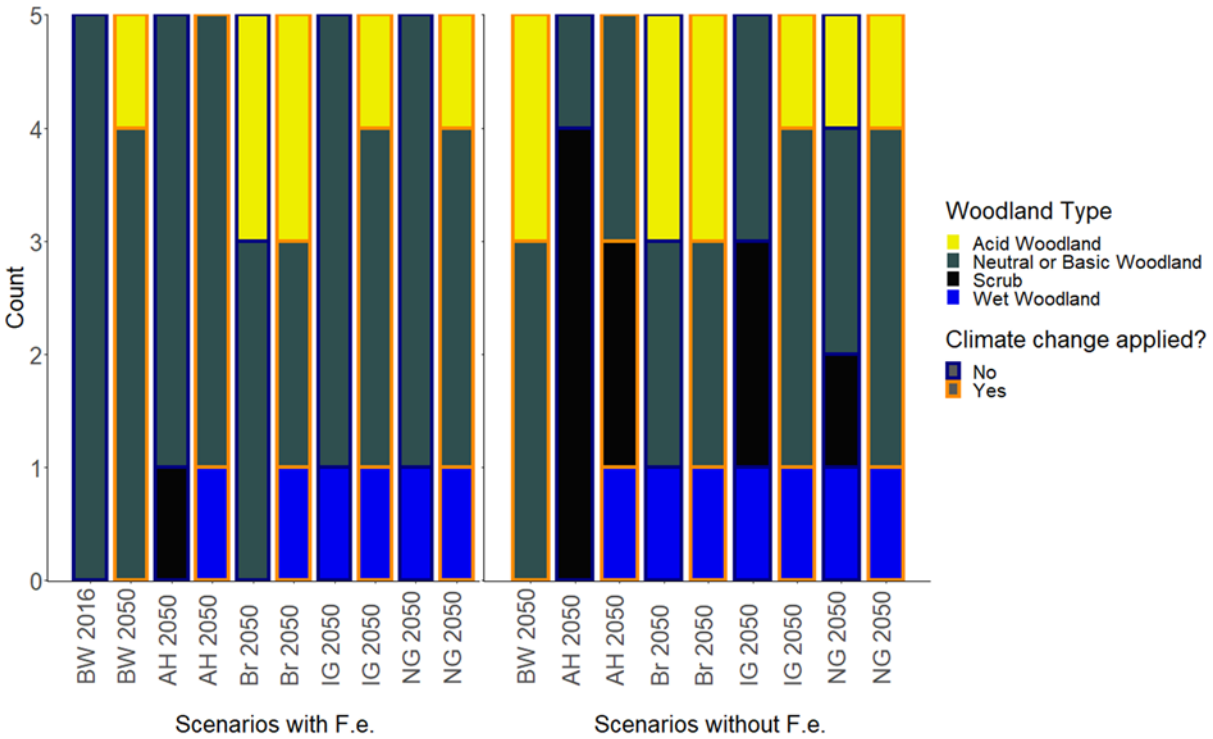


Figure 3.6. For each habitat and year with and without climate change the ***top 6 species*** most suitably predicted species are shown (top 5 if *Fraxinus excelsior* is removed). This only includes plots where weighted model average score suggests *F. excelsior* is more likely to be present than absent, determined by logistic regression. The first 2016 row represents modelled habitat suitabilities in broadleaved woodlands in the baseline year 2016 with all other years representing canopy growth and climate change scenarios. **Broad Habitats**: BW= Broadleaved woodland baseline; AH= Arable & Horticulture; IG= Improved Grassland; NG= Neutral Grassland; Br= Bracken; **Climate change applied?: No** = Baseline climate (white); **Yes** = predicted climate (grey). *See, Appendix B.3.1,* Table B.2 for the top 20 species.

Within baseline broadleaved woodland *A. pseudoplatanus* is consistently predicted as the likely replacement for *F. excelsior* under climate change, as it has the highest suitability scores (**Fig. 3.6**, BW, Climate change scenarios). The vegetation results suggest little change in vegetation type with *F. excelsior* removed (**Fig. 3.7**). However, the predicted, neutral, base-rich woodlands or acid woodlands are likely to be realised as low canopy woodlands or scrub with the species such as *Corylus avellana, Crataegus monogyna, and R. fruiticosus* (**Fig. 3.6**). Scrub as a vegetation type appears more regularly with the removal of *F. excelsior* and more regularly in higher fertility habitats (**Fig. 3.6**).

Results for improved grassland (**Fig. 3.6**, IG) also show that *Crataegus monogyna* and *R. fruticosus* are consistently most suitable. Neutral grassland results in **Fig. 3.6** are similar to the improved grassland but lack the higher scores of the high fertility species (*e.g. Galium aparine*). Neutral grasslands along with bracken habitat also show the largest number of vegetation types in the top vegetation groups (*Appendix B.3.1,* **Table B.2**). The standout feature of the bracken habitat species results is fern species (*Pteridium aquilinum, Dryopteris dilatata, Dryopteris filix-mas*) consistently occurring within the top six species regardless of climate.



Vegetation type description	National vegetation classification units (Rodwell et al., 1998)
Neutral or base rich woodland	W8; W8d; W8e; W8b; W12a; W8a
Wet woodland	W6; W6d
Acid woodland	W10c; W10; W10e; W10a
Scrub	W21; W21a; W21b; W21c; W25a

Figure 3.7. The top five woodland vegetation types for each habitat with Broadleaved Woodland 2016 baseline on the far left for reference, and 2050 for all other scenarios. The left-hand plot shows the predicted vegetation with *Fraxinus excelsior* (**F.e.**) within the species pool and the right plot without F.e., no baseline is shown in the right-hand plot as F.e. is present at the baseline. Woodland types were constructed via National Vegetation Classification units (NVC units, matched using the software MAVIS). *See, Appendix B.3.1,* Table B.**2**, for full data and vegetation group details. The first 2016 row represents broadleaved woodlands at baseline in 2016 with all other years representing canopy growth and climate change scenarios. Broad Habitat: **BW**= Broadleaved woodland baseline; **AH**= Arable & Horticulture; **IG**= Improved Grassland; **NG**= Neutral Grassland; **Br**= Bracken.

3.4 | Discussion

We based our modelling on high-quality, high-resolution soil and vegetation data. As shown here, models can be usefully applied to manage expectations about the potential timescales of achieving conditions suitable for assembling typical understorey communities. This is important because the understorey contributes significantly to forest biodiversity (Brunet *et al.*, 2012; Perring *et al.*, 2020). Our novel inclusion of a measured local species pool (*sensu 2* , West *et al.* (no date)) allows for compositional turnover to arise as the woodland develops in the form of species changing rank based on their habitat suitability score. Hence by modelling habitat suitability of a large suite of potential colonists we can estimate dark diversity at each location over time (Pärtel, Szava-Kovats and Zobel, 2011).

These approaches have allowed us to address the research questions within the following sections.

3.4.1 | Soils

The soil response to afforestation showed mixed results reflecting development from differing starting habitat associated soil conditions (Minasny *et al.*, 2017; Mayer *et al.*, 2020). While our approach used simple and linear empirical models, the results appear plausible over the timescales examined matching research into similar conditions and ecosystems (Poulton *et al.*, 2003; Thomaes *et al.*, 2012). Dynamic biogeochemical modelling would have required either prohibitive data gathering and parameterisation or the use of generalised parameters sets reducing (coarsening) realism of models (Radchuk, Kramer-Schadt and Grimm, 2019), and lowering sensitivity to the fine resolution of the input data (e.g. Davie*s et al.*, 2016).

The three modelled soil variables showed different trajectories. Soil pH started higher than baseline broadleaved woodland in all habitats except the less intensively-managed Bracken (*Pteridium aquilinum*) dominated broad habitat type (see also Seaton *et al.* (2020)) and then increased steadily reflecting adjustment due to recovery from historically acidification from deposition (Emmett, Reynolds, *et al.*, 2016), *sensu 2*, West *et al.* (no date).

Nitrogen (N%) provided an almost opposite story from pH as all habitats except arable were within the baseline range of broadleaved woodland values **Fig. 3.3**, **C**, probably because arable soils lose organic matter due to continued crop harvesting with associated nutrient loss (Jones *et al.*, 2013). However, this habitat makes the greatest gains in N being significantly greater than baseline by 2056. The lack of significant differences (**Fig. 3.3**, **C**) in grassland and bracken habitats from baseline broadleaved woodland soil N is likely due to N being a biologically-limiting nutrient that is competed for in all habitats by biota present (De Graff *et al.*, 2006; Mayer *et al.*, 2020). However, the C:N ratio varies between habitats and as can be seen across **Fig. 3.3** from left to right, broad habitat carbon values are predicted to increase across the time-period. The increasing C:N will filter for species typical of lower fertility than the intensively managed planted habitat's baselines. In summary, using simple models applied to published evidence of the effects of woodland development we predict consistent and substantial increases in C:N ratio where the increase in soil C up to 2050 outweigh increases in soil N, and pH continues to increase in line with recent observations. Coupled with adjustment of the shade filter by simply increasing canopy height and applying climate change, we then determined how these changing model inputs altered habitat suitability for plant species over time (research question ii.). The increase in soil C provides a positive message for forest utilisation to achieve 2050 goals in UK government strategy (HM Government, 2021).

While soil conditions are often discussed in the context of climate change mitigation (De Graff *et al.*, 2006; Mayer *et al.*, 2020), changing conditions also imply change in plant biodiversity and species composition. Moreover land-use legacy effects (e.g. higher N) can result in long-lasting constraints on future woodland development (Dupouey *et al.*, 2002; Valtinat, Bruun and Brunet, 2008; Diedhiou *et al.*, 2009).

3.4.11 | Most habitat creation, versus most change

A more nuanced discussion around ecosystem function and service trade-offs surrounding soil carbon capture *versus* biodiversity gains (Linney *et al.*, 2020) is a comparison of the "most creation" versus the "most change" for differing environmental variables within a habitat. Here we use "most creation" to refer to where the starting habitat has moved closest to the broadleaved woodland baseline, i.e., creating habitat the most similar to it. On the other, hand "most change" to refer to where the greatest positive changes occur in variables.

Looking at a "most change" example, A&H begins with the lowest carbon and nitrogen values at baseline (**Fig. 3.3**) and thus makes the largest gains by 2046 but predicted increases in plant diversity are the least of all the habitats (**Fig. 3.4** & **Fig. 3.5**). However legacy effects of low carbon and high residual fertility can limit the absolute biodiversity change relative to other habitat types, combined with croplands often being the most degraded habitats (Mayer *et al.*, 2020; Berdeni, Williams and Dowers, 2021). Such legacy effects can push community assembly away from desirable endpoints (Falkengren-Grerup, ten Brink and Brunet, 2006).

In contrast, planted Bracken habitats exhibit the greatest predicted forest creation ("most creation") both in terms of progression toward baseline broadleaved woodland soil conditions (**Fig. 3.3**) and predicted dark diversity of forest specialist plants (*Appendix B.3.2,* **Fig. B.7***, B*). Here the similarities of the two broad habitats at baseline has led to forest soils

and ancient woodland indicator species resembling the described target broad habitat closely. Bracken is often thought of as a woodland species that can become dominant after trees are cleared, and there are often woodland species in these habitats within either relict understories, or seedbanks (Marrs and Watt, 2006).

3.4.2 | Climate

Climate filtering effects are noticeable in both the species results (**Fig. 3.4** & **Fig. 3.5**) and vegetation results (**Fig. 3.6**) where differences between climate scenarios are apparent (research question iii.). As predicted temperatures move outside of the range of MultiMOVE model's training data (2046 onwards) predictions after this period become less reliable (*see*, *Appendix B.4,* **Fig. B.10**). The range of the climate training data for MultiMOVE is large given that it covered the full extent of Britain from the temperate continental South-East-England to the boreal conditions of the Scottish mountains. This emphasises the substantial changes in climate predicted for Wales in the next 40 years. Modelling the ecological impacts is an acknowledged challenge and even dynamic approaches need to estimate the uncertain consequences of no-analogue climate space and novel competitive interactions (Williams and Jackson, 2007; Mouquet *et al.*, 2015; J. M. Alexander *et al.*, 2016). *See, Appendix A2.1,* for further details on modelling into future climate space.

3.4.3 | Plant Species

Plantation predicted diversity scores for ecosystem function and service supporting plants all demonstrated deviations from the baseline broadleaved woodland diversity scores (**Fig. 3.4 & Fig. 3.5**). This occurs even in the observed climate scenario where timescales would be expected to produce results similar to the baseline. This suggests that none of the scenarios of future afforestation are likely to replicate the plant assemblages typical of the baseline woodlands in Wales. This implies that expectations require careful management and that

targets based on the present or past may need to be applied loosely to future forest development (research question ii.).

The highest diversity is within the Timber and Woody flora species groups, which is expected as the model workflow is deliberately set up to represent forest establishment, building confidence in its robustness. Comparisons within the results however highlight novel differences under different climates, habitats, and where *Fraxinus excelsior* is removed from the modelled output assuming *H. fraxineus* mortality. The baseline climate scenario shows a steady increase in Timber species diversity across habitats (*Appendix B.3.2,* **Fig. B.8**); with the residual fertility of the grassland starting habitats being the likely cause of their higher scores, also increasing as soil pH is predicted to recover from sulphur deposition (**Fig. 3.3, A**). The lowest scores for timber species coincide with higher temperatures in the predicted climate data (*Appendix B.4,* **Fig. B.10**), this is assumed to be linked to drought stress, already recognised as a concern for UK native timber species (Broadmeadow, Ray and Samuel, 2005). Possible *F. excelsior* loss is a large concern as Broadmeadow *et al.* (2005) suggested it might have been one of the species that would perform better under climate change (alongside *Fagus sylvatica* and *Acer pseudoplatanus*).

For the Woody flora group with and without *F. excelsior* (**Fig. 3.5**) the planting scenario scores under baseline and predicted climate differ much less than for Timber species (*Appendix B.3.2,* **Fig. B.9**, *B&D* varies more than **Fig. B.8** *B&D*). Thus, climate may have less of an effect on over all Woody flora species presence, but is expected to impact abundance or species performance (e.g. Broadmeadow *et al.*, 2005; Hastings *et al.*, 2014). The Timber species (*Appendix B.3.2,* **Fig. B.8**) and Woody flora scores results (*Appendix B.3.2* **Fig. B.9**, A&B to C&D) decrease with the removal of *F. excelsior*, this change is notable in the vegetation type results (**Fig. 3.7**) as the lower canopy or scrubby woody species are modelled as a likely replacement of *F. excelsior*. These results suggests Woody

flora species will be present and prevalent in all future scenarios with climate change and recent empirical work across Europe suggests increases in non-tree woody flora due to changing climate (Perring *et al.*, 2020).

Modelled diversity for Nectar plants and AWI species (**Fig. 3.4**) remain below the baseline broadleaved woodland reference in all habitats and throughout the modelled time interval. The implication is that despite gradual change in soil conditions resulting from forest development, legacy differences in soils persist and inhibit change toward conditions more typical of baseline forest (Valtinat, Bruun and Brunet, 2008). For the modelled dark diversity vegetation to become realised into the future dispersal establishment process would need to facilitate this; for example dispersal from local patches holding species (Brunet *et al.*, 2012) or planting (Ashwood *et al.*, 2019). An improvement on the ENM here would be to model dispersal and establishment to give greater insight into potential future communities (Boulangeat, Gravel and Thuiller, 2012).

The few instances across **Fig. 3.4** where scores are above baseline scores are later years in the scenarios with predicted climate. This is especially notable in the Nectar plants where broadleaved woodland modelled under a predicted climate shows higher scores in 2050 than baseline. This result suggests that Nectar plants are favoured by predicted climates in 2050 and this is notable in individual species results: *Rubus fruticosus* (*Appendix B.3,* **Fig. B.4***, C*); *Hyacinthoides non-scripta* (*Appendix B.3,* **Fig. B.3***, C*), & *Crataegus monogyna* (*Appendix B.3,* **Fig. B.4***, A*). However, this is not consistent across the species group results as these decline in some years suggesting species shuffle as the climate changes.

Within **Fig. 3.4**, no modelled planted habitat reaches the AWI median prior to 2050, so even after three-decades predictions don't reach baseline diversity scores even where climate change appears to increase estimated diversity. However, under planted scenarios less

intensively management starting habitats, Neutral grassland and Bracken (**Fig. 3.4** and *Appendix B.3.2,* **Fig. B.7***, B*) show the most positive response in later years. This applies especially to AWI scores under climate change. As above (*3.4.11*) habitats with starting conditions closest to the desired end habitat provide cases of “most benefit”. While this is a negative answer to research question ii., the “most benefit” & “most change” response narrative suggests some more positive prospects for afforestation aims.

Results for individual species highlight the likely importance of differences in legacy fertility in constraining community assembly (Valtinat, Bruun and Brunet, 2008; Mayer *et al.*, 2020). The main example being improved grassland starting broad habitats (**Fig. 3.6**, IG); and reflecting the habitats residual fertility consistently across years *Urtica dioica* is followed by *Galium aparine* in the IG results.

High residual fertility on ex-agricultural land highlights the likely need for planting of young trees and shrubs. Rather than relying on dispersal and establishment as planting will often be needed to overcome strong space pre-emption by perennial grasses and *Rubus spp.* quickly dominating when agricultural management ceases.

3.4.3.1 | Fraxinus excelsior loss and Vegetation

The results emphasise the importance of *F. excelsior* in UK forests and the impact of its loss is of great concern (Mitchell *et al.*, 2016; Skovsgaard *et al.*, 2017; Carroll, 2020). With young *F. excelsior* trees likely to go as soon as they grow due to ash-dieback, *H. fraxineus* (Skovsgaard *et al.*, 2017), the species that are predicted as the most likely replacements (research question i.) into the future are: *Rubus fruticosus*, *Crataegus monogyna*, *Corylus avellana*, *H. helix*, *Urtica dioica*, & *Galium aparine* (**Fig. 3.6**).

Consistent with established research on *H. fraxineus* (Mitchell *et al.*, 2016) **Fig. 3.6 & Fig. 3.7** suggest that within the next 20-30 years *F. excelsior* dominant forest is likely to remain in the same community type or see an increase in acid woodland (W10 communities) by 2050. This is likely to be realised as low canopy woodland or scrub given the species predicted as replacers (*Rubus fruticosus*, *Crataegus monogyna*, *Corylus avellana*, *H. helix*, *Urtica dioica*, & *Galium aparine*) and the occurrence of scrub in the vegetation type results (**Fig. 3.7**). Mitchell *et al.* (2016) also determined that W10 and W8 sub-communities were the closest ecological analogue to British *F. excelsior*-dominated forest (*see, Appendix B.3.1,* Table B.**2**). We add to Mitchell *et al.* (2016) by modelling the potential composition of newly planted secondary forest in a range of starting points under a scenario of *F. excelsior* loss and climate change (research question iii.).

3.4.3.1.1 Acer pseudoplatanus replacement of Fraxinius excelsior

While *Acer pseudoplatanus* is often an expected beneficiary of *H. fraxineus* (Mitchell *et al.*, 2016; Skovsgaard *et al.*, 2017) it is infrequent in the top 6 species predictions (**Fig. 3.7**). Exceptions to this and the scrub or low canopy woodland predicted above are (within or near) broadleaved woodland habitat where *Acer pseudoplatanus* features more prominently in the top three positions (**Fig. 3.7**). Alternatively, if planted by land-managers it is likely to establish well in grasslands as it can be seen in the top 10 species in the improved and neutral grasslands results (*Appendix B.3.1,* Table B.**2**). Thus, while *A. pseudoplatanus* is not consistently the top ranked replacement species here it is still the likely high canopy replacement amongst the woody flora for *F. excelsior* (research question i.) as all the other species in the top 20 (*Appendix B.3.1,* Table B.**2**) are herbaceous, graminoid or scrubby. However, *Acer pseudoplatanus* casts a heavier shade than *F. excelsior* thus understory ground flora diversity may reduce from current levels observed in woodlands (Mitchell *et al.*, 2016). This is likely to take a decadal time-frame to be observed in woodland communities given successional timescales.

The removal of *F. excelsior* from the species pool is a simplification of reality as the trees would be more likely to decline over time with *H. fraxineus* infection (Pautasso *et al.*, 2013; Mitchell *et al.*, 2016; Skovsgaard *et al.*, 2017). However, we have not applied an incremented reduction in *F. excelsior*. This is due to no data being found on *H. fraxineus* effects on *F. excelsior* abundance with sufficient robustness to estimate change, despite our searching. This is an area that may merit further research to measure dieback impacts at largescale and long-term. Therefore, removal of *F. excelsior* from the plantation scenarios seems to be an at least adequate representation of possible future realities.

Also, Mitchell *et al.* (2016) suggests management response to ash-dieback will be a determining factor in vegetation community realisation as this is effected by the disturbance regime (felling, grazing etc.). Our modelling of dark diversity suggests that planting a range of tree species suited to *F. excelsior* sites will allow for rapid re-establishment of high canopy forests rather than scrub. This, as ever, suggests that higher biodiversity (more high canopy tree species) gives ecosystems more resilience to change.

3.4.4 | Management and Policy

To pursue forest establishment for biodiversity loss mitigation and net zero 2050 goals with climate change and tree disease being influential factors we suggest the following points for management and policy decisions. The literature 30-50 year time range for successional forest establishment that abandonment / no intervention rewilding takes, in comparison with the 20-40 years taken for some variables modelled here to reach broadleaved woodland baseline values, does suggest that in the right context for certain outcomes planting can be a more rapid method of afforestation. To give UK forest ecosystems the best opportunities to establish we make five recommendations for management and policy:

1. Species selection in its simplest form can be done by local observation (10 km, as for the dark diversity method here) of desirable endpoint forest habitats via tree species matching, but would likely be best done by consideration of site environmental conditions or species selection tools e.g. timber species suggested via the Forestry Commission's ESC tool, URL: http://www.forestdss.org.uk/geoforestdss/ (Pyatt, Ray and Fletcher, 2001).
2. Planting method must be of minimum soil disturbance to reduce and possible carbon loss e.g. by spade and hand as suggested in Berdeni *et al.* (2021), this could also reduce negative carbon priming effects (De Graff *et al.*, 2006) especially if this practice happens at scale.
3. Planting adjacent to or in close proximity to established woodland (especially ancient or long term) as older sites are far more likely to have desirable species (as seen in the Broadleaved woodland and Bracken habitat results) that will colonise as plantations establish to forests (Brunet, De Frenne, Holmström, & Mayr, 2012; Di Sacco & Hardwick *et al.*, 2020; Thomaes *et al.*, 2012).
4. Consideration of "most creation" versus "most change" (*see the results discussed in, 3.4.11*) for example planting up a neutral grassland site adjacent to an ancient woodland may provide the "most creation" but greater biodiversity and soil condition recovery ("most change") may come from planting an adjacent arable field.
5. Lastly policy and legislative support (including forest planning support) especially as it is unreasonable to expect land-managers to hold the necessary ecological knowledge to make decisions that are, economically viable for them as well as mitigating biodiversity loss and climate change. While policy documentation to some extend does acknowledge this (Davies, 2016; Defra, 2018), legislation or supportive schemes directly applied to ecosystem management (rather than land management) is rare. However, the new UK Environmental Land Stewardship scheme (ELMs) presents an opportunity to change this (Defra, 2020a).

3.5 | Conclusions and implications

The plant species and vegetation modelling suggests that woodland with *F. excelsior* absent is most likely to establish as scrub or low canopy woodland within the next 30 years. Alternatively, where it is present in the local area within established woodlands, *A.*

pseudoplatanus will become the main replacement. While *F. excelsior* dominated vegetation is likely to shift substantially, new species compositions do not appear likely to emerge, even under predicted climate up to 2050. Likely new replacement dominants (other than *A. pseudoplatanus*) being *Crataegus monogyna*, *Corylus avellana*, *Rubus fruticosus* and in some circumstances *Pteridium aquilinum* and *Dryopteris* Spp.

Plantation scenarios do not show consistent convergence with the baseline across all the species and soil variables. Thus, we cannot say definitively that plantation can establish to equivalent baseline broadleaved woodland conditions even after 30 years. However, as the baseline woodlands are likely to be hundreds-of-years-old (The Woodland Trust, 2020) complete congruence would be unlikely, particularly for Ancient Woodland Indicators. Our results do show some convergence with broadleaved woodland within 20 years for soils and some habitats (Bracken, Improved & Neutral grassland's) show overlapping herbaceous species group diversity scores in their upper ranges from the late 2020s or 2030s onwards.

As results suggest plantations could show establishment within successional time frames for certain contexts, management to achieve this has to be applied correctly at a "by site level" from the right starting conditions (*see, 3.4.4*). This is especially pertinent when modelling dark diversity (species that could potentially colonise), as this is a far more diverse species pool then the observed baseline plots pool. Therefore, a key component of afforestation not well tackled here is a species or seed source for colonisation, natural or otherwise. If this seed source is lacking in areas immediately adjacent to a site intended for afforestation (Brunet *et al.*, 2012; Broughton *et al.*, 2021) then planting or introduction is vital otherwise afforestation will not occur even at times scales over five decades as seen in McGovernor *et al.* (2013) and Marrs *et al.* (2018).

Determining sites to achieve forest establishment within less than successional timeframes would be highly beneficial for 2050 goals and is an important avenue for further research; as availability of land for planting as well as suitability of land is important for afforestation. Lastly given the fact that the UK already has extremely fragmented and degraded habitats (Watson *et al.*, 2011; Hayhow *et al.*, 2019; Forest Research, 2020) it seems unwise to abandon them to already degraded successional processes under the assumption they will sort themselves out.

3 | References

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Chapter four, analysis chapter three

4 | A hard rain's gonna fall: How does deliberate and accidental Nitrogen addition effect temperate grasslands?

The work this chapter is from has also contributed to a Alternet High Impact Award funded project (AHIA, see: "AHIA 2020-21: Demonstrating dependencies between humanity and nature for a sustainable future: A nitrogen case-study" within https://alterneteurope.eu/news/#blogpost) that aims to submit to the journal of People and Nature.

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Contribution statement:
BW and SS conceived the initial ideas, BW constructed most of the modelling workflow with the calibration neural networks created by SS. RM provided soil change data. ST provided the N deposition data. FS assisted and provided guidance on the Bayesian model construction. BW created the original manuscript with subsequent editing and comment from SS, DJ and ST.

4 | Abstract

Nitrogen (N) represents one of the major limiting nutrients to biological growth and its increased availability as a result of the Haber-Bosch process has supported the progressive global increase in food security. However, the prolific use of N fertilisers and the subsequent exposure of natural and semi-natural ecosystems to unused N ('nitrogen surplus') has led to higher biomass production but has also created conditions that favour fewer species, eroding biodiversity. In addition to fertiliser use, gaseous N emissions from agriculture and fossil fuel burning may also subsequently lead to atmospheric deposition and accidental increases of N on land. Fertiliser application as well as N deposition, can be thought of as a 'hard rain' impacting vegetation chemically; positively in stimulating higher crop yields or negatively via lowering diversity. As N change in grasslands is mechanistically tied to soil and plant community composition and state, this work explores links from fertiliser use and N pollution to the state or composition of vegetation and soils. The overall aim is to determine if N change will reflect a shift from high to low N abundance or a reverse of this, explored via changes in plant species groups related to ecosystem service and function. Also, an overall research aim is to determine over what timescale changes in vegetation and soil can (or cannot) be measured. To explore this we have established a modelling workflow of: fertiliser-induced soil change using novel generalised linear mixed effect models; and, Bayesian models to estimate vegetation change caused by N deposition. Hence we created scenarios reflecting change in N abundance as inputs to an ecological niche modelling platform that covers c. 1300 British plant taxa. As expected across the scenarios, results differed between habitats that varied in starting fertility level. The modelled trends showed that responses to change in N abundance were context dependent and specific to both the species groups explored and the habitat they were explored within. A novel result in the context of managing expectations from agri-environment schemes (AES) is that some changes in management are expected to take decadal timescales for measurable change to be observed. The variables and species groups explored often showed little change over the decade modelled.

This suggests that these indicators don’t perform well for determining AES management induced change or determining success over the time modelled. Thus, proof of management change as well indicators are advisable for results-based policy to determine AES outcomes.

4.1 | Chapter introduction

4.1.1 | Nitrogen and global change

The planetary boundaries concept demonstrates a range of global change issues (Rockström *et al.*, 2009; Steffen *et al.*, 2015), with the most prevalent two in discussion being climate change (IPCC, 2018) and biodiversity loss (Díaz *et al.*, 2020). However, closely tied to these is the disruption of biogeochemical cycles with the Nitrogen (N) cycle now containing more anthropogenic-sourced reactive nitrogen (N_r) than natural N_r (Galloway *et al.*, 2008; Gruber and Galloway, 2008). Another key factor is the Haber-Bosch process which generates anthropogenic N_r using 1%-2% of worldwide energy use (Kyriakou *et al.*, 2020). This alongside biogeochemical disruption means that good N_r management (Sutton *et al.*, 2019; Raghuram *et al.*, 2021) is crucial for staying within planetary boundaries (Rockström *et al.*, 2009; Steffen *et al.*, 2015) and ensuring sustainable land management practices are developed for the benefit of future generations (Zhang *et al.*, 2015; Häyhä *et al.*, 2018). In addition to deliberate N_r use, N deposition from the increased N abundance from fossil fuel burning and fertiliser use, results in accidental increases in N_r on land from the atmosphere (Tipping *et al.*, 2019; Hall, Lohse and Matson, 2021).

The positive ecosystem response to a greater abundance of N_r should not be ignored, however. As N is one of the major limiting nutrients to biological growth (Tipping *et al.*, 2019) its increased abundance through the Haber-Bosch process has provided an increase in global food supply (Zhang *et al.*, 2015; Metson *et al.*, 2021). The prolific use of N fertilisers has led to higher productivity land which provides more biomass production for food but also creates conditions that favour fewer species, eroding biodiversity (Stevens *et al.*, 2006, 2016; Emmett, 2007; Maskell *et al.*, 2013).

Fertiliser spreading (manure or chemical spray) as well as N deposition, can be thought of as a 'hard rain' impacting vegetation chemically; positively with greater biomass or negatively via lowering diversity (Emmett, 2007). These two pathways for N_r to enter ecosystems, fertiliser (deliberate) and deposition (accidental), form the focus of this work.

4.1.2 | N pathways

If the above impacts of N_r are considered in the context of where they are best studied, e.g. Europe (Hall, Lohse and Matson, 2021; Henniges *et al.*, 2022) this should allow for the greatest information to be gained to guide sustainable management. Given the N and vegetation data available for the UK (Carey, Wallis, Emmett, *et al.*, 2008; Stevens *et al.*, 2016; Tipping *et al.*, 2019; Levy *et al.*, 2020; Henniges *et al.*, 2022) its data resources make it well suited to exploring the interconnected flows of N and how changes in climate or N use will impact ecosystems over time (Fowler *et al.*, 2013; Galloway *et al.*, 2013).

Past research into the N cycle has provided excellent insight into how N moves through systems (Fernández-Martínez, 2021) both globally (Gruber and Galloway, 2008; Zhang *et al.*, 2015); nationally (Stevens *et al.*, 2016) and: locally, or at fine-scale within landscapes (Maskell *et al.*, 2013; Smart *et al.*, 2017). If we consider two groups of N_r molecules entering the landscape of the UK via specific pathways, similarly to the emitted NO_x molecule example in Gruber and Galloway (2008), this illustrates N pathways at a molecular to national scale. The two N_r groups considered here are the fertiliser molecules (N_{rF}) and the deposition molecules (N_{rD}). Their pathways are both demonstrated in Gruber and Galloway (2008). The N_{rF} group becomes N_r from the Haber-Bosch process capturing atmospheric N and is then available as fertiliser which is applied by the land-manager to increase crop yield. The other group, N_{rD} is formed partly from N_r escape from the N_{rF} pathway but also from fossil fuel burning (and some natural processes, Gruber and Galloway (2008)). This ends up deposited onto the soil surface, freshwaters and vegetation. Then both N_{rF} & N_{rD} enter the

soil N pool also becoming captured within vegetation. This illustrates part of the current N cycle providing the basis of the scenarios explored here.

4.1.3 | Land management

Ecosystem homogenisation through modern agricultural practice lowers biodiversity and reduces ecosystem service provision (Smart *et al.*, 2006; Gossner *et al.*, 2016). Also, in the context of ecosystem services there is a trade-off between fertility and wider ecosystem service provision (Maskell *et al.*, 2013). These factors along with wider environmental degradation (climate change and biodiversity loss) are the reason Agri-environment schemes (AES) were established as policy tools for mitigation of the long-term effects of agricultural intensification (Rose, 2011; Welsh Government, 2016; Defra, 2018; Pe'Er *et al.*, 2019; Rural Payments Agency, 2022a). Specific examples of this include: Glastir Welsh AES options 15,19,26,159 which pay farmers to use less or no fertiliser (Rose, 2011; Welsh Government, 2016); the English Countryside Stewardship organic farming option types OR's OT's and OP's (Rural Payments Agency, 2022a); and the Defra 25-year environment plan aims to "limit inputs of nitrogen-rich fertilisers" (Defra, 2018).

A more recent policy recommendation to promote diversity is to scale up AES from the land parcel to the landscape scale for consistency of biodiversity provision (Gossner *et al.*, 2016). An example of this in current UK policy is the facilitation fund (Rural Payments Agency, 2022b). However, within the UK, measures of environmental variables to confirm the effectives of AES practices for environmental benefit are now being developed (Defra, 2018, 2020a, 2020b). Metrics for this have already been developed for nitrogen in the context of critical loads (Rowe *et al.*, 2016) and wider plant monitoring (Stevens *et al.*, 2006; Payne *et al.*, 2013; Smart *et al.*, 2017; National Plant Monitoring Scheme, 2019).

4.1.4 | N impact versus recovery

A perturbation within an ecosystem takes time to recover from and the duration of the recovery is linked to the size of the impact (Ogle *et al.*, 2015). A change in N abundance (or fertility) in an ecosystem is not always considered a perturbation in the classical ecological succession sense (Novotny *et al.*, 2007) but the response can be: rapid, 3-5 years (Maskell *et al.*, 2014b; Defra, 2015); decadal for returns to pre-perturbation levels (Valtinat, Bruun and Brunet, 2008); while changes in fertility induced by farming can also persist for over 2000 years (Dupouey *et al.*, 2002). This is a key consideration for global change mitigation and AES N management as if implementation times are too short (West *et al.*, no date; Horrocks *et al.*, 2014) to allow for ecosystems to change or for changes to be detected then success or failure cannot be determined or the scheme will have been deemed to fail because the time under intervention was too short. For grasslands, areas where fertiliser use covers a wide gradient, 3 to 10 years appears to be the minimum time for change in vegetation (Maskell *et al.*, 2014b) thus 10 years is the time period modelled here.

4.1.5 | Why Grasslands?

Semi-natural habitats, specifically grasslands cover a wide gradient of management from natural through to heavily fertilised and grazed. They have, however, been identified as places where biodiversity and natural resource production can be traded off to allow for a win-win scenario to be pursued (Lavorel *et al.*, 2011; Simons & Weisser, 2017). Indicators have been identified at the local habitat level in grasslands where N enrichment is becoming a problem for biodiversity and ecosystem function (Stevens *et al.*, 2004; Posch, Aherne and Hettelingh, 2011; Phoenix *et al.*, 2012; Rowe *et al.*, 2016).

4.1.6 | Methodological modelling approach

The dataset here proportionally represents three grassland types across Britain (**Fig. 4.1**) using nested 200m^2 quadrats with soil data taken from the edge of the central 2 × 2 m

quadrat. This provides a high-resolution national scale dataset to model N abundance change effects on soils and plant communities, as these are mechanistically tied together (Stevens *et al.*, 2004; Emmett, 2007; Rowe *et al.*, 2016). Modelling N source effects through different scenarios should provide evidence on when AES management changes may be measurable, helping determine if public money is effectively used for public goods.

Measuring change can, however, be challenging especially where baseline and monitoring data is lacking, as data from past AES effects on plants and soils have rarely been gathered by the statutory authorities adjudicating them. However, the UK vascular flora is one of the best studied in the world (Henniges *et al.*, 2022); with UK climate data available to 1 km resolution (Lowe *et al.*, 2018); deposition data available to 5 km resolution (Tipping *et al.*, 2019); and national plant and soils monitoring data available since the 1970s (Carey, Wallis, Chamberlain, *et al.*, 2008). These provide robust highly suitable inputs to model change at the national scale with a fine resolution (Diekmann and Falkengren-Grerup, 2002).
This level of data availability led to Stevens *et al*. (2016) to explore the impact of N deposition on vegetation Ellenberg fertility score (EbN, (Ellenberg, Dull and Weber, 1992; Hill, Preston and Roy, 2004)) from the past into the future. This approach is emulated here to explore the N_{rD} or N deposition scenario (**Table 4.1**). As Stevens *et al.* (2006) found no significant relationship between top soil N and N deposition, thus modelling EbN provides greater insight (Stevens *et al.*, 2016). The deposition scenario is then compared with the N_{rF}, fertiliser scenarios (**Table 4.1**) that were constructed using the results from a literature review of the effects of fertiliser application on soil properties. This allowed models to be trained to predict soil change with differing levels of fertiliser use. The timescale selected for modelling, 2007 to 2017 is to increase the chance that a signal is detected across the plant community with management change. This is consistent with studies of UK grasslands taking 3-10 years to change (Maskell *et al.*, 2014b; Defra, 2015) and the findings from prior research on agri-environment scheme effects on UK grasslands (West *et al.*, no date;

Horrocks *et al.*, 2014). The end-point of the scenarios modelled as described in the N_{rF} & N_{rD} pathways is the soil and vegetation proxy N availability or N abundance represented by: EbN (Rowe *et al.*, 2016; Stevens *et al.*, 2016); Total soil N% (Stevens *et al.*, 2006; Seaton *et al.*, 2020); leaf N content (Lavorel *et al.*, 2008, 2011; Kattge *et al.*, 2020). Also, plant species diversity change itself will be modelled via use of an ecological niche model, MutliMOVE (Smart *et al.*, 2010; Henrys, Smart, *et al.*, 2015); which will predict how species linked to N abundance respond to change in the scenarios (Rowe *et al.*, 2016; Smart *et al.*, 2017).

Table 4.1. The four scenarios detailed here are listed in decreasing management intensity; however, the baseline is used as a start for the time series of the other three scenarios. Scenarios **L** & **L<50** represent levels of Nitrogen use based on the Soil Nitrogen Supply status for Long-term grassland found in the RB209 Nutrient Management Guide (AHDB, 2021). **Neutral management** refers to management being assumed to be the same as baseline, however other alterations may have been made to the scenario as detailed. **Edaphic GLME's** refers to Generalised Linear Mixed Effect models constructed to represent differing levels of nitrogen application to grasslands. **Bayesian EbN** refers to Bayesian models constructed to represent how Ellenberg nutrient scores (**EbN**) change with nitrogen deposition.

Scenario code	*Scenario description*	*Nitrogen application (kg ha^{-1} yr^{-1})*	*Models used*	*Recovery from acidification applied*	*Deposition represented*	*Years modelled*
L	Management representative of livestock grazing with N applications of 50-100 kg ha^{-1} yr^{-1}	50-100	Edaphic GLME's	No	No	2008-2017
L<50	Management representative of livestock grazing with N applications <50 kg ha^{-1} yr^{-1}	>0 to <50	Edaphic GLME's	No	No	2008-2017
Ndep	Background N deposition with neutral management.	0	Bayesian EbN	Yes	Yes	2008-2017
Baseline	Neutral management.	Baseline	None	No	No	2007

4.1.61 | Environmental condition indicators and metrics

Creation of a common set of environmental indicators to establish standard survey methodologies within ecological research has been a long-term pursuit across branches of ecology (Carey, Wallis, Chamberlain, *et al.*, 2008; Smart *et al.*, 2017; National Plant Monitoring Scheme, 2019; Kattge *et al.*, 2020). However, the idea of pursuing this within AES policy to ensure positive outcomes is newly to be implemented within the UK (Defra, 2018, 2020b). For the sake of robustly established indicators new AES development would do well to explore the established indicators from ecological research.

4.1.7 | Residual fertility

Within the data utilised for this work, three broad habitats are explored as they represent a range of management histories and fertility levels: these are improved grassland (IG); neutral grassland (NG); and acid grassland (AG). These are described in Jackson (2000), Carey *et al.* (2008) and *C.1* where the habitats residual fertility from their history and management varies from the lowest in AG, to higher in NG, and IG representing the highest

levels of fertility (e.g. Willett *et al.*, 2004). The variation in these broad habitats starting points and their management regimes means they are likely to have differing responses to changes in their N abundance or N inputs.

4.1.8 | Research aims

As N abundance varies by multiple factors: management input (one); time (two) and habitat characteristics e.g. residual fertility or species diversity (three); disentangling effects and flows linked to these is contextually dependent. We explore point one through the creation of the scenarios; with modelling over time (2007-2017) exploring point two; and the habitat characteristics (three) are explored by coarse consideration of different starting points via the broad habitat types and location-based species pool construction. Inherent habitat processes altering N abundance are not emphasised or specifically explored as part of the modelling and are likely to take considerably longer periods of time to be detectable (Dupouey *et al.*, 2002; Maskell *et al.*, 2014a).

Here we use N abundance to refer to N within or entering ecosystems, examples include: Improved Grassland has high residual N abundance; fertiliser application provides an increase in N abundance; and with varying starting N abundance levels different broad habitats will respond according to the direction of change. For this reason, we consider the below in the context of an overall hypothesis (1.) and one to three above:

1. Responses to N change will reflect a shift from high to low N abundance or a reverse of this.
    i. Nitrogen fixing species diversity will decrease with higher N abundance.
    ii. Nitrophobic species will decrease with higher N abundance.
    iii. Nitrophilous species will increase with higher N abundance from deposition.
    iv. Modelled Nitrogen held within vegetation will increase with higher nitrogen abundance.

These simple relationship hypotheses should then achieve the research aim to estimate over what timescale change can (or cannot) be measured using the metrics modelled here as indicators. This can inform results-based policy for agri-environment schemes (Defra, 2020a, 2020b) seeking to confirm desirable results empirically.

4.2 | Methods

The map (**Fig. 4.1**) shows the locations that the input data to the modelling workflow represents. The workflow diagram (**Fig. 4.2**) is a methodological representation of the modelling approach used in the study. Each stage of the workflow is numbered after the title in parentheses (as for **Fig. 4.2**) and is described below, covering the modelling period 2007-2017. All modelling and statistical analysis was conducted in R statistical software (R Core Team, 2019).

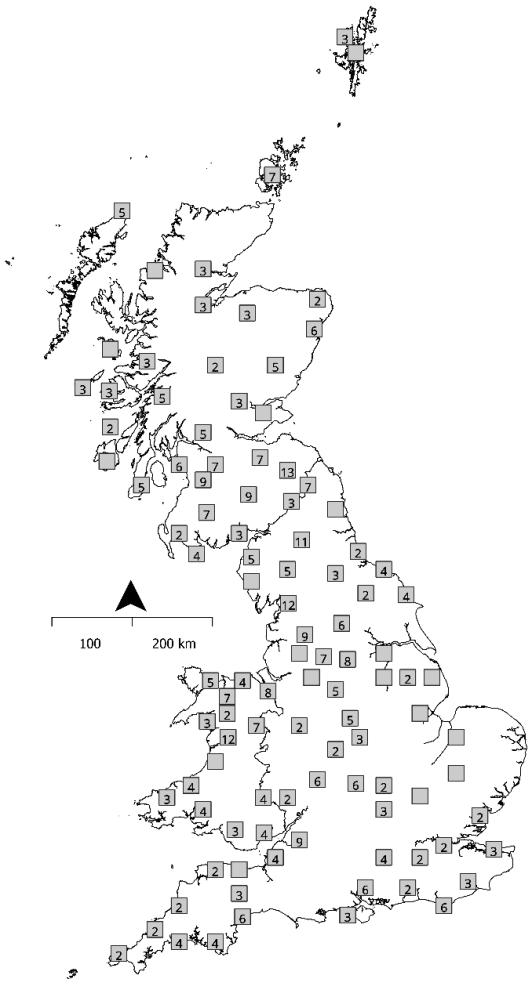

Figure 4.1. Map of the Countryside Survey 1 km squares surveyed across Britain in 2007. Digits within squares represent the number of quadrats within a square when >1 (no. of quadrats = 420). To preserve data confidentiality square locations are represented using the 'Point cluster' function (set to 5 mm) within QGIS Layer Properties.

4.2.1 | Data spatial structure

The spatial structure of the data beginning at 2×2 m quadrats represents the location modelled and where the soil samples were taken from; this sits within a nested quadrat (200 m^2, Maskell *et al.*, 2008).The climate data (Lowe *et al.*, 2018; Met Office Hadley Centre, 2018) is at 1 km resolution (**Fig. 4.2**, 2.0) and the nitrogen deposition data (Tipping *et al.*, 2019; Levy *et al.*, 2020) is at 5 km. The species pool uses the summation of species recorded in each quadrat within the local 1 km cell and those additional species in the wider 10 km pool (**Fig. 4.2**, 3.1) from the Botanical Society of Britain and Ireland Distribution Database (BSBI, 2018). The map (**Fig. 4.1**) shows the Countryside Survey squares (Carey, Wallis, *et al.*, 2008) the quadrats are within.

4.2.2 | Countryside Survey data (1.1)

The Countryside Survey (CS) is a nationally representative survey of Great Britain's plants and soils that has occurred roughly every 10 years since 1978 (Carey, Wallis, *et al.*, 2008; Bunce *et al.*, 2012b; Reynolds *et al.*, 2013; Bunce *et al.*, 2014; Barr, Bunce, Gillespie, Hallam, *et al.*, 2014; Barr, Bunce, Gillespie, Howard, *et al.*, 2014; Barr, Bunce, Clarke, Gillespie, *et al.*, 2014, 2014; Barr, Bunce, Smart and Whittaker, 2014; Brown *et al.*, 2014). The methodology to record the plant and soil survey data can be found in Maskell *et al*. (2008) and Emmet *et al*. (2008), respectively.

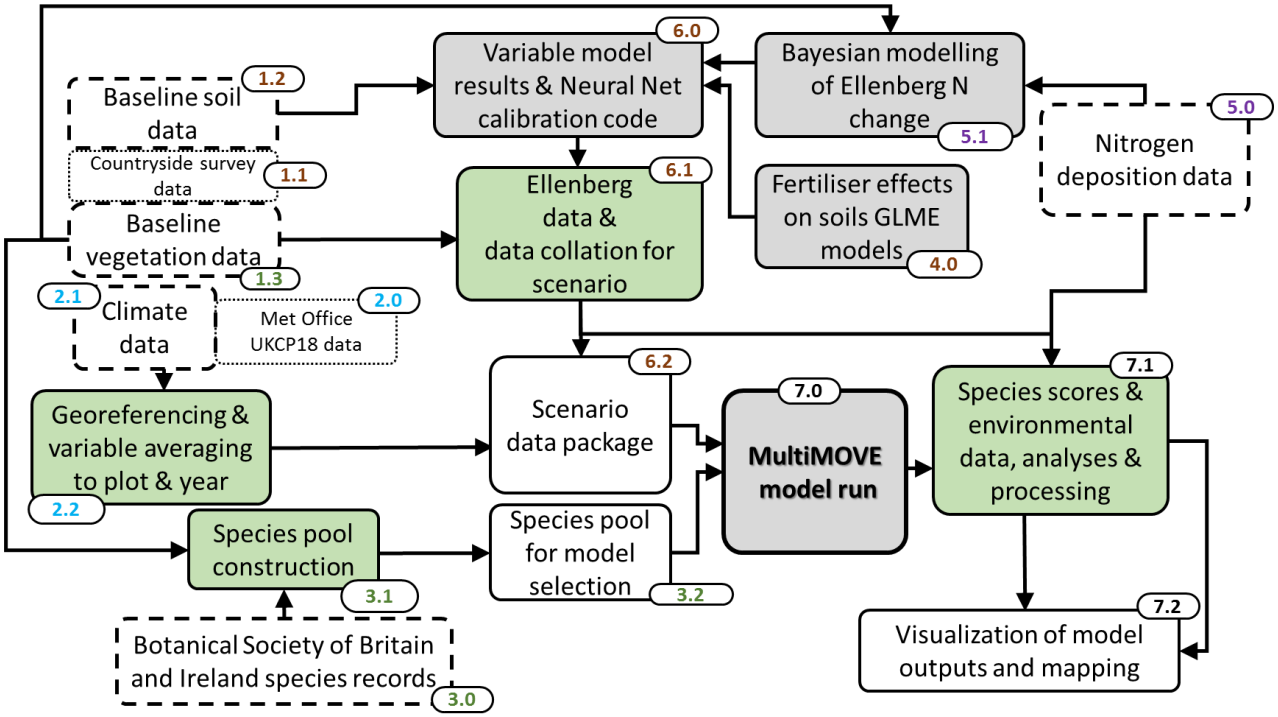

Figure 4.2. Graphical representation of the modelling workflow. Box numbering refers to the relevant text in the methods section: **brown** being soil related; **blue**, climate related; **green**, vegetation related; **purple** being nitrogen deposition related; and **black** numbers refer to ecological niche modelling (7.0) and the results. **Green boxes** represent a coded process; **grey boxes** represent model runs; **white boxes** are datasets; **white boxes with dashed outlines** represent input data.

4.2.3 | Baseline soil conditions (1.2)

Five soil cores (5 cm in diameter, 15 cm deep) were taken from the edge of the 2×2 m quadrat. (Emmett *et al.*, 2008). Here four soil variables derived from each sample were used as model inputs: pH, total soil carbon (%), total soil nitrogen (%) and moisture content (%). These are key soil attributes when differentiating broad habitat types within the UK (Seaton *et al.*, 2020) and thus form fundamental niche dimensions of the plants species we model, *see,* **Fig. 4.2**, 7.0; (Diekmann, Michaelis and Pannek, 2015; Henrys, Smart, *et al.*, 2015). *See*, *C.1 ,* for broad habitat type descriptions.

4.2.4 | Baseline vegetation (1.3)

Within the CS survey data, plant species and vegetation data was recorded within nested quadrats (Maskell *et al.*, 2008). This data includes: species presence and percentage cover;

species average vegetative (non-flowering) canopy height (for **Fig. 4.2**, 6.1) obtained from published sources (Stace, 1997; Hill, Preston and Roy, 2004) as for 2.2.5.

4.2.5 | Met Office Data (2.0)

The climate data we utilised was from the UKCP18 observation datasets (Lowe *et al.*, 2018; Met Office *et al.*, 2019). This was derived from UK land surface observations (HadUK-Grid) interpolated from meteorological station data onto a uniform 1 km grid (Lowe *et al.*, 2018; Met Office *et al.*, 2019).

4.2.6 | Climate data (2.1)

The wider dataset was subsetted by only selecting data for the relevant years and georeferencing CS plot locations. This was averaged from 1981 to each year in the explored years (2007-2017) to give a long-term average that tracks with each modelled year.

4.2.7 | Georeferencing and climate variable averaging (2.2)

Three mean variables (minimum January & maximum July temperature, and total annual precipitation) are the climatic inputs to the ecological niche models (ENM, **Fig. 4.2**, 7.0). Long term annual average values of these three variables were originally used to train the MultiMOVE models and are used as inputs in predictive mode (Smart *et al.*, 2010; Henrys, Smart, *et al.*, 2015).

4.2.6 | BSBI species records and species pool construction (3.0 & 3.1)

To build a species pool from which to filter for dark diversity (Pärtel, Szava-Kovats and Zobel, 2011), a species list was constructed for each 10 x 10 km grid cell (hectads) in which each CS 1 km square was located. This list was based on species recorded by the Botanical

Society of Britain and Ireland distribution database (BSBIdb) covering records till to 2018 (BSBI, 2018). This is the same method as applied in *Chapter 2* (*see, 2.2*).

4.2.7 | Species pool for modelling (3.2)

We focussed our modelling on groups of plant species likely to be especially sensitive to changes in nitrogen availability given their ecology. These groups are as follows (and *see*, C.2):

- Nitrogen fixers (Smart *et al.*, 2017); 21 species.
- Nitrophiles (Rowe *et al.*, 2016; Smart *et al.*, 2017); 68 species.
- Nitrophobes (Rowe *et al.*, 2016; Smart *et al.*, 2017); 273 species.
- Species with leaf N content data from the TRY plant functional trait database (Kattge *et al.*, 2020); 148 species.

4.2.8 | Modelling change in response to nitrogen availability (4.0-6.1)

The ENM (**Fig. 4.2**, 7.0) requires inputs in the form of mean Ellenberg scores. These are scores representing the position of a species along ecological gradients of wetness (Ellenberg F), fertility (Ellenberg N) and reactivity (Ellenberg R) created by Ellenberg *et al.* (1992) and contextualised to the modelling used here by Smart *et al.* (2010).

The intention to model soil and vegetation change with differing N inputs was tackled using two different but complimentary approaches. First, we created generalised linear mixed effect (GLME) models based on analysis of evidence from the literature indicating how direct fertiliser use (N_{rF}) changes soil conditions. Secondly, we revisited the approach used in Stevens *et al.* (2016) and built new Bayesian models conveying the effect of atmospheric N deposition on mean Ellenberg nutrient (EbN) scores (Bayesian modelling). These two approaches reflect the type and form of data and underlying processes of the causes of the change. As soil variables are known to change linearly (Poulton *et al.*, 2003; Thomaes *et al.*, 2012) under fertiliser use they favour the GLME approach. N deposition effects on EbN are

prone to a high amount of noise being dependent on multiple factors, thus favouring a Bayesian approach. Bayesian models were conducted in Stan (Stan Development Team, 2019) in the R environment (R Core Team, 2019) to allow for greater model construct complexity.

For the Ndep scenario (**Table 4.1**) we also included an annual incremental increase in soil pH consistent with long-term recovery from deposition-based acidification. We used trends in Emmett *et al.* (2010) for each broad habitat type, *as for 2.2.4*.

4.2.9 | Soil Generalised Linear Mixed Effect Models (4.0)

In order to build the soil change, fertiliser models a literature review was conducted. This was to find empirical soils data from time-series or chronosequences that measured change in soil conditions where chemical fertiliser had been used (often with liming). Care was taken to ensure the soil variables were measured in the same way as the CS data (Emmett *et al.*, 2008). As a result, we located 15 published data sets. Full datasets were requested from authors where necessary (*see, C.3*).

Once the data was gathered it was categorised into four levels of N use based on the soil nitrogen supply status levels for long-term grass found in the RB209 Nutrient Management Guide (AHDB, 2021). However, as the data contained mostly lower levels of N application (100 <kg ha^{-1} yr^{-1}) the low level was split into above and below 50 kg ha^{-1} yr^{-1}. This led to the creation of four levels:

1. Zero, 0 kg ha^{-1} yr^{-1} applications, level “0”.
2. Less than 50 kg ha^{-1} yr^{-1}, level “L<50”.
3. Low, 50 -100 kg ha^{-1} yr^{-1}, level “L”.
4. Moderate, 100-250 kg ha^{-1} yr^{-1}, level “M”.

The levels were assigned by either taking the kg ha^{-1} yr^{-1} directly or calculating it from the quoted appropriated N g kg^{-1} or equivalent N content if manure was applied with fertiliser.

However, as the control sites used for level 0, likely had fertiliser used on them during historic management it's not a good representation of 0 N management. This in combination with spill over of fertiliser applications from neighbouring sites where plots sizes were small, lead to poor results and rejection for use. The M level was also rejected for use as it also produced poor results most likely as it contained the fewest data points. This left levels, 2 and 3, "L<50" & "L" for modelling, analysis and comparison with the deposition scenario.

As the datasets did not consistently measure all four soil variable inputs to the workflow variables were modelled independently by the creation of individual generalised linear mixed effect (GLME) models using the R package lme4 (Bates *et al.*, 2014). Given the similarity of the study sites and management types within the literature review data, we interpret the change in soil variables as reasonably correlated, although, in reality they interact in varied ways. The GLME model's components were, starting value of the variable modelled, time (years) and N application level. These were the covariates used in each model predicting change over time in each soil variable. Also, all models used a random effect for each study to avoid bias. Due to variation in the datasets of the variables, each was modelled slightly differently. A summary of the constructs of the soil variable models that were selected by seeking low AIC values, significance of model components, producing realistic results and higher R^2 values are below:

- Change in soil pH per year ~ (time * N application level * starting value of pH) + (with random effect for study sites)
- Change in soil Carbon per year ~ (starting value of Carbon * time) + N application level + (with random effect for study sites)
- Change in soil N per year ~ (starting value of N * N application level) + time + (with random effect for study sites)

As soils moisture is not targeted by grassland management this was not modelled here. *See, C.3* for construction data details.

4.2.10 | Nitrogen deposition (5.0)

The N deposition data used within this workflow is the Concentration Based Estimated Deposition (CBED) dataset for years 1986-2018 (Levy *et al.*, 2020), a measurement-derived statistical dataset, with years 1970-1986 inferred from the Fine Resolution Atmospheric Multi-Pollutant Exchange (FRAME) dataset as used in Tipping *et al.* (2019). Both of these are at a 5 km resolution and used to cover 1970 to 2017. This dataset combination uses a similar approach to work exploring direct N deposition impacts on ecosystems across the UK - scaling the CBED distributions by the magnitude of change as modelled by the FRAME model to CBED data to make predictions into the future (Dragosits *et al.*, 2020). We use it here to make predictions about Ellenberg N changes using a method adapted from Stevens *et al.* (2016) and detailed below. The Ellenberg N data was source from grassland habitat plots from the CS years, 1978, 1990, 1998 & 2007 (Barr *et al.*, 2014; Barr, Bunce, Gillespie, Hallam, *et al.*, 2014; Bunce *et al.*, 2014) .

4.2.11 | Bayesian Modelling of Ellenberg Nutrient Score (5.1)

To georeference CS squares with the 5 km square deposition, estimates from both datasets were joined in QGIS (QGIS.org, 2022) then the modelling work was conducted in R (R Core Team, 2019). The same approach with lme4 as Stevens *et al.* (2016) was used to inform model structures but Stan (Stan Development Team, 2019) was used rather than OpenBUGS as it allowed more complex better performing models to be created.

4.2.11.0 | *Data transformations*

Prior to beginning the modelling, the data needed some transformation to align with the methods in Stevens *et al.* (2016) and to prevent the propagation of temporal and spatial autocorrelation relics. Firstly, where the georeferenced CS 1 km squares intersected with

more than one deposition cell a mean of all the cell values at the square intersected was taken.

Next, this square grid average value for each location was then cumulatively summed for each year in the deposition data (**Fig. 4.2**, 5.0) to provide cumulative N deposition values for each of the squares per year within the modelling (CumN).

$$\mathrm{CumN} = \sum_{1970}^{n} (\text{square grid average nitrogen deposition value})$$

Equation 1. Cumulative nitrogen deposition calculation.

Where CumN is generated on a per square basis and “n” is one of the years within the modelling period (1978, 1990, 1998, and 2007-2017).

The prevention of temporal and spatial autocorrelation relics was achieved by transforming CS square CumN values and CS plot EbN values. The transformations below show how the statistical relics were removed from the explanatory (CumN) and response (EbN) variables in the deposition modelling

4.2.11.1 | Explanatory variable statistical relic removal

Square CumN values across the CS years were averaged to get a square mean (SqCumN), this was to remove collinearity between years and locations.

$$\mathrm{SqCumN} = \frac{(CumN_{1978}) + (CumN_{1990}) + (CumN_{1998}) + (CumN_{2007})}{No.\,of\ CS\ years}$$

Equation 2. Explanatory variable transformation.

4.2.11.2 | Response variable statistical relic removal

As the desired outcome of the modelling was a change in EbN per plot for the year modelled, independence from autocorrelation was required. This was achieved by creating a

response variable based on deviation from the cross-year EbN average so that change over time is modelled but spatial differences in the change over time between sites are still retained. The calculations below were conducted per vegetation plot which is a finer resolution than the CS square level, referring to the individual quadrats (Maskell *et al.*, 2008). The plot EbN values were centred and standardised across each plots time series. This involved working out each plot's value per year change from the EbN mean and calculating the standard deviation of the mean.

$$EbN_{nC.S.} = \frac{EbN_n - \frac{\sum_{i=1}^{n}(EbN)}{\mathrm{n}}}{\sqrt{\frac{1}{n}\sum_{i=1}^{n}(EbN_n - \mathrm{MeanEbN})^2}}$$

Equation 3. Response variable transformation.

Where “i” is the first year recorded in the data and “n” is the last (n=4 as CS covers 4 dates). The final value ($EbN_{nC.S}$) is the centred standardised deviation of a plot's EbN value per year from the plot EbN mean over the CS years, giving the required response variable.

4.2.11.3 | Management intensity data division

The dataset was also split into two, reflecting variation in management intensity. Firstly, a high intensity management dataset only including improved grassland (IG) habitat and secondly a lower intensity neutral and acid grasslands (NG & AG) dataset.

4.2.11.4 | Bayesian models construction

The same workflow was applied to both data sets, exploring relationships using lme4 before using the parameters within these as estimates for initial construction parameters for Stan (Stan Development Team, 2019) and brms (Bürkner, 2017) model building.

To aid with convergence increasing the ease of computation SqCumN was transformed as follows:

$$\mathrm{SqCumN}_T = \frac{\mathrm{SqCumN} - 1000}{1000}$$

Equation 4. Convergence aid transformation

4.2.11.5 | *Bayesian models performance*

Beyond ensuring convergence via 10,000 iterations ($^1/_3$ being burn-in), the highest Bayesian R^2 (Gelman *et al.*, 2019) and LOO cross validation (Vehtari, Gelman and Gabry, 2017) values were used to select the best performing models as well as selecting for simpler models. The two final model constructs were:

- For Neutral and Acid grassland:
  $\mathrm{EbN_{C.S.}} \sim \mathrm{SqCumN_T} * \text{year modelled} + (\text{random effect for CS square})$
- For Improved grassland:
  $\mathrm{EbN_{C.S.}} \sim \mathrm{SqCumN_T} * \text{year modelled} + (\text{random effect for CS square})$

4.2.11.6 | *Bayesian model predictions*

To make EbN predictions for the post CS years (2008-2017) their SqCumN data was inputted into the “posterior_predict()” function in brms (Bürkner, 2017) again splitting into IG and NG&AG. Then the posterior predictive estimates were back transformed (undoing Equation 3) then averaged across the iterations giving a dataset of predictions of EbN values per plot per year.

4.2.12 | Variable model results (6.0.1)

The outputs of the **Fig. 4.2**, 4.0, GLME soil models were used as inputs to neural network models (**Fig. 4.2**, 6.0) used to predict Ellenberg community values. Also the Bayesian model predictions were used to provide the Ellenberg N scores for the deposition scenario. Both of these sets of results then provided the Ellenberg scores for their scenarios for inputs to the ENM, **Fig. 4.2**, 7.0 (as for *Chapter 2,* West *et al.* (no date)).

4.2.13 | Neural network calibration code (6.0.2)

To improve on the linear models that use soils variables to predict Ellenberg scores constructed in Smart *et al.* (2010) neural networks were constructed that performed better. This is the same method as in *Chapter 2*, West *et al.* (no date) the details of which can be found in A.3.

4.2.14 | Ellenberg data and data collation (6.1)

The 2007 baseline data was put through the workflow unaltered. However, the L<50 and L scenarios (**Table 4.1**) where constructed by using the baseline data as inputs to the GLME models (**Fig. 4.2**, 4.0) to predict soil variable change. The predicted soil changed data was then inputted into the neural networks (**Fig. 4.2**, 6.0) to gain Ellenberg scores. The Ndep scenario (**Table 4.1**) is constructed differently as pH is the only altered soil variable, having the acid deposition recovery increment applied to it. Then with altered soil pH the rest of the soil baseline data is inputted into the neural networks to gain Ellenberg wetness and reactivity scores. The Ndep Ellenberg nutrient scores are gained for the Bayesian models posterior predictions (**Fig. 4.2**, 5.1).

An additional biotic input to the workflow is cover-weighted canopy height calculated as for the baseline data in **Fig. 4.2**, 1.3*; as for 2*, West *et al.* (no date). This expresses both the successional stage of the plot modelled and the light at ground level.

4.2.15 | Scenarios and model inputs (6.2)

The final model inputs per plot for the plant species ENM were Ellenberg R; Ellenberg N; Ellenberg F; cover-weighted canopy height; minimum January & maximum July temperature, and total annual precipitation. The values of these variables reflect the climate at each location and the way abiotic conditions are expected to vary as fertiliser inputs and N deposition change over the 10-year period modelled as detailed in **Table 4.1**.

4.2.16 | Plant species ENM (7.0, the MultiMOVE R package)

We used the MutliMOVE R package to model the response of each plant species in terms of its movement in ecological niche space. MultiMOVE has been used and validated multiple times (West *et al.*, no date; De Vries *et al.*, 2010; Henrys, Smart, *et al.*, 2015; Rowe *et al.*, 2015; Emmett *et al.*, 2017; Smart *et al.*, 2019). The MultiMOVE ENM consists of a small ensemble of five modelling methods to provide a habitat suitability score for each plant species. The output is a habitat suitability score (weighted model average) that ranges between 0 and 1, where 1 = maximum suitability of conditions. Details of the MultiMOVE R package can be found in Henrys *et al.* (2015) and Smart *et al.* (2019).

4.2.17 | Species scores and soil variables (7.1.0)

Both the outputs from 7.0 and 6.1 (**Fig. 4.2**) are combined to form the modelling results. All results are considered in the context of their trajectory from the baseline in 2007 in response to N abundance change from fertiliser or the atmosphere. The data presented here (**Fig. 4.2**,*7.2* and *Results*) includes: habitat suitability scores from the ENM (**Fig. 4.2**, 7.0); Soil variable results from the GLME models (**Fig. 4.2**, 4.0); EbN values from the Bayesian modelling (**Fig. 4.2**, 5.1); the N deposition data (**Fig. 4.2**, 5.0).

To represent the species group's (**Fig. 4.2**, 3.2) variation between scenarios, all the species per group's habitat suitability scores were summed to give an estimated species diversity score per modelled plot location (Calabrese *et al.*, 2014). An exception to this is species leaf N content data used to calculate a virtual abundance-weighted community mean (vCWM) as for Lavorel *et al*. (2008) used as a proxy for nitrogen stock in the vegetation. The use of vCWM refers to the use of modelled habitat suitability scores being used as a virtual proxy for abundance.

To test model performance two approaches were applied. The first was logistical regression to determine if the species present at the 2007 baseline had significantly higher species, suitability scores than those that were absent. The second was to test, via unpaired t-test, for significant differences between 2007 baseline variables and modelled variables (**Table 4.2**). See *Appendix C.4.*, for these results.

4.2.18 | Visualising the outputs (7.2)

Data plots have been created predominantly as boxplots or mapping. The former where the overall trends in the data vary by habitat, management or year allowing us to show concisely both baseline and modelled results for clarity and ease of comparison. The latter where spatial variation is a key factor in trends of change. The exceptions to this are figures created to synthesise data that are more complex, their subtext provides descriptions of their development.

4.3 | Results

4.3.1 | Scenarios

The three scenarios have been run independently through the workflow, however, a key difference between the (two) fertiliser scenarios and the deposition (Ndep) scenario is the creation of the Ellenberg (Eb) score inputs. The fertiliser scenario Eb scores are driven by the soil models feeding neural networks to generate Eb scores. But, the deposition soil results are held as for the baseline with one exception, pH has a recovery from acidification increment applied for each year. This soil data through the neural network drives the wetness (EbF) and reactivity (EbR) Eb scores but the Eb nutrient score (EbN) is driven by the Bayesian deposition modelling. Thus, due to the differences in the inputs workflows the

soil data is not presented as the Eb scores for the scenarios provides a better comparison (**Fig. 4.3**).

The habitat suitability score outputs (weighted model averages, WMA) generated by MultiMOVE from the environmental inputs) are comparable and the data source for the species group results presented (**Fig. 4.3** & **Fig. 4.5**).

4.3.2 | Baseline observations and modelled results

Logistical regression on the species recorded as present in 2007 versus those included in the modelled pool but absent showed that an increase in a habitat suitability score increases the probability of the species being observed as present. Within the plots, overall predictions from the baseline input data suggests habitat suitability score of 0.386 or more gives a gives a fitted presence value of 0.51 (logistical regression WMA model coefficients P-value <0.001; *Appendix C.4,* **Fig. C.1**).

The tabulated p-values (**Table 4.2**) show little deviation of the modelled results from the baseline results. Exceptions to these occur in later years and more regularly in the fertiliser scenarios, however only the Ellenberg R and N scores show any significant differences (**Table 4.2**, EbR & EbN).

Table 4.2. Significant differences of variables for the years modelled from the 2007 observed baseline values based on an unpaired t-test. Significance indicators: **NS** = Not significant; ***** = p-value<0.05; **-** = Not applicable. Variables: **EbN** = Ellenberg nutrient score; **EbR** = Ellenberg reactivity score; **pH** = soil pH; **C%** = total soil carbon content by percentage; **N%** = total soil nitrogen content by percentage. Scenarios: **Ndep** = Background Nitrogen deposition**; L<50** = Management representative of livestock grazing with N applications of less than 50 kg ha^{-1} yr^{-1}; **L** = Management representative of livestock grazing with N applications of 50-100 kg ha^{-1} yr^{-1}. The increasing shading represents from light to dark and increase in N abundance change within the scenarios. Scenarios **L** & **L<50** represent levels of Nitrogen use based on the Soil Nitrogen Supply status for Long-term grass found in the RB209 Nutrient Management Guide (AHDB, 2021).

Scenario	Year Modelled	Broad Habitat Grassland Type	Significant difference from baseline (2007)				
			EbR	EbN	pH	C%	N%
Ndep	2009	Improved	NS	NS	NS	-	-
Ndep	2009	Neutral	NS	NS	NS	-	-
Ndep	2009	Acid	NS	NS	NS	-	-
Ndep	2013	Improved	NS	NS	NS	-	-
Ndep	2013	Neutral	NS	NS	NS	-	-
Ndep	2013	Acid	NS	NS	NS	-	-
Ndep	2017	Improved	NS	NS	NS	-	-
Ndep	2017	Neutral	NS	NS	NS	-	-
Ndep	2017	Acid	*	NS	NS	-	-
L<50	2009	Improved	NS	NS	NS	NS	NS
L<50	2009	Neutral	NS	NS	NS	NS	NS
L<50	2009	Acid	NS	NS	NS	NS	NS
L<50	2013	Improved	NS	NS	NS	NS	NS
L<50	2013	Neutral	NS	NS	NS	NS	NS
L<50	2013	Acid	*	NS	NS	NS	NS
L<50	2017	Improved	NS	NS	NS	NS	NS
L<50	2017	Neutral	NS	*	NS	NS	NS
L<50	2017	Acid	*	NS	NS	NS	NS
L	2009	Improved	NS	NS	NS	NS	NS
L	2009	Neutral	NS	NS	NS	NS	NS
L	2009	Acid	*	NS	NS	NS	NS
L	2013	Improved	NS	NS	NS	NS	NS
L	2013	Neutral	NS	NS	NS	NS	NS
L	2013	Acid	*	NS	NS	NS	NS
L	2017	Improved	NS	NS	NS	NS	NS
L	2017	Neutral	NS	*	NS	NS	NS
L	2017	Acid	*	NS	NS	NS	NS

4.3.3 | Broad habitats

Differences were apparent between habitats. The residual fertility of Improved grassland (IG); Neutral grassland (NG); and Acid grassland (AG), are best expressed in the baseline 2007 values of the EbN results (**Fig. 4.3**) and Nitrophobic species results (**Fig. 4.5**, D-E).

These show IG to have the highest residual fertility (or EbN), NG to be second to this and AG to have the lowest residual fertility; this reflects the historic management of each habitat and is an expected pattern (*see, Appendix C.1* and *Willet et al.* (2004)). Due to this residual fertility, the results in the following section are presented by habitat.

4.3.4 | Soils

The soils data for each scenario are presented in *Appendix C.4,* **Fig. C.2**. However, the differences between the fertiliser scenarios are described briefly here, these being the < 50 kg^{-1} ha^{-1} yr (L<50), and Low level application (L) 50 – 100 kg^{-1} ha^{-1} yr (**Table 4.1**).

Within the IG and the NG soil variable results the habitats show a stable state for pH and carbon under L<50. The same habitats under L show a slight rise in pH and a stable soil C level. For all IG and NG, L<50 and L results N shows a slight rise. The AG (of the lowest residual fertility) results differ though, under L<50, pH and N rise whereas C drops, and under L all 3 variables drop. *See*, *Appendix C.4,* **Fig. C.2,** for the soil variable results for the scenarios.

4.3.5 | Deposition

The atmospheric N deposition while modelled on a per year per site basis (Tipping *et al.*, 2019; Levy *et al.*, 2020) accumulates over time, hence the use of the cumulative N deposition statistic shown in 2007 (**Fig. 4.6**, D) being lower versus the 2017 maps (**Fig. 4.6**, A-C). This accumulation of N is what drives the Ndep scenario and fuels the deposition-based species trajectories shown in **Fig. 4.4-4.6.**

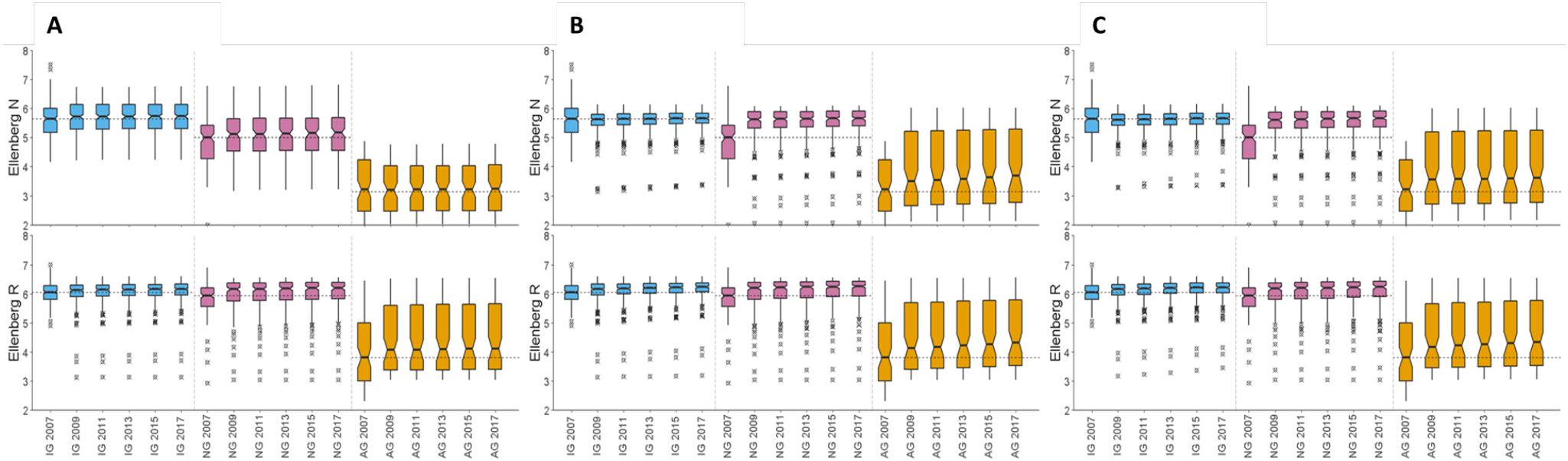

Figure 4.3. Boxplots show Ellenberg Nutrient (N, top row) and Reactivity (R, bottom row) scores under each scenario, broad habitat and year. Columns are nitrogen scenarios: **A** = Nitrogen deposition from Bayesian modelling N deposition effects on Ellenberg N and a recovery from acidification increment applied to pH before generating Ellenberg R from soil variables (field moisture %, pH, C%, N%); **B** = Application of less than (L<50) 50 kg ha^{-1} yr^{-1} of N; **C** = Low (L) level application of N, 50-100 kg ha^{-1} yr^{-1}. Both B&C Ellenberg values are driven by soil variable (pH;C%;N%) generalised linear mixed effect models of different categorised levels of fertiliser applications feeding into neural networks. Broad Habitats (BH): **IG** = Improved grassland (**blue**); **NG** = Neutral grassland (**pink**); **AG** = Acid grassland (**orange**); the dashed line in each part of each plot represents the BH's 2007 median value.

4.3.6 | Ellenberg scores

As the Ellenberg scores are all modelled from the 2007 baseline the plots show the medians of these for each broad habitat as a dashed line from which trajectories can be seen (**Fig. 4.3**). These trajectories are described from the highest residual fertility habitat to the lowest.

The IG results for EbR are consistent across scenarios with a smaller rise under Ndep due to the recovering from acidification increment and a larger rise in the fertiliser scenarios due to lime application in the soils model training data (**Fig. 4.3**). The EbN results for IG however, show a stable trajectory under the fertiliser scenarios and a slight rise under the Ndep scenario.

Broad habitat type NG shows a rise from the observed EbN in 2007 for all three scenarios, the Ndep scenario shows a gradual rise whereas the fertiliser scenarios show a clear step up (**Fig. 4.3**). This reflects the cumulative increase of N deposited (**Fig. 4.6**) and the targeted application of N within the fertiliser scenarios. For EbR in **Fig. 4.3** the move from baseline to the predicted results shows a step up in EbR values, however, within the soil pH results there is more variation in response between the scenarios (*see, Appendix C.4,* **Fig. C.2**).

The AG, EbN and EbR results show increases from the baseline consistent with this being the habitat with the lowest residual fertility moving toward a higher fertility status (**Fig. 4.3**). There is however, a far more marked rise in EbR & EbN in the fertiliser scenarios (**Fig. 4.3**, B&C) results reflecting the change from lower to higher management intensity.

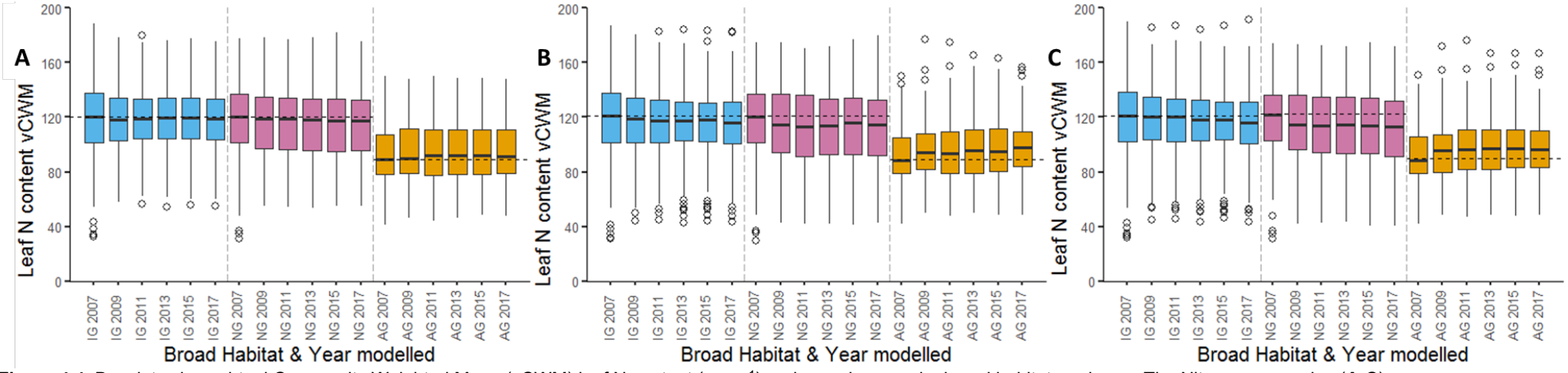

Figure 4.4. Boxplots show virtual Community Weighted Mean (vCWM) leaf N content (mg g^{-1}) under each scenario, board habitat, and year. The Nitrogen scenarios (**A-C**) used Ellenberg values as inputs (alongside climate and vegetation data) for an ecological niche model, this outputted habitat suitability scores that provided the virtual abundance weighting for the vCWM; with leaf N content data from the TRY plant trait database. Nitrogen Scenarios: **A** = Nitrogen deposition (Ndep) from Bayesian modelling N deposition effects on Ellenberg N (EbN) and a recovery from acidification increment applied to pH before generating Ellenberg R (EbR) from soil variables (field moisture %, pH, C%, N%); **B** = Application of less than (L<50) 50 kg ha^{-1} yr^{-1} of N; **C** = Low (L) level application of N, 50-100 kg ha^{-1} yr^{-1}. Both **B&C** Ellenberg values are driven by soil variable (pH;C%;N%) generalised linear mixed effect models of different categorised levels of fertiliser applications feeding into neural networks. Broad Habitats (BH): **IG** = Improved grassland (**blue**); **NG** = Neutral grassland (**pink**); **AG** = Acid grassland (**orange**); the dashed line in each part of each plot represents the BH's 2007 median value.

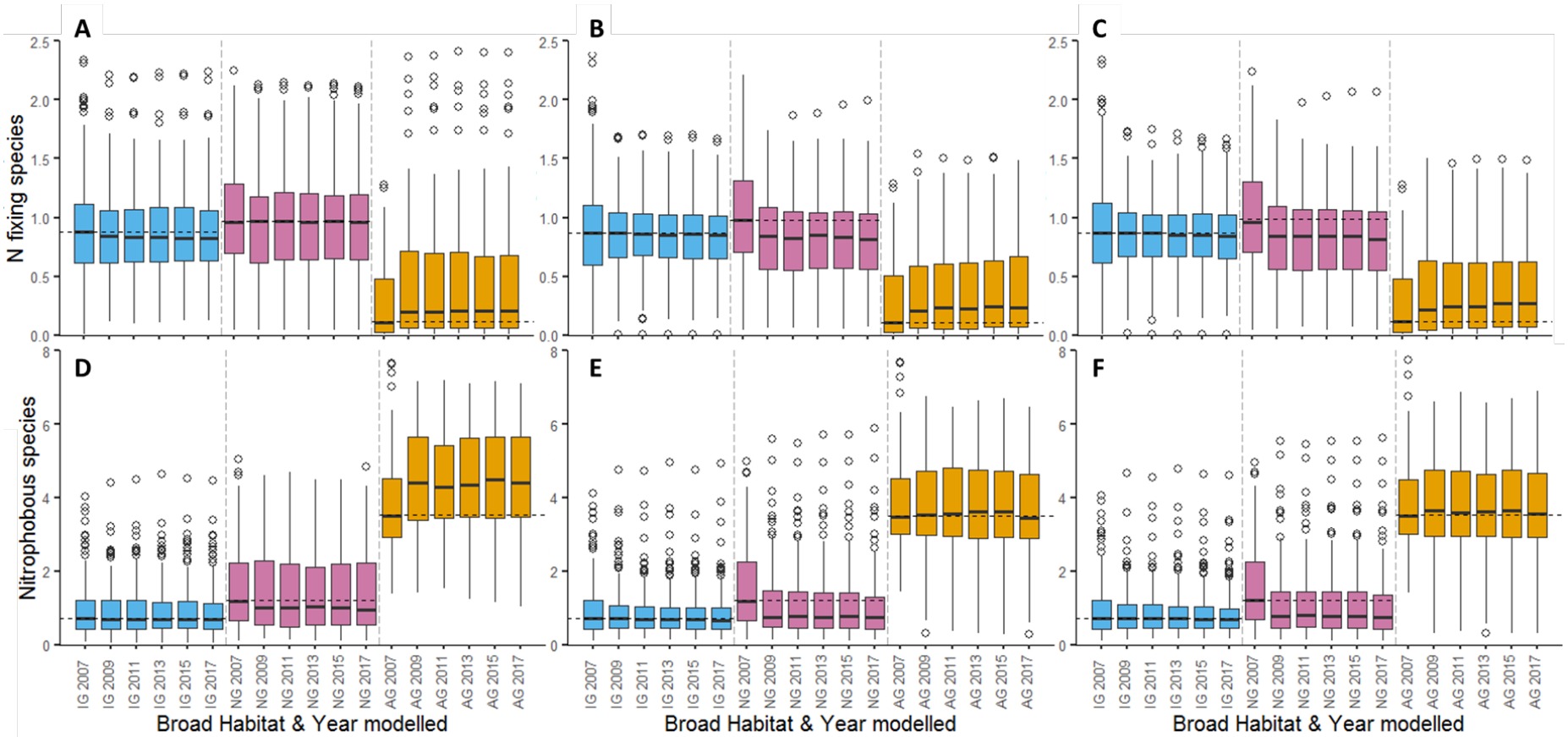

Figure 4.5. Boxplots show diversity scores for the species groups Nitrogen fixers (**A-C**), & Nitrophobes (**D-F**), under each scenario, board habitat, and year. The Nitrogen scenarios used Ellenberg values as inputs (alongside climate and vegetation data) for an ecological niche model which outputted habitat suitability scores that are summed to provide the diversity score for each species group. Nitrogen Scenarios: **A&D** = Nitrogen deposition (Ndep) from Bayesian modelling N deposition effects on Ellenberg N (EbN) and a recovery from acidification increment applied to pH before generating Ellenberg R (EbR) from soil variables (field moisture %, pH, C%, N%); **B&E** = Application of less than (L<50) 50 kg ha^{-1} yr^{-1} of N; **C&F** = Low (L) level application of N, 50-100 kg ha^{-1} yr^{-1}. Plots B,C,E&F Ellenberg values are driven by soil variable (pH;C%;N%) generalised linear mixed effect models of different categorised levels of fertiliser applications feeding into neural networks. Broad Habitats (BH): **IG** = Improved grassland (**blue**); **NG** = Neutral grassland (**pink**); **AG** = Acid grassland (**orange**); the dashed line in each part of each plot represents the BH's 2007 median value.

4.3.7 | Vegetation community

The four species groups show a variety of responses to the scenarios through changes in their group diversity scores (summed, suitability scores / WMA, of each species in the group) as can be seen across the results (**Fig. 4.5**). Also, within the species results is the vCWM leaf N content data (mg g^{-1}) providing an indication (**Fig. 4.4**) of the amount of N that may be held in vegetation.

The vCWM leaf N content results (nitrogen held within vegetation) are a representation of N abundance in the vegetation pool modelled (**Fig. 4.4**). As this represents varying levels of N within vegetation biomass, it also covers a wider range of species growth strategies (Kattge *et al.*, 2020). The IG results shows the least response to the scenarios, but vCWM leaf N content does decline under the fertiliser scenarios (**Fig. 4.4**, B-C). The NG leaf N content vCWM declines under all scenarios but has a more marked step down from baseline under the fertiliser scenarios, particularly under L. The AG results show the opposite trend from the other two habitats showing a rise, with greater change from Ndep to L<50 to L (**Fig. 4.4**, A-C). The Ndep scenario results show the least change for all three broad habitat types vCWM leaf N content (**Fig. 4.4**, A).

The N fixing species diversity results (**Fig. 4.5**, A-C) do not show consistent patterns between the scenarios and habitats. For IG under Ndep (**Fig. 4.5**, A) a slight decline in N fixer diversity is seen and under the fertiliser scenarios (**Fig. 4.5**, B-C), where diversity is fairly stable apart from the final years dropping below the median. With the NG results, diversity is stable under deposition but steps down from the baseline onward in the fertiliser scenarios, these results are representative of the step up in management intensity (**Fig. 4.5**, A-C). For the Ndep scenario AG N fixer diversity steps up from the baseline and for the fertiliser scenarios shows a slight rising trend. This is likely due to conditions changing to favour a greater number of species than in AG broad habitats at baseline (**Fig. 4.5**, A-C).

The nitrophobic species (N-phobe) diversity results are reflective of each habitats residual fertility (**Fig. 4.5**, D-F). Under all three scenarios, IG N-phobe results remain stable around the baseline consistent with the high fertility of the habitat as for the lower N-phobe diversity (**Fig. 4.5**, D-F). Within AG differing trends are seen in the Ndep (rising diversity, **Fig. 4.5**, D) versus the fertiliser scenarios (stable to slight rises in some years, **Fig. 4.5**, E-F). The NG results, however, show the opposite trend to the other two habitats showing declines across the scenarios.

4.3.8 | Deposition and Nitrophiles

Cumulative N shows a clear increase from 2007 to 2017 in **Fig. 4.6** but the Nitrophilous species diversity scores across the broad habitats do not align with this increase. In IG while the number of points decreasing versus increasing is similar in **Fig. 4.6**, A (103 decreasing versus 100 increasing) there are more points with a larger decrease resulting in an overall decline in Nitrophile diversity (*see, Appendix C.4,* **Fig. C.3**). For NG again the number of increasing and decreasing points is similar (56 versus 61) but only a few larger decreases contribute to an overall decline by 2017 of a few decimal points (*see, Appendix C.4,* **Fig. C.3**). The AG results having the lowest residual fertility does, however, show a positive response in Nitrophiles species diversity with considerably more points increasing than decreasing (43 versus 27). The Nitrophilous species diversity across all three grassland broad habitats can be seen (**Fig. 4.6**, D) as varied but with high diversity scores clustered around areas (in blue) where N accumulation is highest, these are most notably the uplands (> 300 m a.m.s.l.) in north Wales and north-west England.

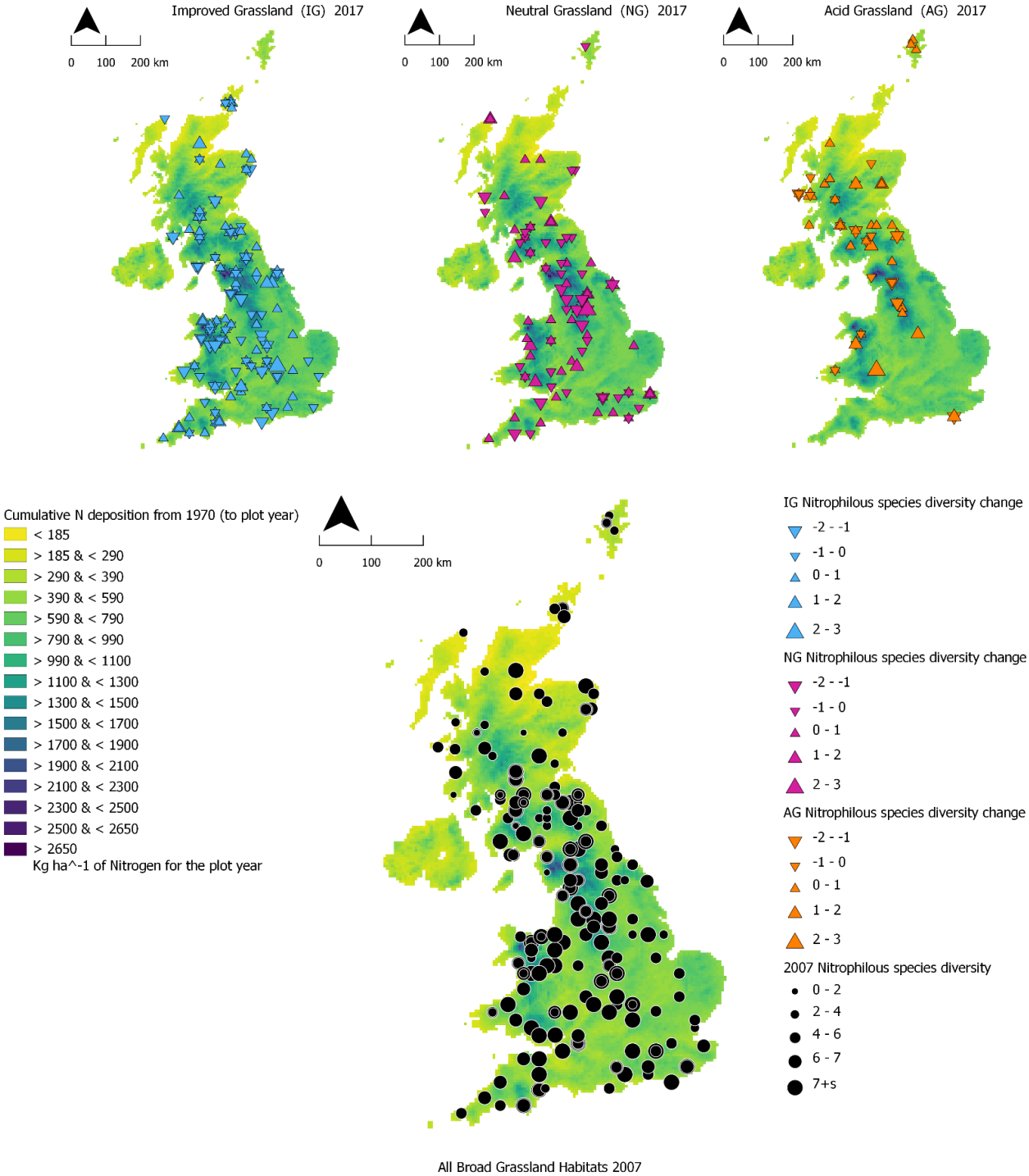

Figure 4.6. Nitrophilous species group diversity and change under nitrogen deposition maps. Cumulative N deposition units are kg ha^{-1} from 1970 to the year mapped, **A-C** (2017) and **D** (2007). The 2007 **species diversity** scores are the summed Nitrophilous habitat suitability scores from an ecological niche model output and the **diversity change** is the 2017 species diversity minus the 2007 species diversity. From 2007 to 2017 triangles pointing up represent positive changes & negative changes are represented by arrows pointing down. Broad Habitats: **IG** = Improved grassland (**blue**); **NG** = Neutral grassland (**purple**); **AG** = Acid grassland (**orange**).

4.4 | Discussion

4.4.1 | Model workflow testing

The logistical regression results (*appendix C.4,* **Fig. C.1**) suggest that at the baseline the workflow produces habitat suitability scores that correlate well with observed species presence building confidence in the modelling approach.

Overall, however, modelling showed surprisingly little response over time with only small deviations from baseline values (e.g. **Table 4.2**).

4.4.2 | Habitat trajectories

As expected across the scenario results with differing habitat residual fertilities responses have varied. Overall results show where residual N abundance is high a positive change in N abundance has led the indicators explored: EbN (**Fig. 4.3**), soil N (*Appendix C.4,* **Fig. C.2**), to remain stable or increase and for Nitrophobous species (**Fig. 4.5**, D-F) to remain stable or decrease. This demonstrates how high or increasing fertility is known to change habitats and have a lasting impact on them as demonstrated in past research (Emmett, 2007; Maskell *et al.*, 2013; Zhang *et al.*, 2015; Tipping *et al.*, 2019).

A novel caveat to this for trying to determine likely measurable change, is that reverse trends to the above are not occurring e.g. there is no obviously lower N abundance relating to lower soil N, lower fertility and higher Nitrophobous species diversity within the results. Within the indicators explored two species groups demonstrate this well: Nitrophobous species increase within lower fertility habitats (acid grassland) under lower N inputs (deposition, **Fig. 4.5**, D); however, Nitrophilious species also increase under lower N inputs (**Fig. 4.6**, C). Despite the responses of the groups being expected to oppose each other.

This inconsistency of expected trends across the results is logical if we consider specifics in the context of the scenarios and habitat types. If we consider higher fertility, improved

grasslands, the EbN results under the highest fertiliser scenario are stable (**Fig. 4.3**, C). This is most likely due to the fact that the L scenario is representative of low fertiliser use in comparison to typically high intensity grassland management (AHDB, 2021). Therefore, little deviation from the baseline median is seen as the input is likely insufficient to trigger a response. Under low fertility, the Nitrophilious species diversity increases in acid grasslands (**Fig. 4.6**, C) representative of them having a low fertility that is increased by deposition. To summarise, the trend for each of these examples respectively are:

A. High N abundance with N input being lower than typical for the habitat results in stability and little change over time in already highly modified and fertile habitats (improved grasslands).
B. Low residual fertility habitats (acid grasslands) with a low N input resulting in fertility increases are reflected by Nitrophilious species diversity increases as expected.

This is reflective of there being a strong dependence on starting conditions and management legacy when exploring vegetation and soil variable change.

4.4.3 | Ellenberg Scores

A possible confounding factor within the results is under improved grassland, where EbN is surprisingly stable under the fertiliser scenarios. While this reflects a possible continuation of typical management it is under low fertiliser application scenarios and applications of over double the values of N kg^{-1} ha^{-1} aren't unknown (AHDB, 2021). This, alongside the rise in EbN under the Ndep scenario, suggests that a change in management or fertiliser use here may take over 10 years to be reflected in a change in fertility in these habitats. Timescale far exceeding this are also not unheard of meaning measurable change maybe a long time coming (Dupouey *et al.*, 2002; Phoenix *et al.*, 2012).

The neutral grassland EbN increases away from baseline reflecting deposition effects congruent with those in Stevens *et al.* (2016), despite N deposition decreasing in some parts of Europe (Stevens *et al.*, 2004). The step-up style increase (**Fig. 4.3**, B&C; and, **Fig. 4.4**,

B&C) is reflective of the management intensity going up pushing neutral grassland closer to the same state as improved grassland, as fertiliser use is known to do (Willett *et al.*, 2004; Emmett, 2007; Gossner *et al.*, 2016). This leads to the same high fertility concerns in neutral grassland as described in improved grassland above; a higher fertility, lower diversity state takes time to move away from.

The consistent pattern in EbR change within neutral grassland across the scenario results does not reflect what might be expected with deposition and fertiliser effects on pH (Phoenix *et al.*, 2012; Xu *et al.*, 2020). This is a result of EbR being reflective of vegetation change under all variables which coarsens the differences observable in the soil pH results (*Appendix C.4,* **Fig. C.2**).

With acid grassland being the habitat with the lowest residual fertility both fertiliser and deposition effects clearly move it toward higher fertility (**Fig. 4.3 & Fig. 4.5**). Within the fertiliser scenarios, this is very much a reflection of the effect of fertilisers on habitats (Diekmann and Falkengren-Grerup, 2002; Emmett, 2007; Phoenix *et al.*, 2012) as the increase in management intensity pushes acid grassland closer to the higher fertility states of neutral and improved. While this has led to higher diversity for N fixers (**Fig. 4.5**, A-C) in acid grassland it also comes with the above concerns surrounding higher fertility and loss of wider diversity (Emmett, 2007; Rowe *et al.*, 2016).

4.4.4 | Soils

The soil variable results (*Appendix C.4,* **Fig. C.2**) are only related to the fertiliser scenarios (L<50 & L) due to the modelling methodology. Fertiliser effects on soils are explored for the sake of monitoring the indicators used here for sustainable land management. The fertiliser application levels here do elicit differing responses. The L<50 scenario, a lower application rate, seems to leave pH stable; and higher application, the L scenario leading to a pH rise in

IG and NG. This is likely due to liming effects (Xu *et al.*, 2020) as this is applied within the soil variable model construction data.

The differences in the L<50 and L; C% and N% are likely due to the capacity of soil to hold onto nutrients (Posch, Aherne and Hettelingh, 2011; Phoenix *et al.*, 2012; Tipping *et al.*, 2017) as the higher drop in soil C under L in acid grassland leads to less N being held in the soil (Novotny *et al.*, 2007; Phoenix *et al.*, 2012). For improved and neutral grasslands, soil C is lower but consistently stable accompanied by a rise in N (*Appendix C.4,* **Fig. C.2**). This is likely due to the management history of these grasslands including some manure and fertiliser application or species compositions meaning extra fertility is utilised by species able exploit this. (Diekmann and Falkengren-Grerup, 2002; Willett *et al.*, 2004; Horrocks *et al.*, 2014). The drop in the L scenario N is likely linked to C also dropping as stoichiometrically the soil cannot hold the extra N coming into the system and may be leached out or lost to biomass harvesting (Novotny *et al.*, 2007; Jones *et al.*, 2017). This is likely due to greater turn-over and net primary production fuelled by the biotic community utilising the increased N availability under lower C:N conditions (Novotny *et al.*, 2007; Jones *et al.*, 2017; Tipping *et al.*, 2019).

The above reflects the need to monitor and manage soils at a national scale to ensure good soil health and function, and the soil indicators used here are shown to be important for this nationally by Seaton *et al.* (2020).

4.4.5 | Plant responses

The plant species responses to the scenarios covered do provide good indications into changing N abundances in habitats as they were selected having been informed by Rowe *et al.* (2016) and Smart *et al.* (2017).

The trajectories of the Nitrophobous and Nitrophilous species group diversity are discussed above but here links are made to the input variables in the differing N scenarios and residual habitat fertilities. For the fertiliser scenario soil and Ellenberg results in improved and neutral grasslands, the rise in the variables relating to fertility and N does tie in with Nitrophobous species diversity decreases. Whereas for Nitrophilous species under deposition (**Fig. 4.6**) the diversity score changes can be linked to, habitats with similarly high residual fertility (improve & neutral grasslands) having declining diversity; and low residual fertility habitats (acid grasslands) having Nitrophile diversity increasing. Also, Nitrophobic species increases in acid grassland under deposition could be a response to increasing pH with the increment applied (*see, 4.2.8*) to represent recovery from deposition based acidification (Emmett *et al.*, 2010; Rose *et al.*, 2016)

Within the N fixing species, the inconsistent response to the scenarios is likely reflective of the variation in habitats residual fertility and plant diversity between habitat types. This is noticeable in N fixing species diversity change under the Ndep scenario (**Fig. 4.5**, A). Here, the decrease in N fixer diversity under high fertility (improved grassland), and the increase in diversity under low fertility (acid grassland); is likely linked to leguminous species being better adapted to taking advantage of systems with low N, using their biological fixation as a competitive advantage (Diekmann and Falkengren-Grerup, 2002; Lee *et al.*, 2003). Whereas when N is high it is not limiting other species are better or as well suited to the conditions (Diekmann and Falkengren-Grerup, 2002; Lee *et al.*, 2003). Within the fertiliser scenarios (although less well defined than in the Ndep scenario), a similar response of N fixer diversity to N abundance is seen in higher versus lower fertility habitats, neutral versus acid grasslands, respectively (**Fig. 4.5**, B&C). As within the higher fertility habitat where N abundance rises N fixers lose their competitive advantage, leading to a decline in diversity (Diekmann and Falkengren-Grerup, 2002; Lee *et al.*, 2003) and in lower fertility, the rise in N abundance brings the habitat closer to the higher fertility habitat and diversity level.

However, this response is likely to be altered for all three grassland habitats under elevated CO_2 levels and climate change (Lee *et al.*, 2003; West *et al.*, 2005).

Foliar biomass N content is known to rise in response to greater N availability (Diekmann and Falkengren-Grerup, 2002; Fernández-Martínez, 2022). However, leaf N content as a plant functional trait is affected by species and functional type identity (Orwin *et al.*, 2010). This means that the interpretation of leaf N content vCWM (**Fig.3**; hereafter, LNvCWM) needs consideration in the context of three key factors: habitat residual fertility, scenario N abundance change and species traits. The LNvCWM response does demonstrate a response to the increasing gradient of scenarios N abundance from **Fig. 4.4**, A (Ndep) to **Fig. 4.4**, C (L, N 50-100 kg ha^{-1} yr^{-1}). Within the Ndep scenario, LNvCWM results in little change, reflective of the least change in fertility (**Fig. 4.3**, A). Whereas under the fertiliser scenarios the habitats typically receiving N inputs in their management (improved grasslands) show minimal change in LNvCWM representing a status quo; whereas a rise in N application for the mid-fertility habitat (neutral grassland) leads to a loss of diversity (*Appendix C.4,* **Fig. C.4**) and lowering of LNvCWM. This is due to N enrichment and has been described in previous research (Emmett, 2007; Maskell *et al.*, 2013). The rise in the lowest fertility habitat (acid grassland) LNvCWM we attribute to its fertility levels and thus LNvCWM moving towards that of the higher fertility habitats, described as ecosystem homogenisation elsewhere (Gossner *et al.*, 2016).

The LNvCWM results here are reflective of species expected to be dominants based on MultiMOVE's outputs and those with high leaf N content values. This may not be reflective of real world typical values due to the species pool being constructed to represent dark diversity thus being larger than expected real pools (Pärtel, Szava-Kovats and Zobel, 2011). The realised species pool is subject to colonisation and establishment filters that determine which species end up present in plots, all species groups modelled here are subject to this.

4.5 | Conclusion

The trends above, mainly within the Habitat trajectories section, show good congruence with the hypothesis (1.); however, there are many exceptions across the results. This variation provides novel insights into factors that confound the research aim, to estimate over what timescale change can (or cannot) be measured. As both N fertilisation and deposition are well known to impact upon soils and plant communities (Willett *et al.*, 2004; Emmett, 2007; Phoenix *et al.*, 2012; Xu *et al.*, 2020) the key insight from this study comes from estimating the detectability of changes over time. This knowledge, however, is critical in the context of designing sustainable land management policies (De Vries *et al.*, 2010; Posch, Aherne and Hettelingh, 2011; Rowe *et al.*, 2016). The finding that none of the measured soil variables were significantly different from baseline values alongside few differences in Ellenberg values (**Table 4.2**) suggests that these indicators don't perform well for determining AES management induced change or determining success over the time modelled (double typical AES prescription times). These indicators could be reinterpreted to be expressed as a percentage change from a start point or toward a desirable point to better represent change but, within the results shown (**Fig. 4.3**) values would still be low. However, within the species results (**Fig. 4.5**) changes are larger suggesting these are better indicators of AES management induced change, especially as plants are responding to multiple environmental variables (model inputs). All the indicators, however, show differences between habitats suggesting that more time may be needed to see change; this negates possible concerns that results are an expression of poor data rather than low performance indicators.

The assumption within the main hypothesis (1.) is that the response to a change in N will be reflective of the direction of change in N abundance. However, our results show a strong dependence of modelled response on starting conditions, meaning the hypothesis is not consistently confirmed. For example, within the improved grassland broad habitats, where

changes in N abundance in either direction in comparison to the habitats past high N inputs regularly fails to elicit a response, by way of little to no deviation from the baseline. Other patterns are summarised below within answering the sub-hypotheses:

i. N fixing species diversity does regularly decrease with higher N abundance in improved and neutral grassland broad habitats. The reverse is true in acid grasslands which is expected to be linked to habitat homogenisation (Smart *et al.*, 2006; Gossner *et al.*, 2016).
ii. With an increase in N abundance and fertility across the scenarios in neutral grassland, Nitrophobic species diversity does drop; although it remains stable or near stable in acid and improved grassland. The one exception to this is a rise in diversity in acid grassland under N deposition where this may reflect decreases in N deposition in some locations (Stevens *et al.*, 2004) as well as recovery from acidification (Emmett *et al.*, 2010; Rose *et al.*, 2016), particularly in the uplands where acid grassland is most common (*see,* **Fig. 4.5** and *4.4.5 , Plant responses*).
iii. Nitrophilous species diversity change is dependent on the broad habitat type and associated residual fertilities. Acid grassland with a low residual fertility which rises under N deposition confirming the main hypothesis and this sub-hypothesis with a rise in diversity. However, neutral grassland with a higher residual fertility shows a decline in diversity.
iv. Modelled N held within vegetation biomass (LNvCWM results) doesn't rise consistently with higher N abundance and often shows little response to change in the scenarios thus this hypothesis is rejected. It is expected to be more closely related to a combination of, species and functional type identity; also N abundance change contextualised to starting conditions and past management (Diekmann and Falkengren-Grerup, 2002; Orwin *et al.*, 2010) as well as previously observed species idiosyncratic responses to N change (Novotny *et al.*, 2007).

While changes (deviations from baseline medians) are observed within some of the results grassland AES agreements typically last 3-5 years, however, N-based changes in ecosystems are hard to measure in under 10 years (Rose, 2011; Rural Payments Agency, 2022a); especially here for soil variables. This is supported by the significance testing of the differences of the modelled results from the baseline and finding few instances of significant deviation. Even with results being habitat and scenario (management history and

management) dependent, decadal timescales for change to be observed can be widely expected.

Our results show that the effect of fertilisers on Ellenberg scores discussed above, as well as the findings of Phoenix *et al.* (2012) suggest that even very low (< 10 kg ha^{-1} yr^{-1}) N addition can accumulate leading to N impacts building up. The recommendation here is, that use of N fertilisers matches the equivalent of L<50 levels specified here (< N 50 kg ha^{-1} y^{-1}), with application limited to habitats that already have higher fertility levels (improved grassland). This could reduce further plant diversity loss. We also make a strong suggestion to policy makers that AES require confirmation of a change of management as well as using established plant species indicators to ensure land-managers are rewarded for environmentally beneficail changes in the practices as well as the results (when observed) of their efforts.

In terms of the research aim looking at measurable changes in the indicators we have focused on here these indicators alone are not likely to be sufficient for results-based policy for agri-environment schemes (Defra, 2020a, 2020b) seeking to confirm desirable results empirically.

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Chapter five, synthesis and conclusion

5 | The only certain thing is change: How can land management work with plants and soils to tackle global change?

5.1 | Land management for global change

The multiple global environmental change issues are well captured within the planetary boundary concept; climate change, land system-change, water use and degradation, biogeochemical cycle disruption, biosphere integrity degradation and polluting novel entities (Rockström *et al.*, 2009; Steffen *et al.*, 2015; Häyhä *et al.*, 2018). While land use change has contributed to the worsening of all these issues (Watson *et al.*, 2011; IPCC, 2018; Hayhow *et al.*, 2019; Díaz *et al.*, 2020), through research-led good practice, land management has the potential to mitigate and reverse these trends (Minasny *et al.*, 2017; Simons and Weisser, 2017; Helm *et al.*, 2020; IUCN, 2020). A concern beyond the issues themselves is the increasing time pressure of their impacts, especially in the context of climate change (Smith, Knapp and Collins, 2009; Zhongming *et al.*, 2022) and ongoing evolution of initiatives such as the European Union (EU) Common Agricultural Policy (CAP) and UN Sustainable Development Goals (Pe'Er *et al.*, 2019). The current state of anthropogenic influences on the planet represents a situation where intentions for the sake of pragmatism should ideally shift from prevention alone to also include damage mitigation.

Achieving ecologically-evidenced sustainable land management represents a top priority for mitigating and preventing the impacts of environmental change. Agri-environment schemes (AES) represent trans-national (EU CAP) policy tools for encouraging implementation of sustainable land management practice (Rose *et al.*, 2016; Oatway *et al.*, 2018; Pe'Er *et al.*, 2019). The novel research work here has aimed to contribute to the ecological evidence base assessing the likely efficacy of AES-prescribed management within the UK when subject to interacting global change drivers. This is highly topical and current as not only are environmental issues becoming more time pressured but also as new policy is required due to the UK's exit from the EU (Brexit) (Arnott *et al.*, 2019; Defra, 2020a).

5.1.1 | Current and future UK AES

The UK AES have been developed in their current form to tackle targeted ecological and environmental goals but need reform in the context of Brexit and the desire to ensure public money is spent on public goods (Defra, 2018, 2020a; Arnott *et al.*, 2019). These goals or aims can be summarised into seven key word-based themes featuring in past, current, and future AES policy documents naming them as key areas for subsidised action:

1. Climate: climate change mitigation or adaptation.
   (Rose *et al.*, 2016; Defra, 2018, 2020a; Oatway *et al.*, 2018)
2. Soil: healthy soil and carbon sequestration.
   (Rose *et al.*, 2016; Defra, 2018, 2020a; Oatway *et al.*, 2018)
3. Biodiversity: maintaining or improving biodiversity.
   (Rose *et al.*, 2016; Defra, 2018, 2020a; Oatway *et al.*, 2018)
4. Water: water quantity and quality.
   (Rose *et al.*, 2016; Defra, 2018, 2020a; Oatway *et al.*, 2018)
5. Flood & Drought: reducing climate-based hazard impacts.
   (Defra, 2018, 2020a)
6. Trees: maintaining forest and planting trees.
   (Rose *et al.*, 2016; Defra, 2018, 2020a)
7. Heritage: sustaining heritage landscape features.
   (Defra, 2018, 2020a)

These are largely implemented by paying land-managers for implementing AES management options, although the individual options are not always specifically linked back to the points above. Example of utilised options can be found in the AES guidance, Welsh Government (2016) and Rural Payments Agency (2022a).

While AES scheme design has been acknowledged as being robust with some positive outcomes evidenced (Keenleyside *et al.*, 2011; Bright *et al.*, 2015; Oatway *et al.*, 2018; Dadam and Siriwardena, 2019; MacDonald *et al.*, 2019) there are many examples of limited success, lack of monitoring, or at best maintenance of the status quo (Kleijn and Sutherland, 2003; Critchley, Burke and Stevens, 2004; Davey *et al.*, 2010; Mountford and Smart, 2014;

Norton, Henrys and Crowe, 2014; Arnott *et al.*, 2018; Staley *et al.*, 2018). These concerns are why a number of land management prescriptions aligned with AES have been modelled here to enable a prospective assessment of the potential performance of interventions given the increasing impact of global change drivers beyond the immediate control of the land-manager.

I explore the near future impact of four generalised AES option types: reducing fertiliser use; reducing livestock density on land; management of vegetation height, and planting native trees species. *Chapters 2 , 3 & 4,* of this thesis focus on these example AES prescription types, through modelling their management effects on plants and soils.

The plant and soil focused models used in this thesis have directly explored ecological outcomes of management directly related to the key word-based AES areas identified here with the numbering used above:

2. By modelling soil variable change with management and fertiliser application change.
3. By using ecological niche modelling (ENM) of plant species and vegetation change.
6. By construction of a modelling workflow emulating tree planting.

There are also links to key word-based AES areas 1, 4 & 5 above: as carbon increase in soil and tree planting can mitigate climate change (Rowe *et al.*, 2016; Minasny *et al.*, 2017; Di Sacco & Hardwick *et al.*, 2020); afforestation can reduce flooding (Marshall *et al.*, 2014; Stratford *et al.*, 2017); and tree planting and fertiliser use reduction is linked to water quality (Emmett, 2007; Horswill *et al.*, 2008).

While ecological monitoring has been part of UK AES for a number of years (Rose, 2011; Oatway *et al.*, 2018), national scale monitoring schemes with methodologies in common are rare. For this reason when large monitoring datasets do become available, it adds value to

the survey efforts to go beyond monitoring and attempt to model into the future; especially in the context of global change (Ormerod, 2012a, no date; Emmett, Alexander, *et al.*, 2016). Thus within the work here, the Glastir Monitoring and Evaluation Program (Emmett *et al.*, 2017) data and the Countryside Survey (Carey, Wallis, Emmett, *et al.*, 2008) datasets alongside the other datasets described in *1.7* have allowed large scale monitoring data to be used for future casting to inform on long-term AES performance.

5.2 | Insights from Modelling AES impacts on plants and soils

This thesis has modelled the management of grassland and creation of woodlands as these respectively represent: semi-natural habitats where anthropogenic land use can be traded off with ecological benefits (Simons and Weisser, 2017); and late stage succession habitats the restoration or creation of which provides biodiversity and carbon capture potential (Green *et al.*, 2005; Stafford *et al.*, 2021). The findings of the work within *Chapters 2 , 3 & 4* are summarised below and synthesised into key ecological considerations at the end of this section then used to make recommendations for application to AES design in section, *5.2.1*.

All three analysis chapters focus on the modelling potential improvement to, creation of or restoring habitats. Within *Chapters* 2 & 4 *,* grassland habitat diversity trajectories are modelled with desirable end-points being biodiversity increases from improved to unimproved grassland habitats. The assumption was when habitats transition from intensively managed improved habitats to reduced intensity management or unimproved habitats, biodiversity gains should be seen; this, however, was not consistently the case (*see, 4.5 & 2.3*). Also, within *Chapter 2 ,* little predicted change in soil conditions were seen. *Chapter 3* modelled tree planting, predicting how several habitats establish to woodland after planting. Within this, biodiversity improvements for both the species groups selected

and soil condition improvements were seen within less than 30 years although not consistently reaching established (baseline) woodland levels.

A consistent theme across the analysis chapters was that for AES options expecting habitat transitions, their agreement times were largely too short for significant ecological change to be completed. This consideration is connected with wider ecological theory of the relationship between intervention (or perturbation) level and the recovery or change timeframe; however, this can be altered by global change drivers as seen in 4 and described in Smith *et al.* (2009). This is also further affected by a site's historic management and ecological state (Dupouey *et al.*, 2002; Ogle *et al.*, 2015). The differences between habitats with shorter-lived versus longer-lived species e.g. grasslands (many annuals) and woodlands (many perennials) explored here, also affects response time (Smith, Knapp and Collins, 2009). This is directly related to the findings of *Chapters 2 & 3* where AES management prescription times are too short for major changes to occur. Given that AES designs are typically determined to be robust, but only occasionally deliver their goals (Keenleyside *et al.*, 2011; Oatway *et al.*, 2018; Dadam and Siriwardena, 2019; MacDonald *et al.*, 2019), their timeframes are a likely cause of their ecologically, inconclusive or poor performance outcomes.

The AES options explored in *Chapter 2* represent a broad-shallow extensification of management, this refers to widely funded AES prescriptions to reduce stocking densities and fertiliser application. *Chapter 3* however represents an intervention (tree planting) to deliberately transition from starting habitats to forest. These two changes in management differ both ecologically and in their level of intervention at the point of implementation, therefore the differences in ecological response are to be expected.

All three modelling chapters (*2 , 3 & 4*) predict changes in habitat suitability of individual species and then sum these to estimate 'dark diversity' (Pärtel, Szava-Kovats and Zobel, 2011) at each modelled quadrat location. By modelling the local species pool drawn from species observed in each quadrat location at baseline and also known to occur in the wider 10km square we estimate the extent to which new soil and climate conditions favour a different subset of plant species to those present at baseline, before and after each intervention is applied. Hence potential future colonisers are those with higher modelled suitability scores. While this is useful for exemplifying restoration potential, realising new assemblages will require dispersal and establishment filters to be overcome (*see, 5.3.1.3*).

The UK has habitats which have become progressively degraded over long time periods and current evidence suggest this trajectory is not changing (Hayhow *et al.*, 2019). This can be addressed in several ways. Firstly, if natural process are to be relied on, then adjacent high quality habitat needs to be present to provide a colonising population source for both forest (Brunet *et al.*, 2012; Di Sacco & Hardwick *et al.*, 2020) and grassland restoration (Stevens, 2010; Wagner *et al.*, 2014). Relying on an already degraded national landscape (Watson *et al.*, 2011; Hayhow *et al.*, 2019; Forest Research, 2020) for natural dispersal processes therefore seems unwise, particularly for afforestation. Alternatives to this regularly explored in grassland and forest restoration is direct seeding or planting of species (Pywell *et al.*, 2007; Wagner *et al.*, 2014; Di Sacco & Hardwick *et al.*, 2020; Berdeni, Williams and Dowers, 2021). This provides a more definite outcome by skipping at least the dispersal stage and, where planting is concerned some of the establishment stage as well.

5.2.0.1 | AES Ecological considerations

The ecological insight gained from modelling and analysis in this work aims to ensure AES interventions are well evidenced. This will also help policy makers expectations to be

realistic. Due to this, three well established aspects of wider ecological theory are provided as key considerations for AES design into the future:

A. Time for change - if ecological restoration is desired then realistic ecological timeframes must be used.
B. Intervention level - lighter management change will result in smaller responses (and longer responses times).
C. Dispersal and establishment - if biodiversity gain goals are to be met, then sources of plant species must be acquired through local population sources or deliberate introduction.

5.2.1 | AES policy and management recommendations

The modelling workflows within the analysis chapters represent a variety of land management scenarios. These have been constructed (using data from literature review) as near matches to AES prescribed management types, thus direct application to management needs careful consideration. The section below, however, provide management and policy recommendations that can be directly applied to AES design for sustainable management of plants and soils.

5.2.1.1 | Habitat restoration and creation, based AES improvement

While the two habitats explored in the analysis chapters differ ecologically, the work here has highlighted two requirements for ecological management of grassland and forests:

I. Extending the length of agreement times and/or offering increased incentives for continually signing up to the same intervention regime or sequentially improving ecological management interventions to increase the chances of positive changes to plant diversity and soil conditions. As *Chapters 2 , 3 & 4* all suggests typical agreement times (3-13 years as in, Rose; Rural Payments Agency, (2011; 2022a)) could be lengthened for more desirable outcomes.
II. Ensuring plants are present to establish, either seeding and planting desirable species; or by dispersal from adjacent sites harbouring target communities. As sections 2.4.1 & 3.4.3 suggest for grasslands and woodlands.

Both of these can be summarised as *longer* and *stronger* interventions, management prescriptions with greater duration and applied targeting. Although as land-managers are more amenable to lighter interventions (Arnott *et al.*, 2018), longer funding times are likely to be more attractive to land-managers if incentivised suitably. The ongoing development of the UK's Environmental Land Management Scheme (ELMS) should consider these opportunities and constraints (Defra, 2020a).

5.2.1.2 | Grassland Management AES improvement

The first (*2*) and third (*3*) analysis chapters both focus on grassland, the first looking specifically at lighter touch AES application and the second on fertiliser use. The findings of both are synthesised below:

5.2.1.2.1 | Fertiliser use

A reduction in fertiliser use modelled in *Chapters 2 & 4* failed to elicit much ecological response in less than 10 years. Therefore, the recommendation here is that fertiliser application is limited only to habitats that already have higher fertility levels (improved grasslands) and application levels do not exceed 50 kg N ha^{-1} yr^{-1} (*see, 4.5*). This allows lower fertility habitats to continue on trajectories uninfluenced by fertilisers, and more fertile habitats to maintain production ecosystem services while slowly transitioning away from high fertility and low diversity states (thus toward AES goals).

5.2.1.2.2 | Detectability

Given the call within newly the developing UK AES, ELMS, for results based schemes a measurable change with the results from government-funded land management prescriptions is required (Defra, 2018, 2020a, 2020b), thus any lack of measurable change is a concern. In both chapters I showed that environmental condition metrics and indicators (Carey, Wallis, Chamberlain, *et al.*, 2008; Emmett *et al.*, 2010; Seaton *et al.*, 2020) often

showed little or no change up with 10 years of modelled intervention. Therefore, the recommendation is lengthening AES (as for *5.2.1.1 I.*) to increase the likelihood of detectable change or results. However, it will remain important to incentivise beneficial management practice prior to this. Therefore, the suggestion to policy makers is that AES implementation should include compliance monitoring (ensuring the intervention has been applied appropriately on the ground and in the right places) plus ongoing monitoring to detect possible ecological change (results-based success) thus ensuring land-manager's sustainable practice efforts are rewarded.

Also, environmental condition metrics and indicators used to determine change need careful consideration. In particular, tension may arise between selecting indicators sensitive to a particular intervention while also achieving backwards compatibility with existing time series. For example, GMEP and ERAMMP use established metrics and indicators (Emmett, Alexander, *et al.*, 2016; Emmett *et al.*, 2017) that date back to the 1970s (Carey, Wallis, Chamberlain, *et al.*, 2008; Reynolds *et al.*, 2013). Also further exploration of plant-based indicators such as those within Rowe *et al*. (2015) could provide vegetation-based indicators that respond faster than decadal time scales.

5.2.1.2.3* | *Stronger interventions

Given the slow response of grasslands to the changes in management modelled in *Chapters 2 & 4 ,* stronger management interventions should lead to more desirable habitat developing faster. Examples of this include: switching to manure or green manure based fertilisation (but keeping below the N application level in *5.2.1.2.1*); stricter vegetation height management with limitation of grazing and cutting; seeding in approved native, seed mixes or spreading of green hay; and manipulation of soil or bare ground to provide colonisation sites. These are all management interventions drawn from grassland restoration ecology (Pywell *et al.*, 2007;

Stevens, 2010; Hayes and Lowther, 2014; Wagner *et al.*, 2014; Staley *et al.*, 2018; Török *et al.*, 2021).

5.2.1.3 | Afforestation AES improvement

The afforestation practices modelled here apply specifically to broadleaved woodlands where we explore benefits for biodiversity and carbon benefits. While I modelled plantation scenarios, aspects of passive afforestation (natural succession) are also included with the AES prescribed management improvements below. A key consideration for afforestation policy is facilitating the "right tree in the right place" narrative (Di Sacco & Hardwick *et al.*, 2020). Achieving this requires the following sequential activities:

1. Site selection.
   As availability and suitability of land for afforestation is needed for successful afforestation; guidance and forest-planning support is key. Therefore, the publishing of regularly reviewed site (and species) selection guidance as well as covering forest planning consultancy fees should improve afforestation success by tailoring planting to the "site level". This is best emphasised in the "most benefit" versus "most creation" contrast in section 3.4.11.
   This is pertinent as not all land-managers can be expected to hold the forest ecology knowledge to make decisions that are, economically viable as well as mitigating biodiversity loss and climate change. While policy documentation does acknowledge this (Davies, 2016; Defra, 2018), schemes that directly address these issues are rare. However, the new UK Environmental Land Stewardship scheme (ELMs) presents an opportunity to change this (Defra, 2020a) that should not be missed.
2. Species selection.
   Next, guidance and forest planning support should also cover which species to establish in a site given its environmental conditions (kept up-to-date with climate change and tree pathogen concerns, Pautasso *et al*. (2010)). Also, while local colonisation (*see, 5.2.1.1: II.*) is a potential tree source, within *Chapter 3*, the time-scales for some variables to reach established woodland values, does suggest that as for *5.2.1.3 : 1.*, well implemented planting schemes at a "by site level" can be a preferable method for accelerated afforestation and restoration.

3. Planting methods.
   To align with AES goals (*5.1.1 : 1., 2. & 6.*), establishing forests to mitigate climate change and improve soil condition (and carbon), minimum soil disturbance planting should be incentivised (*see,* 3.4.4). Planting practices aligning to this can be found in Berdeni *et al*. (2021).
4. Monitoring and restocking.
   To ensure forests establish beyond the AES prescribed management times (*5.2.1.1 : I.*), follow up management should be incentivised. An example of this would be: post-funding tree planting, fund monitoring tree loss at 10-20 years in combination with a further 10 years of competing vegetation management (e.g. removal of, *Clematis vitalba* or *Pteridium aquilinum* removal as well as non-natives such as *Prunus laurocerasus* or *Rhododendron* Sp.), restocking of tree losses and thinning.

5.2.2 | Revisiting the research questions

The new knowledge produced within this thesis helps answer the three research questions posed in the Introduction (*1.7.1*). Below I discuss these and how the results of the research provide novel insight into the performance of agri-environment scheme management:

1. Plant communities will reassemble toward desirable compositions or reference habitats provided they are given suitable management with sufficient time to achieve this. However, the AES prescription tested within this thesis are not of sufficient duration to be consistently successful (*see, Chapters 2 & 4)*.
2. Assembly or reassembly of modelled habitats takes over 10 years for grasslands and over 40 years for forests. However, rare or desirable vegetation types or indicator species were not observed to reach target levels within the timeframes modelled (*see, Chapters 2 & 3*).
3. Ecosystem function and service linked variables (species groups diversity scores and soil conditions) show varied responses depending on the habitat and management. For grasslands minimal response to, or response times longer than the duration of, AES prescriptions occurred regularly in the results (*Chapters 2 & 4*). However, for soil carbon, timber species and nectar-producing species under modelled afforestation results were promising although again at longer than AES prescription times and climate change appears to aid these species groups (*Chapter 3*).

5.3 | Methodological considerations: statistical analysis and monitoring

The methodological approach used within the analysis is only achievable thanks to the environmental data available within the UK. The colloquialism (inclusive of citizen scientists) “There are more botanists in the UK than plant species” is a good reflection of the world class data availability for the UK (K. Walker *et al.*, 2010; Henniges *et al.*, 2022). While a similar turn of phrase can’t be used about soil science or climate modelling, the datasets available are still of a very high standard (Emmett *et al.*, 2010; Lawley, Emmett and Robinson, 2014; Lowe *et al.*, 2018). The datasets linked to the referenced works here and those used in the analyses (*see, 1.6*) are very much representative of the rise of big data in ecology in the past 10-20 years in the UK. However, long-term ecological datasets for ecosystem responses to management and global change in combination are still rare (*see, 5.3.3*).

This rise in data availability is also reflective of the development of MultiMOVE which utilised national datasets as its construction data (Smart *et al.*, 2010; Henrys, Smart, *et al.*, 2015) and can make use of the more recent environmental datasets as inputs e.g. UKCP18 (Lowe *et al.*, 2018). While the ecological modelling workflow is larger than just MultiMOVE, it does form its ecological niche modelling centre.

Both the modelling workflow methodologies for plants and soils applied here; and the ecological monitoring schemes assessing ecosystems and land management practice impacts; have many possibilities available for improvement. Those considered most useful to the work here are described within the following sections.

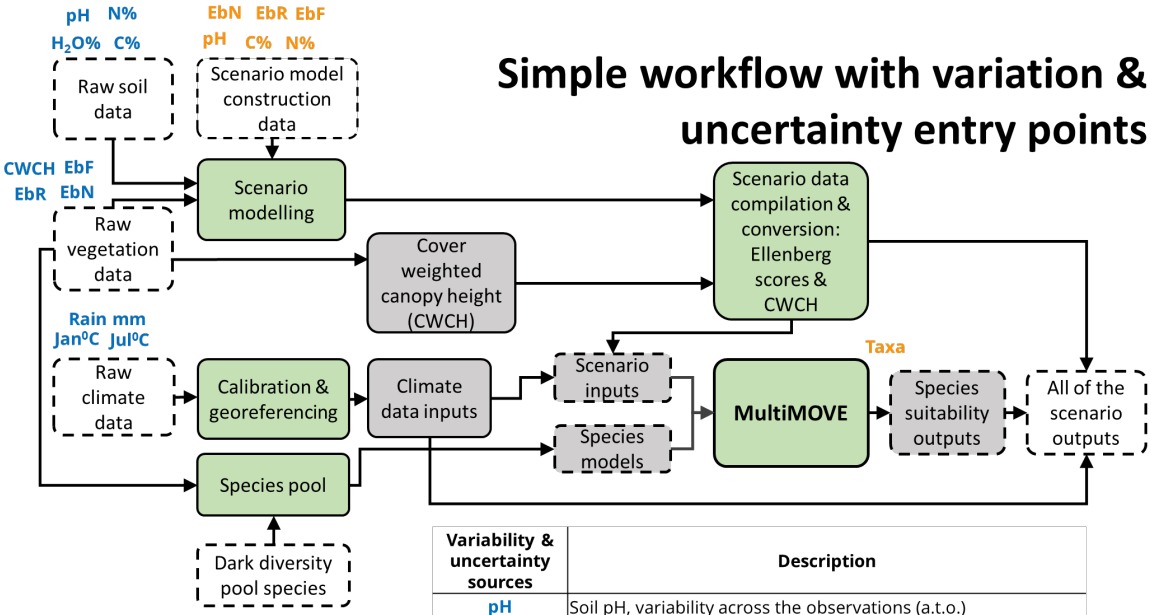
5.3.1 | The land management modelling workflow

The modelling workflow used throughout the data analysis chapters is adapted to fit the research aims of each. However, for *Chapters 2, 3 & 4* the most desirable possibilities for improvement of the model workflow are the same. These are summarised in the following sections.

5.3.1.1 | Uncertainty and variation

The full scale of uncertainty propagated through the empirical and modelled results was not fully explored here, although this would be possible with high performance computing (HPC) clusters (e.g.: Clematis, Mineter and Marciano, 2003; Hallgren *et al.*, 2016). This was not pursued as the focus here is on scenarios with a high degree of reality applied to a specific representation of AES prescriptions. The major disadvantage of this being that the model-generated results are only applicable to the specific real-world scenarios the modelling was based on, matching management and variables equivalent to the baselines here. An example being, within *Chapter* 2 the AES scenarios explored are linked to Welsh grasslands and AES over the short-term (13 years ending in 2029). Thus, the modelled scenarios applied to AES in grasslands here would not be appropriate for generalizing across European grasslands. The trade-off here is that we wished to understand specific regional impacts using a high quality and high-resolution baseline in response to specific interventions. The main ecological findings (*see, 5.2*), can, however, be applied elsewhere, as they are reflective of ecological processes rather than the management or environmental specifics within each analyses chapter's results.

To consider how to explore this, different sources of uncertainty and variation need to be identified across the workflow (Lehmann and Rillig, 2014). These occur at all the entry points of empirical field recorded data or modelled data (**Fig. 5.1**).



Variability & uncertainty sources	Description
pH	Soil pH, variability across the observations (a.t.o.)
C%	Total soil carbon %, variability a.t.o.
N%	Total soil nitrogen %, variability a.t.o.
H_2O%	Soil moisture %, variability a.t.o.
CWCH	Variability from the cover observations made
EbN	Ellenberg vegetation fertility score, variability across plot observed means & uncertainty in the mean values calculated
EbR	Ellenberg reactivity score, variability & uncertainty as for EbN
EbF	Ellenberg wetness score, variability & uncertainty as for EbN
Rain mm	Total annual precipitation, variability from the observations & where predicted climate data is used, uncertainty from the model used for the predictions
Jan°C	Minimum January temperature, uncertainty & variation as for Rain mm
Jul°C	Maximum July temperature, uncertainty & variation as for Rain mm
pH	Predicted pH, uncertainty from the model(s) used (f.t.m.u.)
N%	Predicted N%, with uncertainty f.t.m.u.
C%	Predicted C%, with uncertainty f.t.m.u.
EbN	Predicted EbN, with uncertainty f.t.m.u.
EbR	Predicted EbR, with uncertainty f.t.m.u.
EbF	Predicted EbF, with uncertainty f.t.m.u.
Taxa	Species suitability score from MultiMOVE with uncertainty from the model(s) used to make the prediction

Figure 5.1. A simplified graphical representation of the workflow used across all chapters with uncertainty and variation sources above their respective entry points. Dashed edged boxes represent datasets, white for workflow inputs or output data, grey for mid-workflow datasets. Grey boxes represent data manipulation steps and green boxes represent coded processes. Uncertainty and variability definitions are as for Lehmann and Rillig (2014). Acronyms: **a.t.o**, across the observations; **f.t.m.u.**, for the model(s) used.

Variability across the observed data is captured simply by running all this data through the workflow (the observed plot data). The uncertainty in the species recorded (not the suitability score) and modelled at each site is not included here as it should be captured sufficiently by the modelling of the dark diversity pool (*see, 3.2.34 and* **Fig. 3.2**).

When the models are used predictively to generate change, they introduce uncertainties. These are best represented by the standard deviations around the mean predicted values

(or confidence intervals where SD's are unavailable). Using these it would be possible to represent variability in the outcome of the modelled changes by sampling values from these means and SD. To do this for all variables across the workflow however rapidly multiplies up the number of simulations needed. For example, 100 random draws from the 13 variables uncertainty ranges above (**Fig. 5.1**), goes from 1 to 100^{13} runs needed for the combination of generated values. Hence to achieve this within a reasonable timeframe would require HPC clusters and a workflow tailored to this (e.g. Hallgren *et al.*, 2016 or Bastin *et al.*, 2013).

The above however does not prevent propagation of uncertainty. This means mitigation is needed via correct application of theory and method to avoid error propagation that would lead false conclusions from the results (Hallgren *et al.*, 2016; Bastin *et al.*, 2013). The first key assumption made throughout the modelling here is that working with median or mean values provides a good representation of the observed environmental conditions when specifically applied to the scenarios and habitats analysed. Statistical testing plant and soil results show this has largely been achieved: in *Appendix A.5.1* higher plant habitat suitability scores do suggest species presence to be more likely; and within soils modelling (*Appendix D*, **Table D.1**) there are few significant differences between observations and predictions. *See next section for more details*. This provides confidence that the model outputs are fit for the assumptions made. Although as **Fig. 5.1** shows possible entry points of uncertainty, including as examples: measurement and input parameter; spatial and temporal; model construct and output; and transmission between models' uncertainties (Bastin *et al.*, 2013). Therefore, this does not express how well uncertainties known to enter the workflow may lead to error propagation.

While the scale of possible propagation can only be explored with the HPC methods described earlier in this section, this can affect confidence in the findings. Although the conducted modelling performs well construction parsimony and the complexity of reality

means there are limitations (Bastin *et al.*, 2013), for example: if a site *n* in year *i* in the modelling conducted in the analyses *Chapter 2*, has a low pH, above median soil carbon and above median soil nitrogen with climate variables suggesting *i* to be a warm wet year leading to higher productivity then the vegetation likely to present at the survey could suggest the habitat to be improved grassland. In a different year however, acid grassland might be a better categorisation. If the modelled results in **Fig. 2.3** showing acid grassland to progress to a more diverse range of habitats than improved grassland then when applied to site *n* at *i* then a poor result for AES goals would be expected. This scenario represents a known possible failure of predictions due to uncertainty but true unknows for more outlier sites true unknows are more likely and hard to account for. This makes the specificity of model and application of knowledge generated key. The mitigation for this and the above is rigorous application of statistical methods through: high numbers of replicates, careful data sourcing, multiple techniques for model testing throughout workflows, and specificity of application of results to habitats and scenarios. Although application of HPC techniques to explore error propagation would be a good avenue for future research.

5.3.1.2 | Model Validation

Good model performance is ensured through application of rigorous statistical methodologies, however, validating predictions into the future is challenging. Within the modelling chapters I carried out statistical tests to ensure good performance, for example: AIC comparisons, R^2 and Bayesian R^2. For MultiMOVE predictions of individual species habitat suitability, I used logistic regression to test the ability of the species niche models to predict observed presence and absence data (*see, Appendixes A.5 & C.4, with* **Fig. C.1**). Beyond this the prediction results have been compared to baseline values to ensure realism and build credibility in the modelling approach and the modelled results (e.g., **Fig. 3.3** & **Table 4.2**). However, this doesn't provide model validation and without construction of an independent workflow for comparison (too resource costly to be in scope here) it must be

acknowledged that a robust falsifiable validation method is lacking here. The first challenge in gaining suitable validation data is finding land that has been managed under the same management as the modelled scenarios. Within *4* this initially appears possible as the predictions using the Countryside Survey data (Carey, Wallis, Chamberlain, *et al.*, 2008) could be compared to the GMEP data (Emmett *et al.*, 2017), however ensuring matching management has not been possible and comparison of the datasets shows them as often significantly different; *Appendix D.1* demonstrates an example of this.

Given the time-frame needed (> 10 years) for ecological change the first opportunity to gain real world data for validating the predictions from *Chapters 2 & 4's* workflows is 2026. While comparing the numeric predictions is statistically straightforward e.g. ensuring total soil carbon % or Ellenberg nutrient scores etc. observed in 2026 fall with the standard deviations of the predictions; this is not as simple with the modelling of the species habitat suitability results. Given that workflow species outputs are representative of dark diversity (local potential colonising species) the number of species predicted with habitat suitability scores suggesting occurrence is possible in 2026 (for example *F. excelsior* in *3.3.3*), is far higher than the number likely to be observed. This is useful at the point of prediction as it provides a species pool to consider for ecological restoration as well as representing uncertainty in outcomes. However, this is less useful for predictions of species observations. Thus, while one plot's observed species in 2026 is unlikely to show all the species within the dark diversity pool it is expected that across the number of plots modelled the dark diversity pool would be well, but not completely, represented. Moreover, comparing model predictions with later observed data can specifically focus on species observed at baseline and any extra species appearing at time 1+*n*.

5.3.1.3 | Modelling improvement

Within the modelling workflow the methods used to model management or global change were based on past research. Examples being: the generalised linear mixed effect models used for soil change have been previously proven to robustly represent soil macronutrient change over time (Poulton *et al.*, 2003; Thomaes *et al.*, 2012); and the application of Bayesian models for Nitrogen deposition effects having been previously employed with success (Stevens *et al.*, 2016). Whereas for climate based global change models, the most up-to-date data available for the UK were used (Lowe *et al.*, 2018; Robinson *et al.*, 2022). Thus, these are thought to be well suited to their use here. Improving on these is likely to only be possible with dedicated and specifically applied research efforts applied to the variables and scenarios explored.

The ecological niche modelling package used (MultiMOVE) has undergone several updates since its creation in 2015 (Henrys, Butler, *et al.*, 2015; Henrys, Smart, *et al.*, 2015) and could benefit from further additions beyond the simple inclusion of more taxa or observation data. To bring the ecological modelling here closer to reality, the inclusion of a vegetation abundance predictor and model component(s) representative of dispersal and establishment would be desirable (Boulangeat, Gravel and Thuiller, 2012; Weber *et al.*, 2017).

Ecological niche models have been proven to be able to determine abundance levels where their outputs correlate with training data abundances (Weber *et al.*, 2017). Relating model outputs to abundance via additional modelling would be a worthwhile methodological development within the workflow here to better predict future vegetation communities. This could be achieved by correlating observed cover or frequency estimates in MultiMOVE's training data with habitat suitability predictions for these same data. Functions predicting cover given habitat suitability could then be readily constructed for each species. The exact

relationship could then be modelled (using the ensemble approach for robustness as for the rest of MultiMOVE).

It is also likely to be beneficial to including a categorical variable for the taxa who's abundance is being estimated. This is because relationships between model outputs and rarer species abundances are likely to be less well correlated due to lower data availability. Also, a confidence measure of the abundance predictions would be worthwhile as the training data varies across taxa and new input data may cover sites with differing ecological histories therefore different species responses e.g. competition interactions within different vegetation communities. This, however, does still rely on the assumption that establishment and dispersal factors are accounted for by only modelling species present in the plot or estimating dark diversity (as for, *Chapters 2 , 3 & 4*).

Adding a model layer to MultiMOVE could also allow the incorporation of establishment and dispersal factors; as has been practiced in ecological niche models elsewhere (Boulangeat, Gravel and Thuiller, 2012). Achieving this in combination with abundance estimates would represent a significant step beyond simply estimating dark diversity or modelling species known to be present. But pragmatics of modelling dispersal and establishment are complex, as data would be needed on each taxa's establishment and dispersal ecology although species functional trait data is available (Liu, Cossu and Dickie, 2019; Kattge *et al.*, 2020).

5.3.1.4 | Dynamic mechanistic models

As mentioned within the introduction (*1.4.3.1*), the pursuit of creating dynamic and mechanistic process-based models is desirable although hungry in training data requirements (Kearney and Porter, 2009; Purves *et al.*, 2013; Sillero *et al.*, 2021). Here I explore the likely data requirements for the construction of dynamic mechanistic models that

would match the number of taxa covered across the scale of MultiMOVE (Henrys, Smart, *et al.*, 2015) using a “back of the envelope” calculation estimate.

According to Sillero *et al*. (2021), 20 to 30 species records are needed for good ecological niche model accuracy. MultiMOVE includes 1342 plant taxa (Henrys, Butler, *et al.*, 2015) with 9 environmental variables used to represent the niche space occupied. This (at the low end) suggests 241,560 data points are needed as a minimum. If mechanistic process are to be represented then multiple time-periods will be required (Kearney and Porter, 2009). For example, the current MultiMOVE construction data that includes soil data spans four sampling years across the past few decades (Carey, Wallis, Emmett, *et al.*, 2008) quadrupling the data requirement (to 966,240). As this data does not deliberately include taxa’s life cycles or functional traits, the data requirement (Kearney and Porter, 2009; Benito Garzón, Robson and Hampe, 2019; Radchuk, Kramer-Schadt and Grimm, 2019) for comparable process-based models is easily pushed into the need for millions of points. The current data on which MultiMOVE was constructed spans 50 years (Barr *et al.*, 2014; Barr, Bunce, Gillespie, Hallam, *et al.*, 2014; Bunce *et al.*, 2014). Even with an increased survey effort, this is only likely to decrease to a few decades. Consequently, national scale dynamic mechanistic process-based model construction covering > 1000 taxa remains an admirable and desirable but distant goal (Benito Garzón, Robson and Hampe, 2019; Radchuk, Kramer-Schadt and Grimm, 2019).

Given enough data for enough species, wide-scale dynamic mechanistic process-based models with fine resolution application like MultiMOVE would become possible to construct and utilise. However, this seems unlikely to occur within the next few decades. While HPC cluster-led computing power may be sufficient, the data on species responses to changing conditions, management and global change, and how this effects their ecological function

and the associated processes (e.g. population dynamics) is lacking (Urban *et al.*, 2016; Radchuk, Kramer-Schadt and Grimm, 2019; Sillero *et al.*, 2021).

5.3.2 | Environmental land management informed by monitoring

The EU CAP has adopted monitoring of AES in various forms since the mid-1980s (Geijzendorffer *et al.*, 2016), however a standardised approach to monitoring AES outcomes does not exist across the UK. Here, approaches have been adapted (Ormerod, 2012b; Oatway *et al.*, 2018) to suggest a conceptual model for (**Fig. 5.2**) how monitoring over time could work. This expands beyond a typical monitoring, reporting and validation thematic framework as both ecosystem history and past land management are key priors. Also, predictive modelling, as well as the former components are useful informers for sustainable land management implementation and policy. The following sections are numbered sequentially as for the boxes in **Fig. 5.2** as an illustration, as well as the explanatory text below. **Fig. 5.2** could also be adapted to become an organogram reflecting different sections across a government department (e.g. Defra); for example steps 1-3 & 5-6 could be covered by Natural England and the remaining steps within 1-10 by the Rural Payments Agency.

5.3.2 | 1 Assemble desk based past data on legacy scheme history

With the likes of the Countryside Survey (Carey, Wallis, Chamberlain, *et al.*, 2008) and the long history of biological recording in the UK (K. Walker *et al.*, 2010; BSBI, 2018; Henniges *et al.*, 2022), a desk-based data gathering exercise (**Fig. 5.2**) can act as a start point for information on evidencing AES implementation. This can inform on both the past state of habitats as well as past effects of management. Both of these sources of information can provide training data for models informing on AES outcomes (**Fig. 5.2,** step 9) and have done so within the analysis chapters here. Examples sources of the type of data that would be used for this can be found in *1.6* .

5.3.2 | 2 Historic habitats

Historic habitat data (biotic and abiotic) is widely available in the UK (*see, 1.6*) although, particularly for biological species records, it is likely to need georeferencing or appropriate data handling to allow for referencing to management data and the impacts. Thus, historic abiotic and biotic habitat data often need extraction from wider landscape and land management data when sourcing multiple datasets in step 1 (**Fig. 5.2**). This should provide an environmental dataset, depending on the quality of the data source available, informing on past states of the land in the focus for AES management applications.

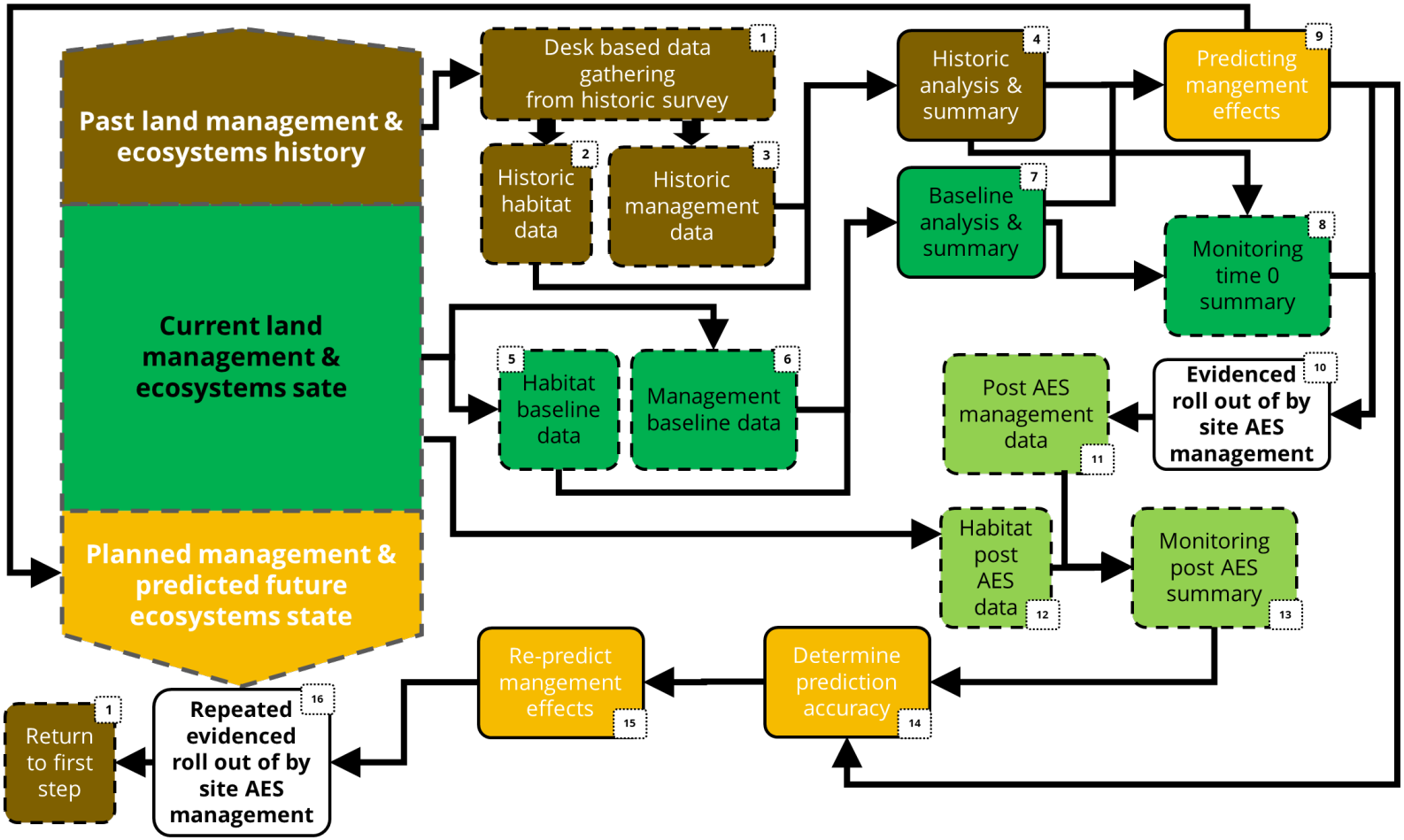


Figure 5.2. Thematic diagram with sequential steps (white numbered boxes) of how information gathering, monitoring and modelling agri-environment scheme (AES) impacts on ecosystems can inform evidenced based AES design and implementation. The left-hand grey dashed vertical strip of boxes are representative of the landscape and land management conceptually in the past (top), current (management regime phase, middle) and future (bottom). Brown boxes represent past aspects of management and environment (M&E); green boxes represent the current management regime phase and aspects of M&E, dark green boxes being the start and light green boxes being the end; orange boxes represent future aspects of M&E. Black outline boxes represent datasets (dashed outline) or processes (plain outline). Step 16 can be considered to become the precursor to step 1 once all steps are completed.

5.3.2 | 3 Historic management

While there is little data on long term management effects (*see, 5.3.3*) on the environment (Chazal and Rounsevell, 2009), in the UK this is changing with the likes of the GMEP and ERAMMP (Emmett, Alexander, *et al.*, 2016; Emmett *et al.*, 2017). Further, while the UK statutory authorities lack data on the success of past AES, old policy and AES documentation does provide information on management prescriptions e.g. Rose (2011); Welsh Government (2016); Rural Payments Agency (2022b). The lack of consistent monitoring of past AES (since their inception in the nineteen-eighties) is, however, a real and serious knowledge gap and oversight by past administrations.

Cumulatively, however, these datasets and information combined with literature reviews of academic research into land management effects can provide (in combination with step 2, **Fig. 5.2**), evidence for improving AES design. This thesis provides an example of having achieved this aspiration for a focussed suite of management interventions.

5.3.2 | 4 Historic analysis & summary

The purpose of step 4 is to compile and summarise information to provide an evidence base for AES design in line with Defra's evidence based policy, policy (Defra, 2011). Therefore, informing step 10 along with step 8 & 9 (**Fig. 5.2**).

5.3.2 | 5 Habitat baseline data

To provide an actual baseline (rather than any proxy space-for-time or chronosequence use, it would be possible to construct from the data in step 4), a field campaign to survey representative landscape and management types to be covered by the AES as well as control non-AES land, is needed. This dataset generated provides the first point in a timeseries as a baseline, forming a robust start point from which to monitor change (L. R. Walker *et al.*, 2010). Examples of project representatives of this can be found in *1.6.1.11* .

However, the information from step 4 can give insights into prior expectation of AES outcomes especially when used for prediction as in step 9.

5.3.2 | 6 Management baseline data

Currently practiced management (as defined in, **Fig. 5.2**) both in and outside AES schemes will also need to be a requirement of baseline data gathering. This is because management preceding AES implementation or conducted separately from it, will provide useful comparators when tailoring AES to by site level implementation (**Fig. 5.2**). Data gathering for this is likely to require major engagement with land-managers across multiple sectors at the same scale as step 5.

5.3.2 | 7 Baseline analysis & summary

Compilation of the data from steps 5 & 6 (**Fig. 5.2**) provides data that can be used to evidence AES design as well as providing data to start step 9.

5.3.2 | 8 Baseline monitoring summary

Evidence compilation from all prior steps. This informs on the impact of past management, the state of ecosystems at the time of baseline survey; and therefore what AES should try to achieve, as well as evidencing AES design.

5.3.2 | 9 Predicting management effects

Predicting the outcomes of AES by statistical modelling and expert opinion using inputs from steps 1-8. This will manage the expectation of policy makers and land-managers alike and give insight into possible outcomes of the AES prescriptions to be implemented.

5.3.2 | 10 Evidence based AES implementation

Roll out of management prescriptions design using evidence from steps 8&9 (**Fig. 5.2**). Here, a site-level management prescription is emphasised as each land parcel under AES will have a different contextual environmental setting that should be accounted for to maximise AES prescription effects.

5.3.2 | 11 Post AES management data

Post the roll out of an AES scheme, data on the number of participants, landscape and ecosystem types involved, and actual AES option implemented by land-managers will narrow expected outcomes, again informed by steps 8&9 (**Fig. 5.2**). Here GMEP (Emmett *et al.*, 2017) provides an example of steps 5-7 and ERAMMP (Emmett, Alexander, *et al.*, 2016) steps 11-13 (*see, 1.6.1* , for further details on GMEP and ERAMMP).

5.3.2 | 12 Habitat monitoring post AES

Step 12 (**Fig. 5.2**) is a second field campaign to survey representative landscape and management types covered by the AES as well as resurvey of the control non-AES land. This provides a time 1 as a continuation of step 5 (a second iteration of steps 1-16 would provide a time 2 etc.; **Fig. 5.2**).

5.3.2 | 13 Monitoring summary post AES

A summary of the complied data from the timeseries generated by steps 5-8 and 10-13. This provides a robust outcome post AES management with background changes that can be unpicked from the control surveys. This does not only determine the success of AES but also informs on better and worse design components. A dataset of this level of spatial and temporal detail for land management does not exist in the UK, although this is expected to change with the completion of ERAMMP (*see, 1.6.1.11*).

5.3.2 | 14 Predictions accuracies

Informed by the data and evidenced from step 13, the accuracy of the predictions can be determined, and further predictions can be improved for step 15 (**Fig. 5.2**).

5.3.2 | 15 Re-prediction

Reworking of prediction techniques to improve on or remove errors from those in step 9 (**Fig. 5.2**), evidenced by steps 13 and 14. This is to be combined with step 13 to inform step 16.

5.3.2 | 16 Repeated AES development

The final step in the cycle would be to reflect on multiple years of AES development that should result in, well evidenced, robust and pragmatic, bespoke to location, AES design. This needs to be a cyclical process for continued robust design with new iterations required due to on-going global change and any development of new technologies. Hence the linking of step 16 back to 1 in **Fig. 5.2**.

5.3.3 | Long-term ecological monitoring data

The desk-based study of ecological data in "5.3.2 | 1" above as well as the environmental change models for soil and vegetation fertility change in *Chapters 2, 3 & 4* are good representations for the need for long term ecological data. This is required both within stable ecosystems e.g. the Environmental Change Network with long-term monitoring established at sites with constant ecosystem management (Tso *et al.*, 2021) and within more anthropogenically managed or disturbed ecosystems e.g. Rothamsted (Rothamsted Research, 2016) or the Newcastle University's research farm (Kidd *et al.*, 2017). Finding such sites with relevant data has been challenging throughout this work and De Chazal &

Rounsevell (2009) has also noticed the lack of long term ecological data on management effects. However the Ecological Continuity Trust website's "sites" page (https://www.ecologicalcontinuitytrust.org/sites) was a valuable starting resource for finding long term land management based ecological monitoring datasets within this work (Ecological Continuity Trust, 2020).

A further point of concern involves the length of time for ecological cycles to run their course, for example many tree species live for centuries (e.g. the *Quercus robur* stand in Pitman *et al.* (2014)) covering multiple human generations. Further, biogeochemical processes can take even longer e.g. the N cycle Fowler *et al.*, (2013). Given this and the timescale and theoretical insights in, figure 1 in Colwell and Rangel (2009): an example of a 100,000 year climatic cycle effecting species abundance's depending on their niche conservatism or adaptation strategies; what we currently define as long term data is inadequate in the context of long term environmental processes. While this is mitigated by paleoecology or historical environmental science techniques, with example including: dendrochronology (e.g.: Jansma *et al.*, 2012; Solomina *et al.*, 2022); sediment pollen records (e.g.: Rackham, 1980; Seppä and Bennett, 2003); ice core atmosphere composition (e.g.: Wolff, 2011; Bauska, Marcott and Brook, 2021); it is still the case that any timeseries data started now is only likely to increase in value into the future. With the likes of the Rothamsted Broadbalk Wheat Experiment being the longest continuously running agricultural experiment in the world (Fan *et al.*, 2008). It would be beneficial not only for ecological science but also society, for global change mitigation insights if experiments of this timescale became more frequent across more biomes, ecosystems and natural resource management systems. The likes of government AES (for example the approach in *5.3.2*) could help provide this data.

5.4 | Hectares not words: Big data in ecology to landscape scale restoration

A key component of sustainable land management research is the application or delivery of its findings to policy and practitioners. This exemplifies the on the ground impact of environmental science research being as important as its findings (Lavery *et al.*, 2021). The novelty and utility of the work in this thesis concerns the application of established predictive methodological tools across wider spatial and temporal scales than previously used and inclusion of global change factors. However, sustainable land management research does not often tackle the actual pragmatics of implementation at the scales required for change (regional and up). The following discussion aims to outline how nature-based solutions (IUCN, 2020) could be applied to actual land holdings for transformative change (Díaz *et al.*, 2019). While novel research into mitigating or reducing environmental issues is admirable, a substantial amount of ecological restoration is achievable through pragmatic implementation of established science. This can be alternatively phrased as: focusing on hectares of restored habitat rather than words on novel research, although the two are partly congruent here.

However, there is a varying level of political and practitioner willingness to pursue this due to economic complexity or (lack of) ease of implementation reasons (Arnott *et al.*, 2018, 2019). However, if these socioeconomic reasons can be surpassed (Cortina-Segarra *et al.*, 2021) especially at landscape scales, then transformative change could be achieved. An example of who this may be achieved by outside of governance is nature conservation organisations. This is because they often have, at the scale's needed, the economic, pragmatic and willingness, required. The Landscape Partnership's (TLP), landscape-scale conservation workshop (The Future of Landscape-scale Conservation in Europe workshop, 2015; The

Landscape Partnership, 2018) is an example of this. This at-scale conservation partnership concept is progressed here into an ‘ecological pipedream’ aimed at achieving ecological transformative change across the hectares owned by The Landscape Partnership’s members.

With UK forest cover being amongst the lowest in Europe and its habitats continually reported as being degraded, the need for at-scale ecological restoration is widely acknowledged (The Future of Landscape-scale Conservation in Europe workshop, 2015; Hayhow *et al.*, 2019; Forest Research, 2020). The four main organisations involved in the TLP workshop (The Future of Landscape-scale Conservation in Europe workshop, 2015): RSPB (Royal Society for the Protection of Birds), The Wildlife Trusts (WTs), National Trust (NT), The Woodland Trust (TWT), represent the major conservation organisations in the UK and in combination the major land holder (The Landscape Partnership, 2018). This also means they have the greatest capacity (economic, pragmatic and willingness) and land to achieve landscape-scale ecological restoration. While all of these four have strategies to achieve this individually (e.g. National Trust, 2022), the TLP appears to have been the only attempt to achieve this a as a networked partnership. However, the NT has conducted some work following the ”right tree in the right place” philosophy, this is a good restoration example: identify land where tree planting would not have a large impact on existing land-use or other nature conservation efforts by mapping and modelling these to locate sites where minimum or no trade-offs are needed for planting to take place (Halls and Heard, 2021; National Trust, 2021, 2022). This identification of suitable land is a common crux of wide scale ecological restoration efforts (Di Sacco & Hardwick *et al.*, 2020) but a progression of the TLP by, RSPB, WTs, NT and TWT could overcome this. The next step after identifying land, with the approach of the NT (Halls and Heard, 2021; National Trust, 2021, 2022) being exemplar, is to target specific ecosystems which can be restored towards to: compliment

historic conditions and land use as well as ecosystem service provisions. This conceptual approach is tailored towards a nature-based solutions (NbS) approach (IUCN, 2020; Stafford *et al.*, 2021), using ecosystems processes to mitigate global change and increase ecosystem service provision.

The considerations of site histories to aid restoration efforts is another aspect where both the UK and the four organisations mentioned have an advantage, baseline data and long-established classifications and surveys. These provide a wide variety of options to the four conservation organisations to consider at the local to national level for starting conditions to improve landscape condition.

These environmental information sources include:

1. National long term UK datasets such as: the Countryside Survey (Carey, Wallis, Chamberlain, *et al.*, 2008; Bunce *et al.*, 2014; Emmett, Reynolds, *et al.*, 2016), Botanical Society of Britain and Ireland vegetation records (Walker *et al.*, 2010; BSBI, 2018); UK Soil Observatory (Lawley, Emmett and Robinson, 2014); can provide site data or proxy site data (where data is lacking locally) that can inform on starting points for possible habitat trajectories.
2. The UK is fortunate to have established plant community types in the form of the National Vegetation Classification (NVC, Rodwell, 1998). This provides a wide range of target plant communities that management can move toward or away from dependant on local (to national) management and manager goals (set by RSPB, WTs, NT or TWT on their land holdings).
3. The four organisations have their own internal environmental datasets and land use histories, both empirical and anecdotal. Also, within the organisation's staff, the institutional knowledge likely to be held is valuable for adapting to local conditions.

It should be noted that the combination of: historic environmental conditions; baseline data; target habitat types within the NVC, does not assist with continuing land use or ecosystem service provision. The progression of this on from the baseline date sourcing (in 1-3 above) would be to explore possible ecosystem service provision within NVC community units.

While this connection has not been made, methodologies to connect environmental variables and vegetation directly to ecosystem services does exist (Lavorel *et al.*, 2011; Grigulis *et al.*, 2013; Kohler *et al.*, 2017). Examples of this within grasslands conducted by the Laboratoire d'Ecologie Alpine in Grenoble include: ecosystem service mapping across differing land use types (trajectories) using plant functional traits and soil variables to map ecosystem service hot and cold spots in Lavorel *et al.* (2011); also using sites measured plant and microbial functional properties to gain models of ecosystem service production within Grigulis *et al.* (2013); also Kohler *et al.* (2017) used data and models from these studies for predicting different habitat trajectories and potential ecosystem service provision. This approach could be adapted to make ecosystem service provision estimates for NVC community units when used in combination with the Countryside Survey datasets (Carey, Wallis, Chamberlain, *et al.*, 2008; Bunce *et al.*, 2014) where more botanical and soil data is needed. Field survey proportionally representative of the land to undergo restoration will still be needed to gain plant trait data (and soil data where it is lacking), to account for where local conditions differ from proxy baseline data.

This so far provides: suitably resourced organisations able to take on restoration efforts (the four conservation organisations); a range of habitats to aim restoration efforts at (the NVC); baseline data from which to predict suitable target habitats (national monitoring datasets and the organisation's internal data); and while a research gap, the connection between NVC community units to ecosystem service provision to compliment local land use and management goals. This staged process provides a conceptual but possible approach to achieving transformative change at a landscape scale using a NbS approach (restoration toward specific NVC units) to both mitigate global change and assist in sustainable ecosystem service provision.

The above provides a brief conceptual overview of a large-scale complex restoration effort. The following attempts to outline a staged methodology of the work required to attempt this:

i. Identification of land for restoration by TLP members and local mangers and desired land use and ecosystem service requirements. This should lead to establishment of clear end goals for land selected.
ii. Baseline (or proxy baseline) data taken from national monitoring datasets with data geographically near to the selected site. Alternatively (or additionally), taking site baseline data (botanical and soil data) where it is lacking locally in the national datasets.
iii. Identification of which NVC habitats are likely to establish under the local conditions and the land-managers goals. Also, identification of species lacking in the local species pool that will need to be sourced for restoration efforts.
iv. Determining the frequencies (or proxy for abundance) of species in the baseline and the target vegetation to estimate ecosystem service provision. This ties the approach of Kohler *et al.* (2017) to determine potential ecosystem service provision, via community weighted mean calculations of traits (Lavorel *et al.*, 2008) to the established frequencies within the NVC unit communities (Rodwell, 1998).
v. Identification of multiple end points to allow for dynamic decision making for a pragmatic approach to evolving conditions for flexible management.
vi. National site strategies for local staff and managers within TLP member organisations to implement on the ground restoration efforts.
vii. Following the above restoration efforts, continued monitoring and management will be required at the decadal timescale to both ensure end goals are reached and to account for changing conditions e.g. under global change.

The modelling methodologies applied through out this thesis provide a suite of examples for the above. This provides some proof that at least the desk-based work required to achieve *i.* to *iv.* above is possible. The fine resolution data used to model species responses to management change alongside the predictions used for MultiMOVE's input data to represent global change in the analysis chapters can be applied to provide for *ii.* to *v.* in the above.

While the text here does little to emphasise the scale and number of hectares this could be applied across, it is important to acknowledge the difficulty of the task. Although a conceptually promising avenue to mitigate global change, the amount of further work and trade-offs needed to achieve this is huge. It would also require a very significant buy-in from the partnership and organisations described.

However, if this partnership for pragmatic implementation could be achieved it would be a nature-based solutions approach to ensure ecosystem service provision and mitigate global change, achieving transformative change at a near-national scale.

5.5 | Conclusion

The findings here which concern the applied exploration of AES via modelling can be summarised as a recommendation to fund longer and stronger prescriptions to ensure the interventions achieve their goals (*see, 5.1.1*). It is arguable that the ecological and environmental science to inform good AES design and implementation is already in existence. Thus, given the data availability and long-standing ecological research history within the UK, novel findings are, that despite evidence of good practice being possible, our current management is often insufficient. Therefore, the wider suggestion to improve AES delivery is regular monitoring and evaluation to inform ongoing adaptation-based design for global change (*e.g. 5.3.2* and **Fig. 5.2**).

Areas for future work should include the increase and improvement of long-term ecological monitoring not only for informing on environmental change and its drivers but, specifically for effective sustainable land management. A major area for future (at scale) ecological restoration and research efforts could be the application of big data techniques providing

land-managers with well evidenced management prescriptions suited to their own goals and local sites. A grassroots level up but widescale approach like this could provide the restoration forests and grasslands need.

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A | Appendix A. Supporting information and data for Chapter two and three

A.1 | Appendix A: Description of grassland Broad Habitat Types

The three broad habitats, improved grassland, neutral grassland and acid grassland are described in Jackson (2000). During the baseline Glastir Monitoring and Evaluation Programme (GMEP) survey areas of land were assigned to these three broad habitats among others using a vegetation key available online at: http://nora.nerc.ac.uk/id/eprint/5194/1/N005194CR.pdf.

The top 10 most common species in quadrats surveyed in GMEP and assigned to each broad habitat were as follows:

- **Improved grassland:** *Lolium perenne, Trifolium repens, Ranunculus repens, Holcus lanatus, Cerastium fontanum, Taraxacum agg., Poa trivialis, Agrostis capillaris, Poa annua, Rumex obtusifolius*
- **Neutral grassland:** *Holcus lanatus, Agrostis capillaris, Trifolium repens, Lolium perenne, Ranunculus repens, Cerastium fontanum, Anthoxanthum odoratum, Taraxacum agg., Cynosurus cristatus, Rumex acetosa*
- **Acid grassland:** *Rhytidiadelphus squarrosus, Galium saxatile, Anthoxanthum odoratum, Festuca ovina, Agrostis capillaris, Potentilla erecta, Deschampsia flexuosa, Pleurozium schreberi, Vaccinium myrtillus, Hylocomium splendens*

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A.2 | Appendix A: Downscaled climatic variables.

The 1 km climate variables for future projections were taken from a single member (01) of the CHESS-SCAPE ensemble (Robinson *et al.*, 2022). This was downscaled from the corresponding member (01) of the UKCP18 regional climate model perturbed parameter ensemble (RCM-PPE) (Met Office Hadley Centre, 2018). This is an ensemble of RCM variants, nested within perturbed parameter variants of the HadGEM3-GC3.05 global climate model (GCM) (Murphy *et al.,* 2018). This nesting allows better projection of the dynamics of regional UK and European climate without the prohibitive computational cost of running the model globally at the high resolution. Ensemble member 01 uses the default model parameters (Murphy *et al.,* 2018) and CO^2 concentrations prescribed by RCP8.5 (van Vuuren *et al.*, 2011). The RCM-PPE data are distributed at 12 km resolution. To produce CHESS-SCAPE, these were then downscaled to 1 km using an adapted version of the CHESS methodology (Robinson *et al.*, 2017), which interpolates variables to a finer resolution while adjusting for local topography using physically-based and empirical methods (Robinson *et al.*, in prep.). The resulting files cover the UK land surface, but exclude Shetland due to data availability. Variables were reduced from the grid box elevation of the climate model to mean sea level, interpolated from 12 km to 1 km, then readjusted to the elevation at 1 km resolution given by the Integrated Hydrological Digital Terrain Model (IHDTM) (Morris *et al.*, 1990). Daily mean, minimum and maximum air temperatures were adjusted using a lapse rate of -0.006 K m^{-1} (Hough & Jones, 1997), and the interpolation was carried out separately for each variable. Rainfall was not interpolated but was adjusted for long-term averages in local rainfall rates using a 1 km resolution map of Standardised Area Average Rainfall (Spackman, 1993). In this study we use the climate projection without bias-correction.

The RCM-PPE has a strong climate sensitivity and is at the high end of the range of the CMIP5 ensemble, but it is consistent with the current generation of climate models in CMIP6 (Lowe *et al.*, 2018), particularly the related model HadGEM3-GC.3.1 (Williams *et al.*, 2017). Although the overall trend is for warming temperatures, the interannual variability of the climate model projection is such that 2029 is cooler than 2026. Additionally, there was a particularly warm period in the climate model projection from 2017 to 2027, which resulted in 2026 being outside of the baseline range. While this is unusual, it is consistent with climate variability. The projected trend in rainfall is for an overall decrease in mean annual rainfall by 2080 (with an increase in winter rainfall but a bigger decrease in summer rainfall), although there is little change by the end of the study period (Murphy *et al.,* 2018). Again, interannual variability can be seen with higher rainfall in 2021 and 2026, followed by lower in 2029.

A2.1 | Modelling into future climate space unknowns

Given the substantial unknowns of attempting this type of work into the future under global change the ecological modelling community has a challenge to achieve reliable predictions regardless of the methods used (Williams *et al.*, 2017; Williams *et al.*, 2007; Veloz *et al.*, 2012; Smith *et al.*, 2013; Fitzpatrick & Hargrove, 2009). Considering novel environmental space occurrence into the future, we do not attempt to predict climate effects on biogeochemical processes here e.g. carbon priming effects (Smith *et al.*, 2013) as we restrain consideration of results to those that do not fall outside MultiMOVE operating space thus is not expected to be impactful. A greater concern maybe that early successional or disturbed ecosystems are at greater risk to climate change impacts (Kröel-Dulay *et al.*, 2015) this maybe be mitigated by consideration of species beyond natives but that are likely to be ecological functional and non-damaging e.g. tree species examples in Read *et al.* (2009).

A.2 | References

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A.3 | Appendix A: Ellenberg indices neural network calibration

MultiMOVE accepts Ellenberg indices as inputs. These convey the ecological position of the soil and vegetation along gradients of soil moisture, fertility and pH (MultiMOVE species niche viewer Shiny app here https://shiny-apps.ceh.ac.uk/find_your_niche/). Because we were interested in how changes in soil conditions change habitat suitability for the plant assemblage we constructed neural network models that could predict mean Ellenberg indices from measured or modelled soil variables. The latter step was achieved by constructing a model per abiotic gradient where the predictors were the soil measurements from the 5% of the training data for MultiMOVE that comprised fine resolution joint recording of soil and plant species composition. These co-located samples came from a high quality unbiased and representative sample of British vegetation types (Carey *et al.*, 2008; Smart *et al.*, 2010). Models were tuned, trained and tested using the neural network R package (Ripley, 1994). Predictors were standardised by their range to vary between 0 and 1 and the data split at random into 70% training and 30% testing.

The neural network method was chosen because we were interested in constructing the predictive model with the greatest accuracy but based on a small set of predictors all with strong ecological justification for their inclusion. Given the possibility of overfitting we tested the transferability of each model by compared the predictions from the final neural networks against a similarly designed but totally separate survey of soil and vegetation carried out across Wales between 2013 and 2016.

The below is an R markdown filed included here from supplementary material in West *et al.* (no date) to provide the method and code for the neural network construction, titled:

Creating neural network models that translate soil variables into mean Ellenberg values

S. Smart, 23/06/2021

Aim

Here we build models to produce estimates of mean Ellenberg values for soil moisture, pH and fertility given soil %C, %N and gravimetric moisture. A re-working could usefully add in canopy height too as we know shade is a also an influential filter on the way the species assemblage responds to other abiotic gradients.

Building the Neural Networks

The code below derives a new calibration of mean Ellenbergs given soil data. The resulting neural network models can then be applied in predictive mode given new soil inputs. To build the models we use the Countryside Survey 2000 dataset of mean Ellenberg scores based on plant species composition (not weighted by cover/abundance) and co-located soil data that were used to produce the first set of transfer functions reported in Smart et al (2010).

We train models on a random 70% and test on a random 30% of the data. First we need to carry out a sensitivity analysis to determine the best number of hidden layers to use in our black-box models. We selected neural networks because we have less interest in the form of the regression relationships between predictors and response but more interest in generating a model that can best fit training and new independent test data. The last step is critical because we need to ensure transferability to new areas and samples.

Some of the following code was modified from: http://www.michaeljgrogan.com/neural-network-modelling-neuralnet-r/

How many hidden layers and neurons do we need?

"There are some empirically-derived rules-of-thumb, of these the most commonly relied on is 'the optimal size of the hidden layer is usually between the size of the input and size of the output layers'. Jeff Heaton, author of 'Introduction to Neural Networks in Java' offers a few more. In sum, for most problems, one could probably get decent performance (even without a second optimization step) by setting the hidden layer configuration using just two rules: (i) number of hidden layers equals one; and (ii) the number of neurons in that layer is the mean of the neurons in the input and output layers."

So here, we experiment with 1 or 2 hidden layers and with 2 or 3 neurons in the first layer. See here for further information

https://stats.stackexchange.com/questions/181/how-to-choose-the-number-of-hidden-layers-and-nodes-in-a-feedforward-neural-network

```
library(neuralnet) # NOTE THAT 'COMPUTE' HAS BEEN REPLACED WITH 'PREDICT'
library(caTools)
library(dplyr)
library(haven)
library(ggplot2)
```

Loop to select best Neural network model based on different number of neurons and hidden layers and using a number of measures of model performance.
The search for the best model is done separately for each mean Ellenberg score.

```
## Build the best models
Soils_and_Ebergs98<- read.csv("C:\\CS98_input.csv")
```

Independent testing against data from the Welsh GMEP survey carried out between 2013-'16

Here we compare the predictive performance of the original GBMOVE equations in Smart et al (2010) with the hopefully better performance of the neural networks.
We do each Ellenberg score in sequence as follows:

1. Ellenberg Wetness scores:

```
#load NNet models
   load(file =
\C:\\simon\\UKSCAPE\\UKSCAPE_IMP\\Updated_Ellenberg_calibration\\nn_EbW.rda\)

   #Read GMEP data for model testing
   GMEP<-
read.csv(\C:\\simon\\UKSCAPE\\UKSCAPE_IMP\\Updated_Ellenberg_calibration\\Test_gm
ep_soils_bergsx1.csv\)
   Test<-GMEP[,c(4,13,10,9,11)]

   # Calculate Ebergs based on GBMOVE calibration formulae

   Test$GbmW <- (log((Test$MC/(100-Test$MC)))+3.27)/0.55

   # Examine
   plot(Test$GbmW, Test$EbW)
   # Delete NAs and preds outside range

   Test1<-subset(Test, GbmW<=12 & GbmW>=1)
   plot(Test1$EbW, Test1$GbmW)

   # Now solve using NNet

   #MAX-MIN NORMALIZATION
   normalize <- function(x) {
     return ((x - min(x)) / (max(x) - min(x)))
   }
   normTest <- as.data.frame(lapply(Test1, normalize))

   # Compute Predictions off Test Set
   predicted.EbW.values <- compute(EbW, normTest[2:5])
```

```
   results <- data.frame(obs = Test1$EbW, GLM_EbW=Test1$GbmW, prediction =
predicted.EbW.values$net.result)
   # Note here that the back-transformation requires the values of range and min
from the
   # original dataset used to create the neural net - see below for a list of
these.

   results$predicted<-(results$prediction * 4.866667) + 4.333333

   # Now calculate the separate diagnistic stats. Needed for each comparison of
   # obs v GLM_Eb* and obs v predicted

   results$GLM_deviation<-((results$obs-results$GLM_EbW)/results$obs)
   results$GLM_abs_deviation<-(results$obs-results$GLM_EbW)

   GLMmEb_diff=mean(results$GLM_abs_deviation)
   GLMaccuracy=1-abs(mean(results$GLM_deviation))

   results$NN_deviation<-((results$obs-results$predicted)/results$obs)
   results$NN_abs_deviation<-(results$obs-results$predicted)

   NNmEb_diff=mean(results$NN_abs_deviation)
   NNaccuracy=1-abs(mean(results$NN_deviation))

   GLMaccuracy
   GLMmEb_diff
   NNaccuracy
   NNmEb_diff

plot(results$obs, results$predicted)
plot(results$obs, results$GLM_EbW)
```

```
|                                                  | Neural Nets | GLM (Smart et
al 2010) |
|--------------------------------------------------|-------------|----------------
--------|
| \% agreement pred v observed                     | 0.96        | 0.86
|
| Mean deviation in Ellenberg scores (obs v pred) | 0.30        | 0.79
|
```

Higher accuracy with the Neural network and much lower average absolute difference in mean Ellenberg values such that the difference between obersved and predicted is on average 0.3 of an Ellenberg unit.

```
## 2. Ellenberg N scores:

#load NNet models
```

```
load(file = "nn_EbN.rda")

#Read GMEP data for model testing
GMEP<- read.csv("Test_gmep_soils_bergsx1.csv")
Test<-GMEP[,c(2,13,10,9,11)]

# Calculate Ebergs based on GBMOVE calibration formulae

Test$GbmN <- exp(0.7751 - (0.00006*Test$MC) - (0.00009*(Test$MC^2)) -
(0.01475*Test$C) + (0.000099*(Test$C^2)) + (0.2639*Test$pH)
                    - (0.01684*(Test$pH^2)) + (0.1908*Test$N))

# Examine
plot(Test$GbmN, Test$EbN)

# Now solve using NNet

#MAX-MIN NORMALIZATION
normalize <- function(x) {
  return ((x - min(x)) / (max(x) - min(x)))
}
normTest <- as.data.frame(lapply(Test, normalize))

# Compute Predictions off Test Set
predicted.EbN.values <- compute(EbN, normTest[2:5])

results <- data.frame(obs = Test$EbN, GLM_EbN=Test$GbmN, prediction =
predicted.EbN.values$net.result)
# Note here that the back-transformation requires the values of range and min
from the
# original dataset used to create the neural net - see below for a list of these.

results$predicted<-(results$prediction * 6.083333) + 1.166667

# Now calculate the separate diagnistic stats. Needed for each comparison of
# obs v GLM_Eb* and obs v predicted

results$GLM_deviation<-((results$obs-results$GLM_EbN)/results$obs)
results$GLM_abs_deviation<-(results$obs-results$GLM_EbN)

GLMmEb_diff=mean(results$GLM_abs_deviation)
GLMaccuracy=1-abs(mean(results$GLM_deviation))

results$NN_deviation<-((results$obs-results$predicted)/results$obs)
results$NN_abs_deviation<-(results$obs-results$predicted)

NNmEb_diff=mean(results$NN_abs_deviation)
NNaccuracy=1-abs(mean(results$NN_deviation))
```

```
GLMaccuracy
GLMmEb_diff
NNaccuracy
NNmEb_diff

plot(results$obs, results$predicted)
plot(results$obs, results$GLM_EbN)
```

	Neural Net's	GLM (Smart et al 2010)
% agreement pred v observed	0.88	0.85
Mean deviation in Ellenberg scores (obs v pred)	-0.25	-0.29

Neural network model outperforms the GLM on both counts but there is less to separate them than for the Ellenberg W models above.

3. Ellenberg R (pH) scores

```
#load NNet models load(file = "nn_EbR.rda")

#Read GMEP data for model testing\
GMEP<- read.csv("Test_gmep_soils_bergsx1.csv")
Test<-GMEP[,c(3,13,10,9,11)]

# Calculate Ebergs based on GBMOVE calibration formulae

Test$GbmR <- 0.5293 - (0.02503*Test$MC) + (1.665*Test$pH) - (0.1061(Test$pH^2)) -
(0.00566*Test$C)

# Examine

plot(Test$GbmR, Test$EbR)

# Now solve using NNet

#MAX-MIN NORMALIZATION normalize \<- function(x) { return ((x - min(x)) / (max(x)
- min(x))) } normTest \<- as.data.frame(lapply(Test, normalize))

# Compute Predictions off Test Set

predicted.EbR.values <- predict(EbR, normTest[2:5])
```

```
results <- data.frame(obs = Test$EbR, GLM_EbR=Test$GbmR, prediction =
predicted.EbR.values$net.result)

# Note here that the back-transformation requires the values of range and min
from the  original dataset used to create the neural net - see below for a list
of these.

results$predicted<-(results$prediction * 5.25) + 2

# Now calculate the separate diagnistic stats. Needed for each comparison of

# obs v GLM_Eb\* and obs v predicted

results$GLM_deviation<-((results$obs-results$GLM_EbR)/results$obs)
results$GLM_abs_deviation<-(results$obs-results$GLM_EbR)

GLMmEb_diff=mean(results$GLM_abs_deviation) GLMaccuracy=1-
abs(mean(results$GLM_deviation))

results$NN_deviation<-((results$obs-results$predicted)/results$obs)
results$NN_abs_deviation<-(results$obs-results$predicted)

NNmEb_diff=mean(results$NN_abs_deviation) NNaccuracy=1-
abs(mean(results$NN_deviation))
GLMaccuracy
GLMmEb_diff
NNaccuracy
NNmEb_diff

plot(results$obs, results$predicted)
plot(results$obs, results$GLM_EbR)
```

	Neural Net's	**GLM (Smart et al 2010)**
% agreement pred v observed	0.90	0.84
Mean deviation in Ellenberg scores (obs v pred)	-0.28	-0.41

The range of the GLM predictions is substantially narrower than observed values although accuracy does not differ much hugely compared to the neural network largely because of the residual variation around the observed values between EbR = 3 and 5. However, on balance the neural network is again better. The neural network predictions also have a much lower average absolute difference from the observations.

A.3 | References

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A.4 | Appendix A: Modelling change in soil variables given management intervention

Determining how soils change in response to management was done via constructing generalized linear mixed-effects models trained on data gathered from literature review where the effects of interventions on soil variables had been measured over time and where interventions could be equated with the AES options that were the focus of our study.

The use of biogeochemistry models to dynamically process the impact of management change was not adopted because the necessary soil measurements do not exist for each modelled location. Using average inputs coarsely resolved to larger grid squares and dominant soil type would have greatly decreased the accuracy and realism of the modelling process removing the benefit of filtering the observed plant species composition at our very high-resolution sampling sites. The four soil variables (C, N, pH, moisture) were also modelled independently of each other as no study measured all these variables together over long enough time periods. Hence, our results are strongly dependent on the representativeness of the studies selected from literature review and the realism of the

modelled change in each variable. A consequence is that we derived separate empirical models for each variable even though in reality we know they respond as an intercorrelated complex. To some extent, the lack of such long-term fundamental datasets is surprising. Despite a number of long-term experiments existing across the UK and ecological science being an endeavour that is at least 200 years old there is a lack of fundamental information on long-term soil and vegetation changes in response to human management. This is notable in the literature with many studies relying on chronosequences and space-for-time differences in habitats and management. Despite data availability falling short of the representativeness and redundancy we would have liked for our three habitat types, a clear benefit is that the models created here summarise changes in soil conditions that have been observed to result from management intervention on soil and vegetation starting points that equate with the soils and vegetation of the GMEP baseline. Readers can therefore inspect the underlying data and assess the representativeness of the observations and the robustness of the estimated soil changes.

A.4.1 | Literature sources

Care was taken to closely match the methods of each study found during literature review to the GMEP methods or ensure data values could be converted to match. Non-UK studies were omitted. This search resulted in datasets of varying size as requests were made to study authors to provide full datasets but not always yielded, and also including relevant open access data; these are:

- Project supplementary material from grassland restoration from arable (Pywell *et al.*, 2007)
- UK Department for Environment, Food and Rural Affairs (Defra) report (Wagner *et al.*, 2014)
- Rothamsted Research, Park Grass long-term experiment data (Rothamsted Research, 2016)

- Project on restoration from farmland (Pywell, Webb, & Putwain, 1994)
- Full data set provided by author from Marrs *et al.*, (2018).
- Summary data published in McGovern *et al.*, (2014).
- Defra project on managing grassland diversity (Defra, 2015)
- Elan Valley grasslands report (Hayes & Lowther, 2014)
- A 12-year fertiliser and lime experiment, supplementary material from (Kirkham, Dunn, Tallowin, Bhogal, & Chambers, 2011)

A.4.2 | Data categorisation and model construction

Data was categorised in two ways in order to ensure robust fitting to scenarios; by management strategy derived from the practices described in the study and management intensity level. The two data categorisation types were used as insufficient data on nitrogen was found for it to be modelled per management category.

The levels of management intensity were:

- High (H, with constant or near constant grazing or with at least annual cutting and chemical/organic fertiliser application to the land)
- Medium (M, intermittent grazing and cutting and minimal to no fertiliser application)
- Low (L, treatments with very low grazing density (<6 animals ha^{-1} or 0 ha^{-1}) with no fertiliser applications in an upland environment)

The management categories were defined as:

- Mid-intensity management with intermittent grazing and cutting and minimal chemical/organic fertiliser application to the land (MIG)
- Extensification management with intermittent grazing and cutting with no applications (EA)

Table A.1. Below summarises the data in the categories, the number of data points taken from the data matched as the values at 0 years.

Intensity or Management	No. of studies	No. of data points	No. of studies with pH	No. of pH data points	No. of studies with total carbon	No. of total carbon data points	No. of total nitrogen data points	No. of studies with total nitrogen
All	10	260	9	158	6	95	6	71
High intensity	5	100	4	82	3	42	3	43

Medium intensity	8	71	7	39	4	18	5	25
Low intensity	4	89	3	37	3	35	2	3
MIG	5	28	4	22	3	7	3	10
EA	2	32	2	6	0	0	1	4

Models using L and H intensity were not used, as L was atypical and not good representations of an AES option, and H as it did not represent management relatable to typical high intensity agriculture. Level and intensity were assigned per-treatment per-study, where studies used chronosequences data for the cumulative effects of treatments in different parts of the experiment including control plots were used to represent change over time.

Calculating the change in variables was done by subtracting the value at start time (or matched time 0 chronosequence data) with the values at treatment end time and dividing by years duration of the study to give a change of X in a variable per year (delta-X). This approach takes advantage of the correlation between variables within sites. As a result, between-site differences were accounted for by a study site random effect. The delta-X per year change was the variable modelled.

Modelling changes in moisture was attempted but returned values very close to the mean (no change) or impossible values, confirming the decision to hold moisture constant (no change to the observed mean Ellenberg F value) as it is not targeted by management.

Table A.2. Scenario's details. **M** = medium intensity, minimal fertiliser inputs and intermittent grazing; **EA** = extensification management with intermittent grazing and cutting with no fertiliser inputs; **MIG** = mid-intensity management with intermittent grazing and cutting. As ***Low inputs*** and ***Reduced Stocking*** scenarios vegetation height should be reduced to promote plant diversity cover weighted canopy heights were set as follows: **Low** = ~1 CWCH or held constant if observed <1 CWCH at baseline to match management; **High** = set to 2 CWCH or left constant if over 1 CWCH at baseline to match management, (CWCH, 1 = <100 mm, 2 = 101-299 mm). Both M&MIG scenarios included adjustment of vegetation height via cutting or grazing. Two climate states were applied: **H.Clim**=High emissions (RCP 8.5 UKCP18 downscale modelled 1 km); and **B.Clim**=Baseline average climate (1981 to 2016). Model categorical settings: **M** = medium intermittent grazing and cutting and minimal to no fertiliser application; **MIG** = mid-intensity management with intermittent grazing and cutting and minimal chemical/organic fertiliser application to the land; **EA** = extensification management with intermittent grazing and cutting with no applications. The **Glastir options** represent nearest matches as the model construction data could not be directly matched to their exact management prescriptions.

Scenario	Management	Glastir options (nearest match)	Soil models categorical setting	Recovery from acidification applied	Scenario versions	Years modelled
Baseline	Observations from the GMEP survey.	NA	None	No	Observed climate averaged (1981 to 2016).	2016
Low inputs (LU)	Management using a reduced amount of fertiliser application, with sward height managed to promote plant diversity.	15b, 15d	All: M	Yes	Low, B.Clim; Low, H.Clim; High, B.Clim; High, H.Clim	2021,2026,2029
Reduced stocking	Grassland with a reduced number of livestock, with sward height managed to promote plant diversity.	41a, 41b & 411	Carbon and pH: MIG nitrogen: M	Yes	Low, B.Clim; Low, H.Clim; High, B.Clim; High, H.Clim	2021,2026,2029
No inputs	No chemical inputs applied.	15a	pH: EA Carbon and nitrogen: M	Yes	B.Clim; H.Clim	2021,2026,2029

A.4.3 | Model construction and formula code

Model 1, for Delta pH per year by management type:
Formula: Change in pH per year ~ (Management category * pH value at start) + random effect for study. Used for Reduced Stocking and No Inputs scenarios. Ig=MIG.

```
> pHMcatXT0=lmer(YrDelta_pH~(Manage_cat.*pH.Matched.0years)+(1|source.code)
+                ,data=pHdt,REML = T);pHMcatXT0
Linear mixed model fit by REML ['lmerModLmerTest']
Formula: YrDelta_pH ~ (Manage_cat. * pH.Matched.0years) + (1 | source.code)
   Data: pHdt
REML criterion at convergence: -539.4186
Random effects:
 Groups      Name        Std.Dev.
 source.code (Intercept) 0.05401
 Residual                0.02577
Number of obs: 137, groups:  source.code, 8
Fixed Effects:
                      (Intercept)                      Manage_cat.Ig
                           0.7694                            -1.0365
                  Manage_cat.Igna                     Manage_cat.uEx
                          -0.7069                            -0.7926
                pH.Matched.0years    Manage_cat.Ig:pH.Matched.0years
                          -0.1448                             0.1939
Manage_cat.Igna:pH.Matched.0years   Manage_cat.uEx:pH.Matched.0years
                           0.1382                             0.1422
> summary(pHMcatXT0)
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerT
est']
Formula: YrDelta_pH ~ (Manage_cat. * pH.Matched.0years) + (1 | source.code)
   Data: pHdt

REML criterion at convergence: -539.4

Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.8923 -0.4907 -0.0383  0.4754  3.4956

Random effects:
 Groups      Name        Variance Std.Dev.
 source.code (Intercept) 0.002917 0.05401
 Residual                0.000664 0.02577
Number of obs: 137, groups:  source.code, 8

Fixed effects:
                                  Estimate Std. Error        df t value Pr(>|t|)
(Intercept)                        0.76938    0.32765 123.66581   2.348  0.02045
*
Manage_cat.Ig                     -1.03655    0.33129 122.83732  -3.129  0.00219
**
Manage_cat.Igna                   -0.70694    0.33060 122.83293  -2.138  0.03447
*
Manage_cat.uEx                    -0.79257    0.33067 122.62590  -2.397  0.01805
*
pH.Matched.0years                 -0.14477    0.05813 126.15768  -2.490  0.01406
*
Manage_cat.Ig:pH.Matched.0years    0.19394    0.05861 126.29457   3.309  0.00122
**
Manage_cat.Igna:pH.Matched.0years  0.13821    0.05856 126.34836   2.360  0.01980
*
Manage_cat.uEx:pH.Matched.0years   0.14223    0.05863 126.36157   2.426  0.01668
*
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
Correlation of Fixed Effects:
                 (Intr) Mang_ct.Ig Mng_ct.Ign Mng_.E pH.M.0 Mng_ct.Ig:pH.M.0 Mng_
ct.Ign:H.M.0
Manag_ct.Ig      -0.989
Mang_ct.Ign      -0.991  0.986
Manag_ct.Ex      -0.991  0.984      0.985
pH.Mtchd.0y      -0.993  0.982      0.984      0.984
Mng_ct.Ig:pH.M.0  0.985 -0.990     -0.977     -0.976 -0.992
```

```
Mng_ct.Ign:H.M.0  0.985 -0.974     -0.990     -0.977 -0.993  0.985
Mn_.E:H.M.0       0.984 -0.973     -0.975     -0.989 -0.992  0.983            0.9
84
```

Model 2, for Delta pH per year by management intensity
Formula: Change in pH per year ~ (years duration * pH value at start) + management intensity + random effect for study. Used for Low Inputs scenario.

```
> pHYrXT0Ins=lmer(YrDelta_pH~(years.from.origin*pH.Matched.0years)+Intensity+(1|s
ource.code)
+                 ,data=pHdt,REML = T);pHYrXT0Ins
Linear mixed model fit by REML ['lmerModLmerTest']
Formula: YrDelta_pH ~ (years.from.origin * pH.Matched.0years) + Intensity +
    (1 | source.code)
   Data: pHdt
REML criterion at convergence: -502.6846
Random effects:
 Groups      Name        Std.Dev.
 source.code (Intercept) 0.05317
 Residual                0.02886
Number of obs: 137, groups:  source.code, 8
Fixed Effects:
                       (Intercept)                    years.from.origin
                        -0.1227562                            0.0030531
                  pH.Matched.0years                           IntensityL
                         0.0267155                           -0.0572121
                         IntensityM  years.from.origin:pH.Matched.0years
                        -0.0298726                           -0.0005747
> summary(pHYrXT0Ins)
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerT
est']
Formula: YrDelta_pH ~ (years.from.origin * pH.Matched.0years) + Intensity +
    (1 | source.code)
   Data: pHdt

REML criterion at convergence: -502.7

Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.61000 -0.40084 -0.03089  0.64032  2.89936

Random effects:
 Groups      Name        Variance  Std.Dev.
 source.code (Intercept) 0.0028267 0.05317
 Residual                0.0008331 0.02886
Number of obs: 137, groups:  source.code, 8

Fixed effects:
                                      Estimate Std. Error         df t value Pr(>
|t|)
(Intercept)                         -1.228e-01  4.441e-02  7.939e+01  -2.764 0.00
7093 **
years.from.origin                    3.053e-03  1.054e-03  1.283e+02   2.898 0.00
4421 **
pH.Matched.0years                    2.672e-02  7.140e-03  1.301e+02   3.742 0.00
0273 ***
IntensityL                          -5.721e-02  2.518e-02  7.353e+01  -2.272 0.02
6012 *
IntensityM                          -2.987e-02  8.304e-03  1.294e+02  -3.598 0.00
0456 ***
years.from.origin:pH.Matched.0years -5.747e-04  2.057e-04  1.284e+02  -2.794 0.00
6003 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
Correlation of Fixed Effects:
            (Intr) yrs.f. pH.M.0 IntnsL IntnsM
yrs.frm.rgn -0.672
pH.Mtchd.0y -0.874  0.718
IntensityL  -0.172 -0.044  0.062
IntensityM  -0.047  0.002 -0.049  0.061
yrs..:H.M.0  0.649 -0.943 -0.746 -0.013 -0.004
```

Model 3, for Delta carbon percentage per year by management intensity
Formula: Change in carbon percentage per year ~ (management intensity * C% value at start) + years duration + random effect for study. Used for Reduced Stocking and No Inputs scenarios.

```
> CPCim13=lmer(CPCdt$YrDelta_C ~ (Intensity*C.Matched.0years)+years.from.origin
+              +(1 | source.code),data=CPCdt,REML = T)
> summary(CPCim13)
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerT
est']
Formula: CPCdt$YrDelta_C ~ (Intensity * C.Matched.0years) + years.from.origin +
    (1 | source.code)
   Data: CPCdt

REML criterion at convergence: -33.6

Scaled residuals:
    Min      1Q  Median      3Q     Max
-3.5579 -0.1663 -0.0633  0.2198  3.3315

Random effects:
 Groups      Name        Variance Std.Dev.
 source.code (Intercept) 0.09018  0.3003
 Residual                0.01397  0.1182
Number of obs: 59, groups:  source.code, 5
Fixed effects:
                             Estimate Std. Error         df t value Pr(>|t|)
(Intercept)                 0.8959917  0.2178622  7.9705284   4.113 0.003405 **
IntensityL                 -0.3706922  0.1484784 50.7574350  -2.497 0.015827 *
IntensityM                 -0.1367721  0.1980646 50.8212039  -0.691 0.492995
C.Matched.0years           -0.0995763  0.0246210 51.9935396  -4.044 0.000174 ***
years.from.origin          -0.0146191  0.0042731 15.0718376  -3.421 0.003767 **
IntensityL:C.Matched.0years  0.0994388  0.0246415 51.9476422   4.035 0.000180 ***
IntensityM:C.Matched.0years  0.0005473  0.0309115 49.6696321   0.018 0.985945
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
Correlation of Fixed Effects:
            (Intr) IntnsL IntnsM C.Mt.0 yrs.f. IL:C.M
IntensityL  -0.420
IntensityM  -0.200  0.138
C.Mtchd.0yr -0.602  0.611  0.165
yrs.frm.rgn -0.497 -0.143  0.069  0.120
IntnL:C.M.0  0.583 -0.624 -0.163 -0.994 -0.108
IntnM:C.M.0  0.127 -0.091 -0.942 -0.100 -0.042  0.099
```

Model 4, for Delta nitrogen percentage per year by management intensity
Formula: Change in nitrogen percentage per year ~ (management intensity * N% value at start) + random effect for study. Used for Low Inputs, Reduced Stocking and No Inputs scenarios.

```
> NPCim11=lmer(YrDelta_N ~ (Intensity*N.Matched.0years)+(1 | source.code),data=NP
Cdt,REML = T)
> summary(NPCim11)
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerT
est']
Formula: YrDelta_N ~ (Intensity * N.Matched.0years) + (1 | source.code)
   Data: NPCdt

REML criterion at convergence: -252.2

Scaled residuals:
    Min      1Q  Median      3Q     Max
-3.7592 -0.2131 -0.0442  0.1360  3.1300

Random effects:
 Groups      Name        Variance  Std.Dev.
 source.code (Intercept) 0.0005973 0.02444
 Residual                0.0001159 0.01077
Number of obs: 49, groups:  source.code, 5
Fixed effects:
                             Estimate Std. Error        df t value Pr(>|t|)
(Intercept)                 0.043373   0.015868 10.516691   2.733  0.02020 *
IntensityL                 -0.031562   0.014851 41.475345  -2.125  0.03957 *
IntensityM                 -0.018501   0.017154 36.260943  -1.079  0.28792
```

```
N.Matched.0years            -0.070606   0.021202 42.999959  -3.330  0.00179 **
IntensityL:N.Matched.0years  0.058143   0.025051 42.982285   2.321  0.02510 *
IntensityM:N.Matched.0years  0.009155   0.028098 38.126062   0.326  0.74634
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
Correlation of Fixed Effects:
            (Intr) IntnsL IntnsM N.Mt.0 IL:N.M
IntensityL  -0.436
IntensityM  -0.489  0.251
N.Mtchd.0yr -0.633  0.563  0.356
IntnL:N.M.0  0.496 -0.717 -0.284 -0.839
IntnM:N.M.0  0.409 -0.207 -0.936 -0.294  0.234
```

A.4.4 | Literature data and sources for the edaphic variable modelling constructions

The collation of data from the literature below can be found in the file:

Table A.3.Appendix A.4.4.Soil change with management change data from literature.csv

listed with this document but available at the DOI: http://dx.doi.org/10.13140/RG.2.2.10410.90560.

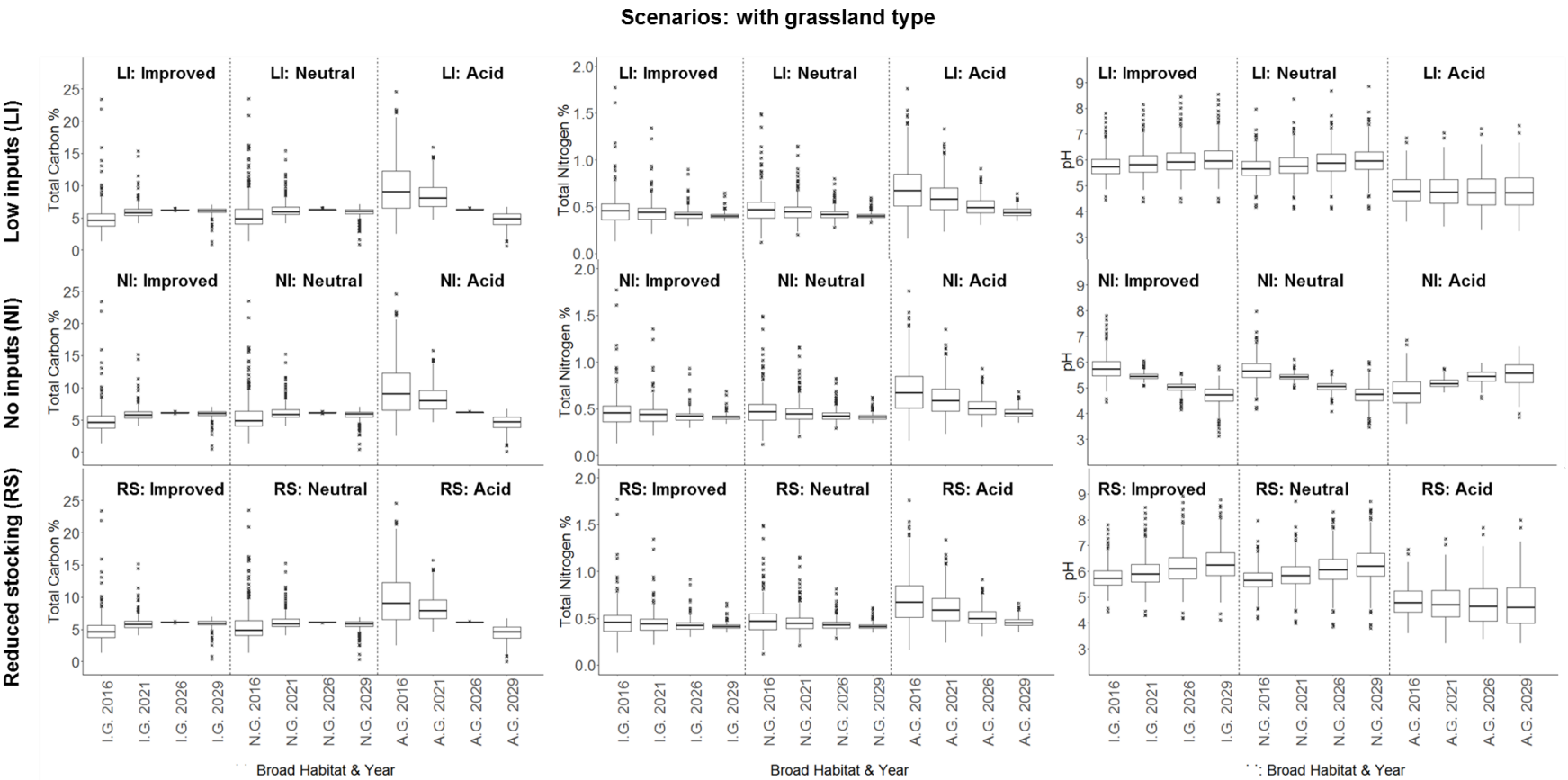

Figure A.1. Boxplots (median, IQ range and range) of grassland soil variables (%C, %N and pH) by year, scenario and broad-habitat type in each GMEP quadrat at baseline and modelled. Scenarios (LI, NI, RS) represent three groups of grassland management options representative of agri-environmental scheme option. Broad-habitat type and year are displayed on the X-axis of each plot: I.G. = improved grassland; N.G. = neutral grassland; A.G. = acid grassland. Soil variables were measured in 2016 as part of the Glastir Environmental Monitoring Program with subsequent years' values modelled.

A.4 | References

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Kirkham, F., Dunn, R., Tallowin, J., Bhogal, A., & Chambers, B. (2011). BD1468 Appendix 2, Are inputs of fertilizer and lime compatible with the restoration of species diversity to hay meadows? Evidence from a 12 year fertilizer and lime experiment. Retrieved from Department for Environment, Food and Rural Affairs (Defra), Nobel House, 17 Smith Square, London SW1P 3JR helpline@defra.gsi.gov.uk website: http://sciencesearch.defra.gov.uk/Default.aspx?Module=More&Location=None&ProjectID=16130

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McGovern, S., Evans, C. D., Dennis, P., Walmsley, C., Turner, A., & McDonald, M. A. (2013). Resilience of upland soils to long term environmental changes. Geoderma, s 197–198, 36–42. doi: 10.1016/j.geoderma.2012.12.018

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Wagner, M. ., Bullock, J. M. ., Hulmes, S. ., Hulmes, L. ., Peyton, J. ., Amy, S. ., … Pywell, R. F. (2014). BD1459: Techniques to enhance the establishment and persistence of poor-performing species in grassland restoration - RP00199. Retrieved from http://publications.naturalengland.org.uk/publication/5700071847886848?category=513173

A.5 | Appendix A: Workflow output graphical plots.

A.5.1 | Model testing

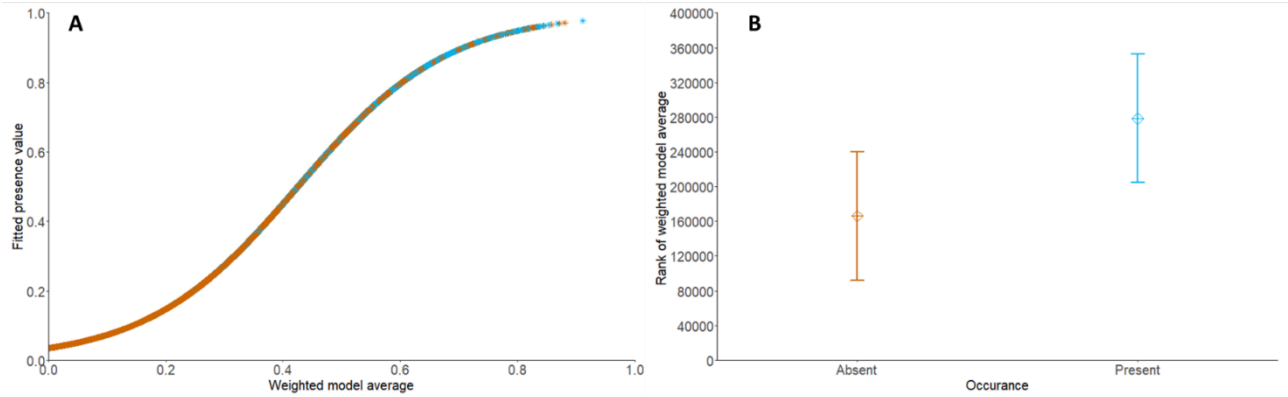

Figure A.2. Results of testing the species ecological niche model MultiMOVE outputs against the observed baseline. **A.** Logistic regression (LR) of weighted model averages (WMA) of species per X-plot observed as present (**light blue**) or not present (**brown**). A species within a plot having a WMA of 0.43 or over according to the LR is more likely to be observed as present (fitted presence of 0.51) than absent within the input data (logistical regression WMA model coefficients P-value <0.001). **B.** Average rank plots of WMA values with rank standard deviations for absent species (**brown**, Absent) versus present in each modelled quadrat (**light blue**, Present).

Logistical regression showed that an increase in a habitat suitability score increases the probability of the species being observed as present in a plot within the input data (0.43 or over gives a fitted presence value of 0.51, logistical regression WMA model coefficients P-value <0.001; **Fig. A.2**).

The grassland broad habitat summarised vegetation NVC unit grouping within the paper's **Fig. 2.3**, "Plant community profiles of modelled baseline (2016) versus scenario-driven species composition (2029)" can be found within the file:

Table A.4. Appendix A.5.1.MASTER_NVC_grouping and scenario counts.csv listed with this document but available at the DOI: http://dx.doi.org/10.13140/RG.2.2.10410.90560.

A.5.2 | Modelling workflow outputs

The full species list MultiMOVE uses with the categorisation columns of the ecosystem functions or services species groups can be found within the file:

Table A.5. Appendix A5.1.MultiMOVE and ecosystem functions or services species list.csv listed with this document but available at the DOI: http://dx.doi.org/10.13140/RG.2.2.10410.90560.

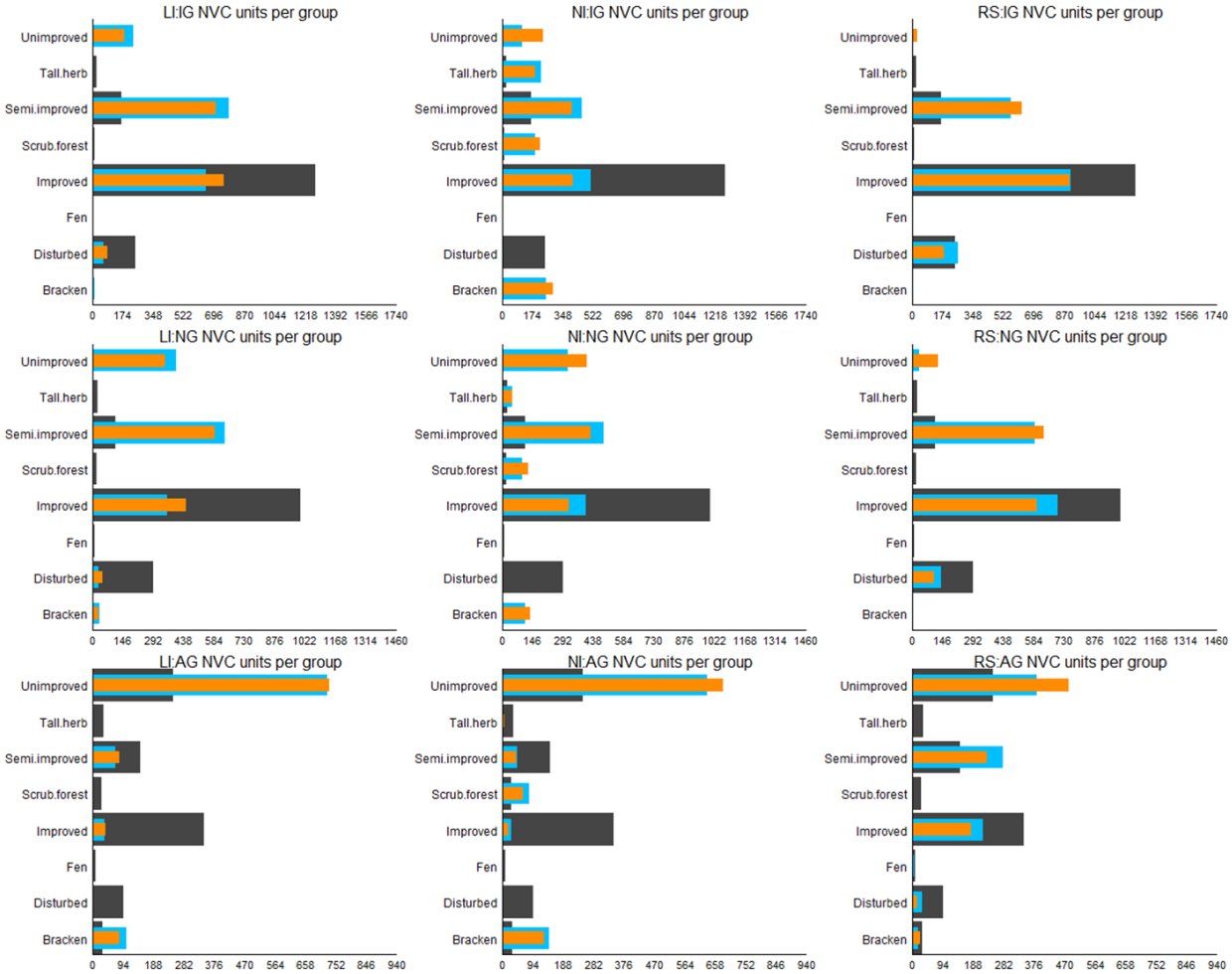

Figure A.3. Modelled, baseline versus scenario (2021) vegetation. Grassland broad habitat plot's top five closest National Vegetation Classification (NVC) unit matches counted into summarised vegetation groups: modelled baseline (dark grey, 2016); scenarios observed climate (blue, 2021) & predicted climate (orange, 2021). Broad habitat types (rows): IG = Improved grassland (348 plots); NG = Neutral grassland (292 plots); AG = Acid Grassland (188 plots). X-axes show counts of fits to each NVC community

group from the top 5 matching coefficients for each plot. Observed climate (grey & blue) = UKCP18, HadUK-Grid 1981-2016 (averages); projected climate= UKCP18 (RCP 8.5) downscaled data for 2021 (orange). Management scenario (columns): LI = Low inputs; NI = No inputs; RS = Reduced stocking. For Low inputs & Reduced stocking, vegetation height is as stipulated in the Glastir agri-environment scheme (at ~ 7 cm). Summarised vegetation was derived by grouping (*see, Appendix A.5.1,* Table A.**4**) NVC unit matches for the baseline and modelled GMEP plots, matches are from MAVIS processing of the habitat suitability outputs from ecological niche modelling.

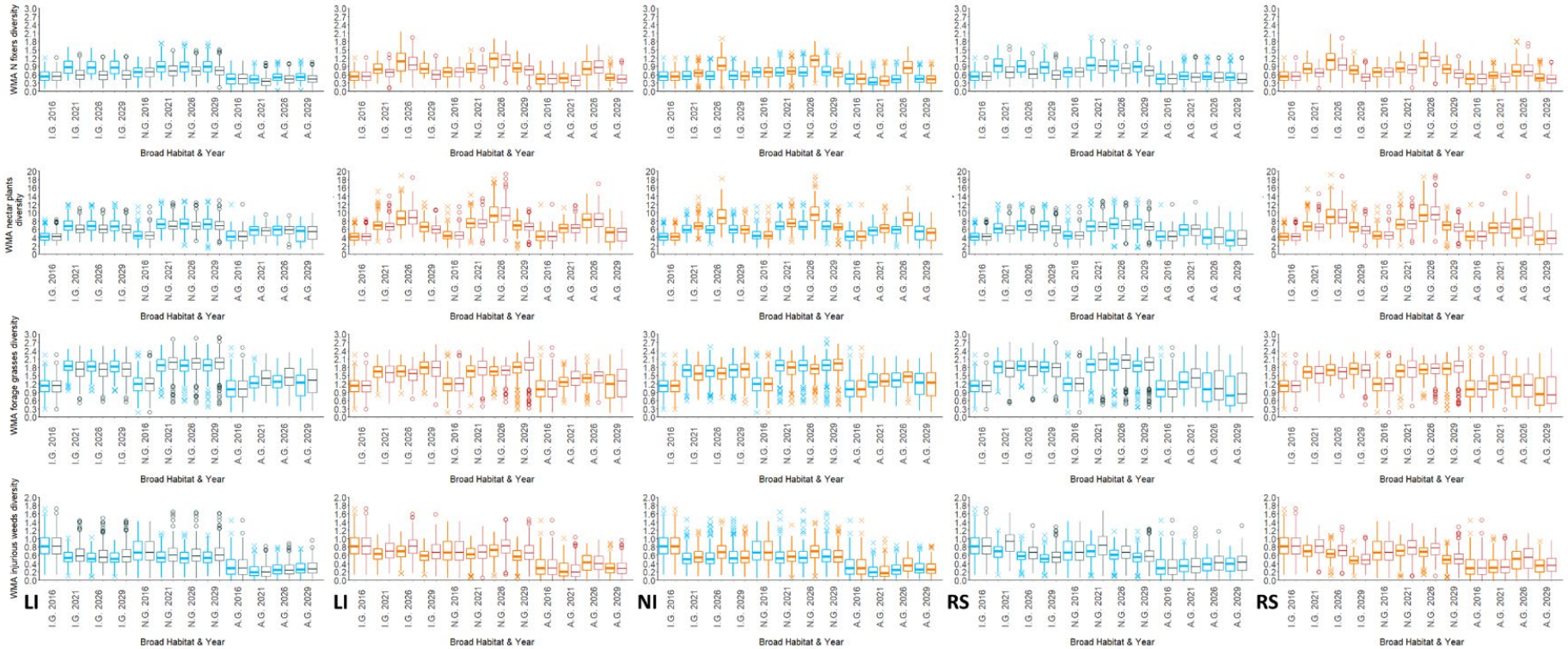

Figure A.4. Boxplots of diversity scores of species groups providing ecological functions, disservices or services (Smart *et al.*, 2017). Data modelled represents different climate and management scenarios using the Glastir Monitoring and Evaluation Program data as a modelled baseline (2016) and as inputs for future year scenarios. The three broad habitat types shown are improved (I.G.), neutral (N.G.) and acid (A.G.) grasslands. Scenarios (columns) were created by using observed (2016, *see, Fig. A.6*) and predicted climate data (UKCP18, temperatures spike in 2026 outside of modelling space so are excluded from interpretation) along with soil variable change with management change models as inputs for species ecological niche modelling in the R package MultiMOVE, which uses these to predict plant habitat suitability to changing soil, vegetation height and climate conditions. Scenarios representing one of the three management types: LI = Low input (representative of Glastir agri-environment scheme options 15b entry & advanced, also 15d advanced); RS = Reduced stocking (representative of Glastir options 411&41b advanced, also 41a entry & advanced); NI = No inputs (representative of

Glastir options 15a entry & advanced). Boxplots show the species group weighted model average (WMA) diversity score for X-plots in the broad habitat type and year shown on the x-axis, rows show results for each species group as follows: N fixers = nitrogen fixing species (top); nectar plants = nectar producing plants (second); forage grasses, species for livestock forage (third); injurious weed species (bottom). The plot y-axes (WMA "group" diversity) is a dark diversity estimate created via summing WMA probabilities output from the MultiMOVE ensemble. Within each scenario for climate and cover weighted canopy height colours of boxplots represent: LI & RS light blue represents cover weighted canopy height set to 1 (equivalent to < 100 mm) or held constant if observed lower with observed climate & orange represents the same cover weighted canopy height as light blue but with predicted climate, dark blue represents cover weighted canopy height over 1 (set to 2, equivalent to 101-299 mm, where observed as under 1) with observed climate and dark red represents the same cover weighted canopy height but with predicted climate; NI, light blue represents observed climate & orange represents predicted climate, both NI colours cover weighted canopy height is left as the observed.

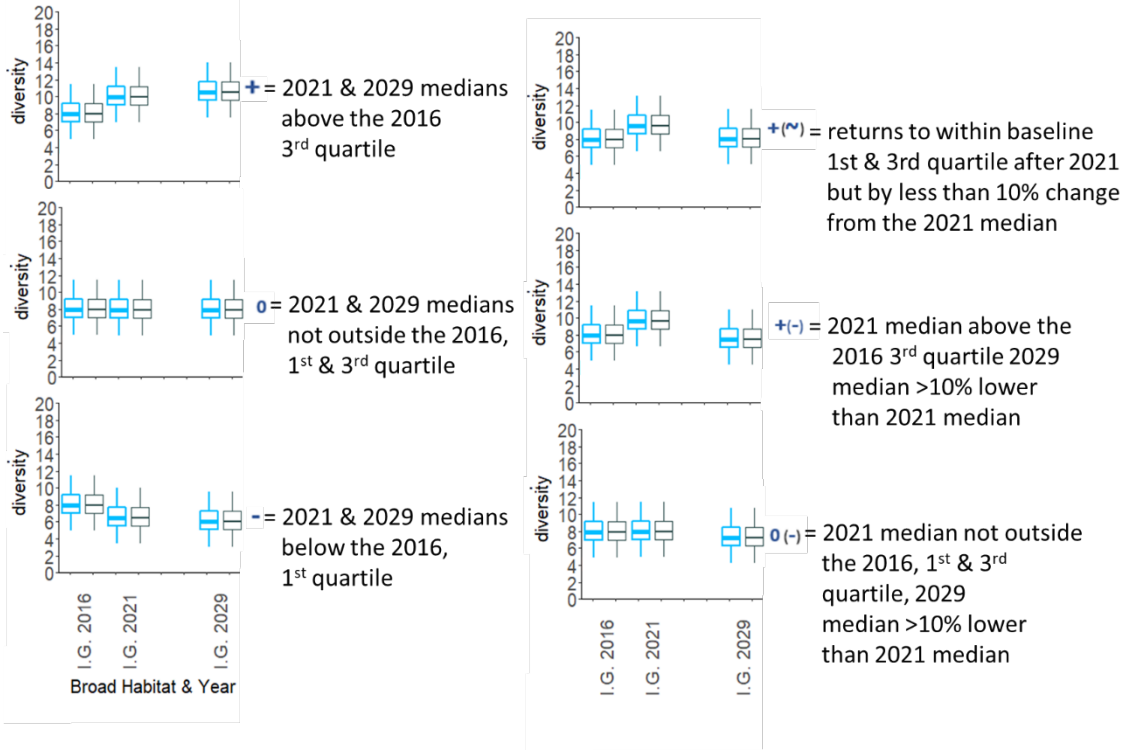

Figure A.5. Example boxplots of diversity scores of for a given species group with a legend showing how modelled dark diversity trends across years (2016, 2021, 2029) are defined and appear in a box-plot form.

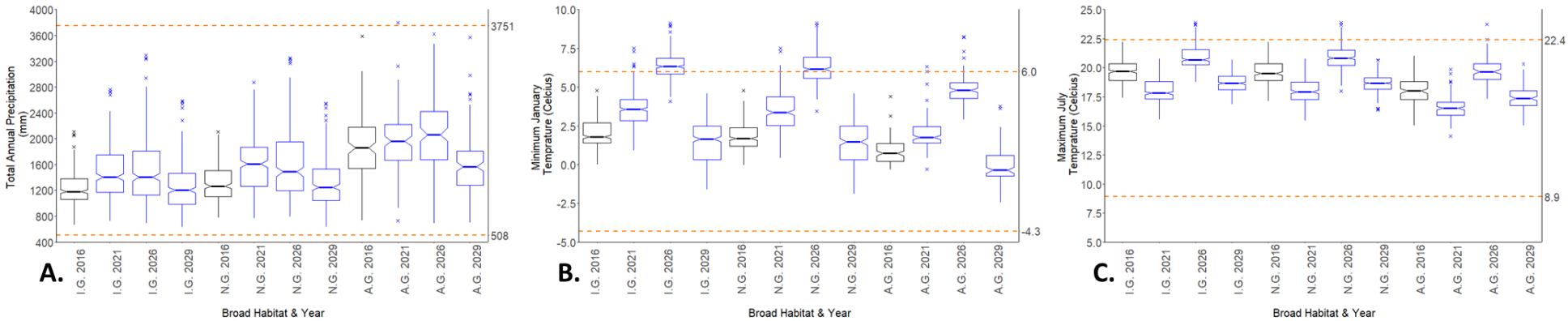

Figure A.6. Boxplots showing Glastir Environmental Monitoring Program X-plot climate data from UKCP18 at 1 km square scale from 2016 (averaged from 1981 to 2016 as a baseline) through subsequent predicted years up to 2029. Observed (2016) data was sourced from Met Office HadUK-Grid, 1 km climate data and averaged. Predictions data from the UKCP18 high emissions scenario, RCP8.5, UK regional 12 km scale probabilistic data, was downscaled to 1km. A. Total annual precipitation in mm, B. minimum January temperature in °C and C. Maximum July temperature in °C; georeferenced to the 1 km square each X-plot was within. Left hand Y-axes shows variable ranges to derive boxplot values from (black observed average for 2016; blue beyond 2016 predicted). The dashed orange lines show the top and bottom of ranges the R package MultiMOVE was constructed within. X-axis labels show the X-plot groups of year and board habitat type: I.G. = improved grassland; N.G. = neutral grassland; A.G. = acid grassland.

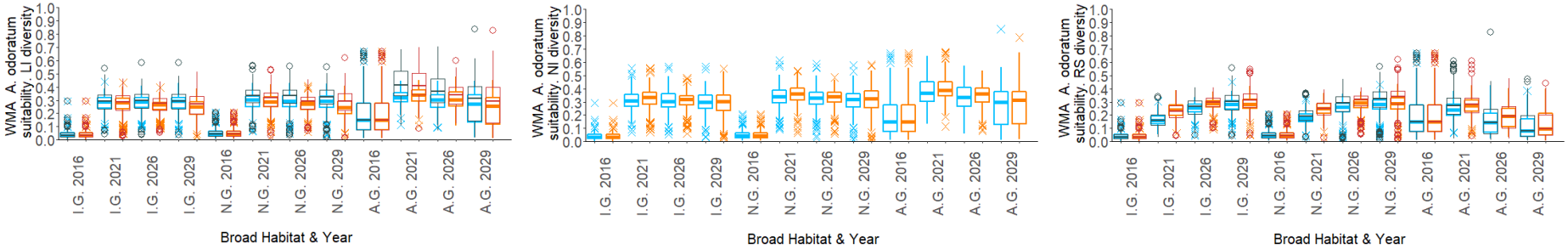

Figure A.7. Boxplots of Anthoxanthum odoratum MutliMOVE output results. Data modelled represents different climate and management scenarios using the Glastir Monitoring and Evaluation Program data as a modelled baseline (2016) and as inputs for future year scenarios. The three broad habitat types shown are improved (I.G.), neutral (N.G.) and acid (A.G.) grasslands. Scenarios (columns) were created by using observed (2016, *see, Fig. A.6*)) and predicted climate data (UKCP18, temperatures spike in 2026 outside of modelling space so are excluded from interpretation) along with soil variable change with management change models as inputs for species ecological niche modelling in the R package MultiMOVE, which uses these to predict plant habitat suitability to changing soil, vegetation height and climate conditions. Scenarios representing one of the three management types: LI = Low inputs management left; RS = Reduced stocking density management centre; NI = No inputs management right. Boxplots show the species weighted model average (WMA) or suitability score for X-plots in the broad habitat type and year shown on the x-axis. Within each scenario for climate and cover weighted canopy height colours of boxplots represent: LI & RS light blue represents cover weighted canopy height set to 1 (equivalent to < 100 mm) or held constant if observed lower with observed climate & orange represents the same cover weighted canopy height as light blue but with predicted climate, dark blue represents cover weighted canopy height over 1 (set to 2, equivalent to 101-299 mm, where observed as under 1) with observed climate and dark red represents the same cover weighted canopy height but with predicted climate; NI, light blue represents observed climate & orange represents predicted climate, both NI colours cover weighted canopy height is left as the observed.

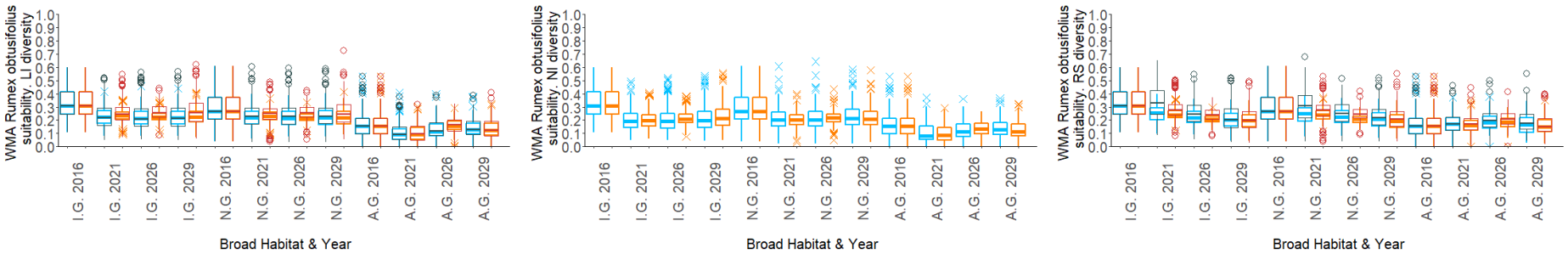

Figure A.8. Boxplots of Rumex obtusifolius MutliMOVE output results. Data modelled represents different climate and management scenarios using the Glastir Monitoring and Evaluation Program data as a modelled baseline (2016) and as inputs for future year scenarios. The three broad habitat types shown are improved (I.G.), neutral (N.G.) and acid (A.G.) grasslands. Scenarios (columns) were created by using observed (2016, *see, Fig. A.6*)) and predicted climate data (UKCP18, temperatures spike in 2026 outside of modelling space so are excluded from interpretation) along with soil variable change with management change models as inputs for species ecological niche modelling in the R package MultiMOVE, which uses these to predict plant habitat suitability to changing soil, vegetation height and climate conditions. Scenarios representing one of the three management types: LI = Low inputs management left; RS = Reduced stocking density management centre; NI = No inputs management right. Boxplots show the species weighted model average (WMA) or suitability score for X-plots in the broad habitat type and year shown on the x-axis. Within each scenario for climate and cover weighted canopy height colours of boxplots represent: LI & RS light blue represents cover weighted canopy height set to 1 (equivalent to < 100 mm) or held constant if observed lower with observed climate & orange represents the same cover weighted canopy height as light blue but with predicted climate, dark blue represents cover weighted canopy height over 1 (set to 2, equivalent to 101-299 mm, where observed as under 1) with observed climate and dark red represents the same cover weighted canopy height but with predicted climate; NI, light blue represents observed climate & orange represents predicted climate, both NI colours cover weighted canopy height is left as the observed.

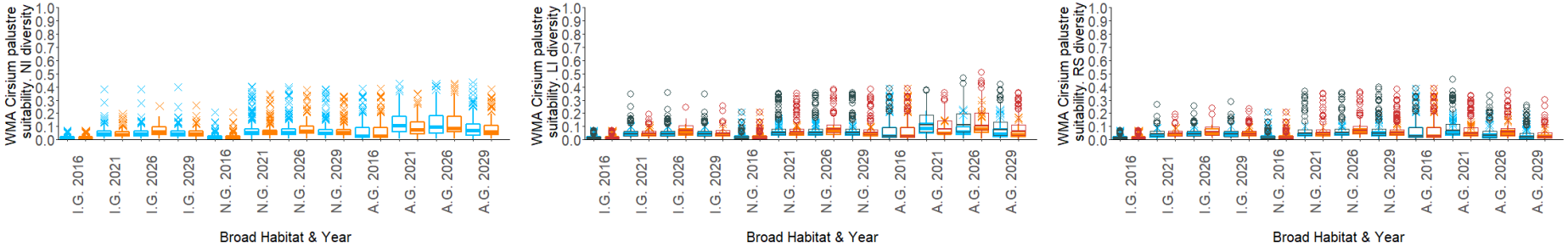

Figure A.9. Boxplots of Cirsium palustre MutliMOVE output results. Data modelled represents different climate and management scenarios using the Glastir Monitoring and Evaluation Program data as a modelled baseline (2016) and as inputs for future year scenarios. The three broad habitat types shown are improved (I.G.), neutral (N.G.) and acid (A.G.) grasslands. Scenarios (columns) were created by using observed (2016, *see, Fig. A.6*)) and predicted climate data (UKCP18, temperatures spike in 2026 outside of modelling space so are excluded from interpretation) along with soil variable change with management change models as inputs for species ecological niche modelling in the R package MultiMOVE, which uses these to predict plant habitat suitability to changing soil, vegetation height and climate conditions. Scenarios representing one of the three management types: LI = Low inputs management left; RS = Reduced stocking density management centre; NI = No inputs management right. Boxplots show the species weighted model average (WMA) or suitability score for X-plots in the broad habitat type and year shown on the x-axis. Within each scenario for climate and cover weighted canopy height colours of boxplots represent: LI & RS light blue represents cover weighted canopy height set to 1 (equivalent to < 100 mm) or held constant if observed lower with observed climate & orange represents the same cover weighted canopy height as light blue but with predicted climate, dark blue represents cover weighted canopy height over 1 (set to 2, equivalent to 101-299 mm, where observed as under 1) with observed climate and dark red represents the same cover weighted canopy height but with predicted climate; NI, light blue represents observed climate & orange represents predicted climate, both NI colours cover weighted canopy height is left as the observed.

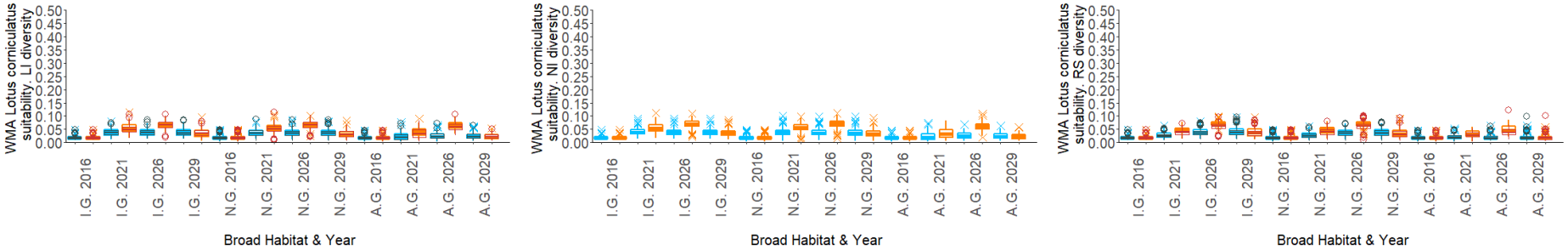

Figure A.10. Boxplots of Lotus corniculatus MutliMOVE output results. Data modelled represents different climate and management scenarios using the Glastir Monitoring and Evaluation Program data as a modelled baseline (2016) and as inputs for future year scenarios. The three broad habitat types shown are improved (I.G.), neutral (N.G.) and acid (A.G.) grasslands. Scenarios (columns) were created by using observed (2016, *see, Fig. A.6*)) and predicted climate data (UKCP18, temperatures spike in 2026 outside of modelling space so are excluded from interpretation) along with soil variable change with management change models as inputs for species ecological niche modelling in the R package MultiMOVE, which uses these to predict plant habitat suitability to changing soil, vegetation height and climate conditions. Scenarios representing one of the three management types: LI = Low inputs management left; RS = Reduced stocking density management centre; NI = No inputs management right. Boxplots show the species weighted model average (WMA) or suitability score for X-plots in the broad habitat type and year shown on the x-axis. Within each scenario for climate and cover weighted canopy height colours of boxplots represent: LI & RS light blue represents cover weighted canopy height set to 1 (equivalent to < 100 mm) or held constant if observed lower with observed climate & orange represents the same cover weighted canopy height as light blue but with predicted climate, dark blue represents cover weighted canopy height over 1 (set to 2, equivalent to 101-299 mm, where observed as under 1) with observed climate and dark red represents the same cover weighted canopy height but with predicted climate; NI, light blue represents observed climate & orange represents predicted climate, both NI colours cover weighted canopy height is left as the observed.

B | Appendix B. Supporting information and data for Chapter three only

B.1 | Appendix B. Description of Broad Habitat Types

The six broad habitats are described in Jackson (2000). During the baseline Glastir Monitoring and Evaluation Programme (GMEP) survey areas of land were assigned to these six broad habitats among others using a vegetation key available online at: http://nora.nerc.ac.uk/id/eprint/5194/1/N005194CR.pdf.

The top 10 most common species in quadrats surveyed in GMEP and assigned to each broad habitat were as follows:

- **Broadleaved woodland (BW),** Broadleaved, Mixed and Yew Woodlands being the full name: *Rubus fruticosus, Dryopteris dilatata, Hedera helix, Fraxinus excelsior, Thuidium tamariscinum, Corylus avellana, Hyacinthoides non-scripta, Dryopteris filix-mas, Sorbus aucuparia, Pteridium aquilinum.*
- **Coniferous Woodland (CW):** *Picea sitchensis, Dryopteris dilatata, Vaccinium myrtillus, Thuidium tamariscinum, Plagiothecium undulatum, Mnium hornum, Rubus fruticosus, Rhytidiadelphus loreus, Deschampsia flexuosa, Sorbus aucuparia.*
- **Arable and Horticulture (A&H):** *Poa annua, Poa trivialis, Ranunculus repens, Trifolium repens, Lolium perenne, Agrostis stolonifera, Taraxacum agg., Persicaria maculosa, Rumex obtusifolius, Triticum aestivum.*
- **Improved grassland (IG):** *Lolium perenne, Trifolium repens, Ranunculus repens, Holcus lanatus, Cerastium fontanum, Poa trivialis, Taraxacum agg., Agrostis capillaris, Poa annua, Rumex obtusifolius.*
- **Neutral grassland (NG):** *Holcus lanatus, Agrostis capillaris, Trifolium repens, Lolium perenne, Ranunculus repens, Cerastium fontanum, Anthoxanthum odoratum, Taraxacum agg., Cynosurus cristatus, Rumex acetosa.*

- **Bracken (Br):** *Pteridium aquilinum, Agrostis capillaris, Rhytidiadelphus squarrosus, Pseudoscleropodium purum, Anthoxanthum odoratum, Galium saxatile, Holcus lanatus, Festuca ovina, Potentilla erecta, Pleurozium schreberi.*

B.1 | References

Jackson, D. L. (2000). Guidance on the interpretation of the Biodiversity Broad Habitat Classification (terrestrial and freshwater types): Definitions and the relationship with other habitat classifications. Joint Nature Conservation Committee, Peterborough, UK.

B.2 | Appendix B. Modelling change in soil variables under afforestation

Determining how soils change in response to afforestation via planting or natural succession was completed by constructing generalized linear mixed-effects models trained on data gathered from a review of the literature where the effects of afforestation on soil variables had been measured under time series or chronosequences. The use of biogeochemistry models to dynamically process the impact of afforestation was not adopted because the necessary soil measurements do not exist for each modelled location. Using average inputs coarsely resolved to larger grid squares and dominant soil type would have greatly decreased the accuracy and realism of the modelling process removing the benefit of filtering the observed plant species composition at our very high-resolution sampling sites.

The four soil variables (C, N, pH, moisture) were modelled independently of each other as an insufficient number of studies measured all the variables together so there was too little data to account for relationships. A consequence is that we derived separate empirical models for each variable even though in reality we know they respond as an intercorrelated

complex. Thus, the modelled results are strongly dependent on the studies selected from the literature and the realism of the modelled change in each variable.

Despite data availability falling short of the representativeness and robustness we would have liked for the study habitat types, a clear benefit is that the models created here summarise changes in soil conditions that have been observed resulting from afforestation on soil and vegetation starting points that equate with the soils and vegetation of the GMEP baseline. Readers can therefore inspect the underlying data (see below) and assess the representativeness of the observations and the robustness of the estimated soil changes. The collation of data from the literature below can be found in the file:

Table B.1. Appendix B.2.afforestation_soils_change.csv listed with this document but available at the DOI: http://dx.doi.org/10.13140/RG.2.2.10410.90560.

To some extent, the lack of such long-term fundamental datasets is surprising. Despite a number of long-term experiments existing across the UK and ecological science being an endeavour that is at least 200 years old, there is a lack of fundamental information on long-term soil and vegetation changes in response to human management.

B.2.1 | Literature sources

Care was taken to closely match the methods of each study found during the literature review to the GMEP methods or to ensure that data values could be converted to match. Non-UK studies were omitted. This search resulted in datasets of varying size. Requests were made to study authors to provide full datasets, while we also included relevant open access data; A summary of the studies is as follows:

- A 100 year chronosequence of 40 plots in Kielder forest (Vanguelova *et al.*, 2019)
- Forest conditions development under different tree species in a chronosequence (Ovington, 1953)

- A pooled selection of former agricultural sites planted up with broadleaves (Ashwood *et al.*, 2019)
- Rothamsted regenerating broadleaved woodland post-abandonment from arable (Jenkinson, 1971; Poulton *et al.*, 2003)
- A study of succession on lowland heaths (Mitchell *et al.*, 1997)
- Plots extracted from the UK Centre for Ecology and Hydrology's Countryside Survey data showing vegetation trends (increase in scrub, bracken or tree species cover) as having undergone afforestation (Reynolds *et al.*, 2013)
- Dataset of afforestation provided by Aidan Keith from work on short rotation forestry soil development (Keith *et al.*, 2015; R. L. Rowe *et al.*, 2016)

B.2.2 | Data categorisation and model construction

Data was categorised in two ways (for: total C%, total N%, pH) in order to ensure robust fitting to scenarios, by afforestation type (planted broadleaved, planted conifer, or succession), and by taxon (gymnosperm trees, angiosperm trees, or bracken). The two different data categorisation types were used as insufficient data on nitrogen was found for it to be modelled according to its afforestation type. This categorisation was done per-treatment within each study. Where studies used chronosequences, controls e.g. grassland or arable sites, were used as time 0 matches for each variable. Also where multiple controls or multiple treatments were replicated the variables of these were averaged to become start or end values as appropriated. This was also done where samples had been taken from multiple soil depths e.g. samples taken from 0-5, 5-10 and 10-15 cm where averaged to give a 0-15 cm depth value. All soil data recovered during the literature review was taken from within the O horizon to match the baseline GMEP data which was taken from the field layer (0-15 cm).

Calculating the change in variables was done by subtracting the value at start time (or matched time 0 for chronosequence data) with the values at treatment end time and dividing

by years duration of the study to give a change of X in a variable per year. This approach takes advantage of the correlation between variables within sites, between-site differences were accounted for by a study site random effect. However, given the variability in the data different model constructions were used these being:

- pH change per year as determined by afforestation type & time are predictors
- Change in total carbon per year was transformed then afforestation type & value at the start were used as interacting terms alongside time as predictors
- Total nitrogen was the same as carbon but time & value at start were used as interacting terms alongside afforestation type

Exact model constructions can be found in the **Boxes 1-4** below.

As the poorest data was found for soil field moisture% with only a few treatments with this data gathered this data was categorised by habitat type (conifer forest or broadleaved forest). Also as this data was so noisy, no good model could be made for the raw field moisture data thus the neural networks used in the model workflow to calculated Ellenberg wetness (EbF) were used to gain EbF values and these were modelled. The model construction can be found in **Box 4**. The planted results from the Ellenberg wetness model show no convergence (*Appendix B.2.2,***Fig. B.1**) towards baseline woodland most likely due to planted forest holding onto underlying soil properties from the baseline habitats, thus are not explored in the main body of work.

In grassland and bracken habitats N is modelled to reach 0 or negative values for a handful of plots from 2046 onwards. These plots' values represent where the model fails to reproduce a possible reality and are thus excluded from all the plant results.

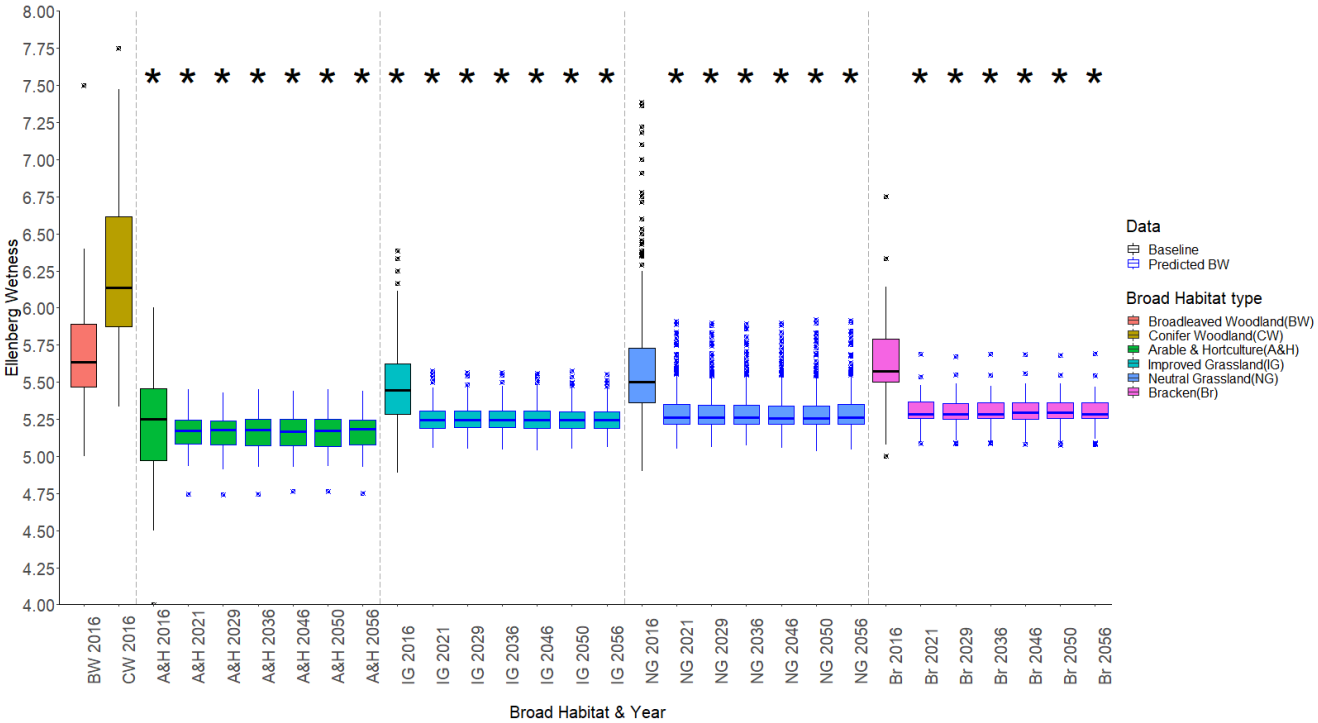

Figure B.1. Box plots of Ellenberg Wetness per Broad Habitat (BH) type and year. The year 2016 for each BH type represents the observed data (black boxes), subsequent years data were predicted by using 2016 data as inputs to generalised linear mixed effect models of broadleaved woodland plantation (blue boxes). Asterisks (*) at Y=7.5 represent significant differences (p-value=0.05) of logged variables of the 2016 Broadleaved Woodland baseline compared to the Broad Habitat type and year below each asterisk.

B2.3 | Model construction and formula code

Box 1. pH model construction and summary from R. Formula: Change in pH per year ~ afforestation type + years from start year + random effect for treatment site; planted_vs_succession = afforestation type.

```
> formula(pHMX2a)
YrDelta_pH ~ planted_vs_succession + Years_From_Origin + (1 |
    Source_Code)
> summary(pHMX2a)
Linear mixed model fit by REML. T-tests use Satterthwaite's method
['lmerModLmerTest']
Formula: YrDelta_pH ~ planted_vs_succession + Years_From_Origin + (1 |
Source_Code)
   Data: pHdt

REML criterion at convergence: -454.7

Scaled residuals:
    Min      1Q  Median      3Q     Max
-4.2257 -0.4419 -0.0919  0.5194  4.0527

Random effects:
 Groups      Name        Variance  Std.Dev.
 Source_Code (Intercept) 0.0002494 0.01579
 Residual                0.0005705 0.02388
Number of obs: 109, groups:  Source_Code, 9

Fixed effects:
                                        Estimate Std. Error         df t value
Pr(>|t|)
(Intercept)                           -1.998e-02  9.170e-03  1.437e+01  -2.178
0.0465 *
planted_vs_successionplanted conifer  5.165e-03  6.422e-03  1.050e+02   0.804
0.4231
planted_vs_successionsuccession      -1.251e-02  1.326e-02  9.632e+00  -0.943
0.3687
Years_From_Origin                     2.783e-04  1.099e-04  1.001e+02   2.531
0.0129 *
Signif. Codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
              (Intr) pln__c plnt__
plntd_vs_sccc -0.501
plntd_vs_sccs -0.449  0.303
Yrs_Frm_Org   -0.468  0.143 -0.084
```

Box 2. Carbon model construction and summary from R. Formula: transformed total soil carbon change per year ~ (afforestation type + total soil carbon at start year) + years from start year + random effect for treatment site. Transformation: $(X+5)^{2.6}$, where X is total soil carbon change per year; planted_vs_succession = afforestation type.

```
> formula(CPCim13)
CPCdt$T_CPC ~ (planted_vs_succession * Percent_C_Matched_0Yrs) +
    Years_From_Origin + (1 | Source_Code)
> summary(CPCim13)
Linear mixed model fit by REML. T-tests use Satterthwaite's method
['lmerModLmerTest']
Formula: CPCdt$T_CPC ~ (planted_vs_succession * Percent_C_Matched_0Yrs) +
    Years_From_Origin + (1 | Source_Code)
   Data: CPCdt

REML criterion at convergence: 285.9

Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.0777 -0.1764 -0.0215  0.1116  4.0838

Random effects:
 Groups      Name        Variance Std.Dev.
 Source_Code (Intercept) 101.4    10.07
 Residual                382.0    19.54
Number of obs: 35, groups:  Source_Code, 4
```

```
Fixed effects:
                                                          Estimate Std. Error
df t value
(Intercept)                                               69.73412   10.59073
2.34748   6.584
planted_vs_successionplanted conifer                       6.26961   10.93693
28.99879   0.573
planted_vs_successionsuccession                           80.09064   23.74397
28.95766   3.373
Percent_C_Matched_0Yrs                                    -0.40362    1.49225
28.99626  -0.270
Years_From_Origin                                          0.04571    0.17815
8.44266   0.257
planted_vs_successionplanted conifer:Percent_C_Matched_0Yrs -0.34601    1.53944
27.69725  -0.225
                                                          Pr(>|t|)
(Intercept)                                                0.01460 *
planted_vs_successionplanted conifer                       0.57089
planted_vs_successionsuccession                            0.00213 **
Percent_C_Matched_0Yrs                                     0.78871
Years_From_Origin                                          0.80364
planted_vs_successionplanted conifer:Percent_C_Matched_0Yrs  0.82381
Signif. Codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
              (Intr) pln__c plnt__ P_C_M_ Yr_F_O
plntd_vs_sccc -0.441
plntd_vs_sccs -0.075 -0.107
Prcn_C_M_0Y   -0.352  0.581 -0.420
Yrs_Frm_Org   -0.327 -0.180  0.241 -0.414
p__c:P_C_M_    0.298 -0.656  0.430 -0.978  0.402
fit warnings:
fixed-effect model matrix is rank deficient so dropping 1 column / coefficient
```

Box 3. Nitrogen model construction and summary from R. Formula: transformed total soil nitrogen change per year ~ (Years from start year * Total soil carbon at start year) + taxon + random effect for treatment site. Transformation: $(X+1)^{4.9}$, where X is Total Soil Nitrogen change per year.

```
> formula(NPCimYrT1Man1)
T_NPC ~ (Years_From_Origin * Percent_N_Matched_0Yrs) + taxon +
    +(1 | Source_Code)
> summary(NPCimYrT1Man1)
Linear mixed model fit by REML. T-tests use Satterthwaite’s method
[‘lmerModLmerTest’]
Formula: T_NPC ~ (Years_From_Origin * Percent_N_Matched_0Yrs) + taxon +      +(1
| Source_Code)
   Data: NPCdt

REML criterion at convergence: -36.4

Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.4144 -0.3123 -0.0083  0.1783  3.9178

Random effects:
 Groups      Name        Variance Std.Dev.
 Source_Code (Intercept) 0.008763 0.09361
 Residual                0.008369 0.09148
Number of obs: 41, groups:  Source_Code, 5

Fixed effects:
                                        Estimate Std. Error         df t value
Pr(>|t|)
(Intercept)                            1.1242621  0.0596648  3.1052138  18.843
0.000264 ***
Years_From_Origin                     -0.0008210  0.0007631 25.1889857  -1.076
0.292194
Percent_N_Matched_0Yrs                -0.2888201  0.0409102 30.6600991  -7.060
6.68e-08 ***
taxongymnosperm                        0.0312140  0.0390797 32.2923006   0.799
0.430284
```

```
Years_From_Origin:Percent_N_Matched_0Yrs  0.0029235  0.0015408 24.3850602   1.897
0.069676 .
Signif. Codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) Yr_F_O P_N_M_ txngym
Yrs_Frm_Org -0.404
Prcn_N_M_0Y -0.341  0.340
txngymnsprm -0.193  0.103 -0.191
Y_F_O:P_N_M  0.063 -0.631 -0.495 -0.123
```

Box 4. Ellenberg wetness (EbF) model construction and summary from R. Formula: over all change in EbF ~ (Habitat type * EbF at start year) + random effect for treatment site; conifer_broadleaved_openscurb = Habitat type.

```
> formula(GWCNPCim11)
GWCdt$delta_EbF ~ (conifer_broadleaved_openscurb * EbF_Matched_0Yrs) +
    (1 | Source_Code)
> summary(GWCNPCim11)
Linear mixed model fit by REML. T-tests use Satterthwaite’s method
[‘lmerModLmerTest’]
Formula: GWCdt$delta_EbF ~ (conifer_broadleaved_openscurb * EbF_Matched_0Yrs) +
    (1 | Source_Code)
   Data: GWCdt

REML criterion at convergence: 18.6

Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.94916 -0.15189  0.04419  0.26634  3.14888

Random effects:
 Groups      Name        Variance Std.Dev.
 Source_Code (Intercept) 0.01316  0.1147
 Residual                0.07987  0.2826
Number of obs: 32, groups:  Source_Code, 3

Fixed effects:
                                                        Estimate Std. Error      df
t value Pr(>|t|)
(Intercept)                                               3.3695     1.1140 19.8506
3.025  0.00673
conifer_broadleaved_openscurbconifer                     -2.4103     1.2445 24.0523
-1.937  0.06461
EbF_Matched_0Yrs                                         -0.6549     0.2072 18.7795
-3.161  0.00520
conifer_broadleaved_openscurbconifer:EbF_Matched_0Yrs     0.4461     0.2279 21.9075
1.958  0.06312

(Intercept)                                             **
conifer_broadleaved_openscurbconifer                    .
EbF_Matched_0Yrs                                        **
conifer_broadleaved_openscurbconifer:EbF_Matched_0Yrs .
Signif. Codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) cnfr__ EF_M_0
cnfr_brdlv_ -0.886
EbF_Mtch_0Y -0.994  0.899
c__:EF_M_0Y  0.899 -0.995 -0.917
```

B.2 | References

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B.3 | Appendix B. Workflow outputs and graphical plots.

B.3.1 | *Fraxinus excelsior* plot Species and NVC units

Results within the *Fraxinus excelsior* plots and NVC units table are a subset of the total data, only including sites where *Fraxinus excelsior* habitat suitability scores (weighted model average) of 0.383 or over suggest the species is likely to be present (>0.51) according to logistic regression conducted on baseline scores.

Within *Fraxinus excelsior* plots the top 20 species by the number of plots they occur in and National Vegetation Classification (NVC, matched using the software MAVIS) units determined with and without *F. excelsior* can be found in the file:

Table B.2. Appendix B.2.Top_20Sp._in_*Fraxinus_excelsior*_plots_and_NVCunits.xlsx

listed with this document but available at the DOI:
http://dx.doi.org/10.13140/RG.2.2.10410.90560.

B.3.2 | Species within MultiMOVE and the ecosystem function and service groups

The full species list MultiMOVE uses with the categorisation columns of the ecosystem functions or services species groups can be found within the file:

Table B.3. Appendix B.2.MultiMOVE and forest ecosystem functions or services species list.csv

listed with this document but available at the DOI:

http://dx.doi.org/10.13140/RG.2.2.10410.90560.

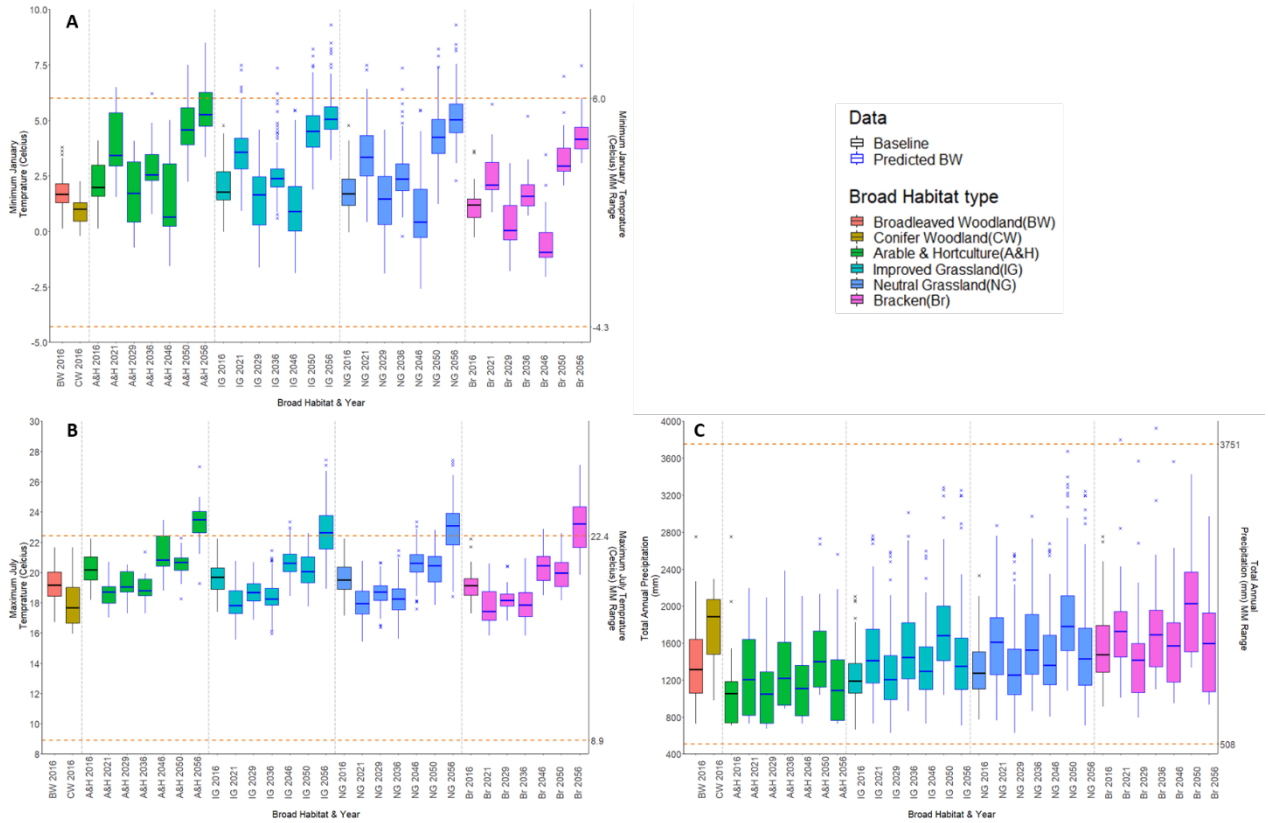

Figure B.2. Boxplots showing Glastir Environmental Monitoring Program X-plot climate data from UKCP18 at 1 km square scale from 2016 (averaged from 1981 to 2016 as a baseline) through subsequent predicted years up to 2056. Observed (2016, black edged box plots) data was sourced from Met Office HadUK-Grid, 1 km climate data and averaged. Predictions data (blue edged box plots) from the UKCP18 high emissions scenario, RCP8.5, UK regional 12 km scale probabilistic data, was downscaled to 1km. A. Total annual precipitation in mm, B. minimum January temperature in °C and C. Maximum July temperature in °C; georeferenced to the 1 km square each X-plot was within. Left hand Y-axes shows variable ranges to derive boxplot values from (black observed average for 2016; blue beyond 2016 predicted). The dashed orange lines show the top and bottom of ranges the R package MultiMOVE was constructed within. X-axis labels show the X-plot groups of year and board habitat type: A&H = arable and horticulture; I.G. = improved grassland; N.G. = neutral grassland; Br = Bracken.

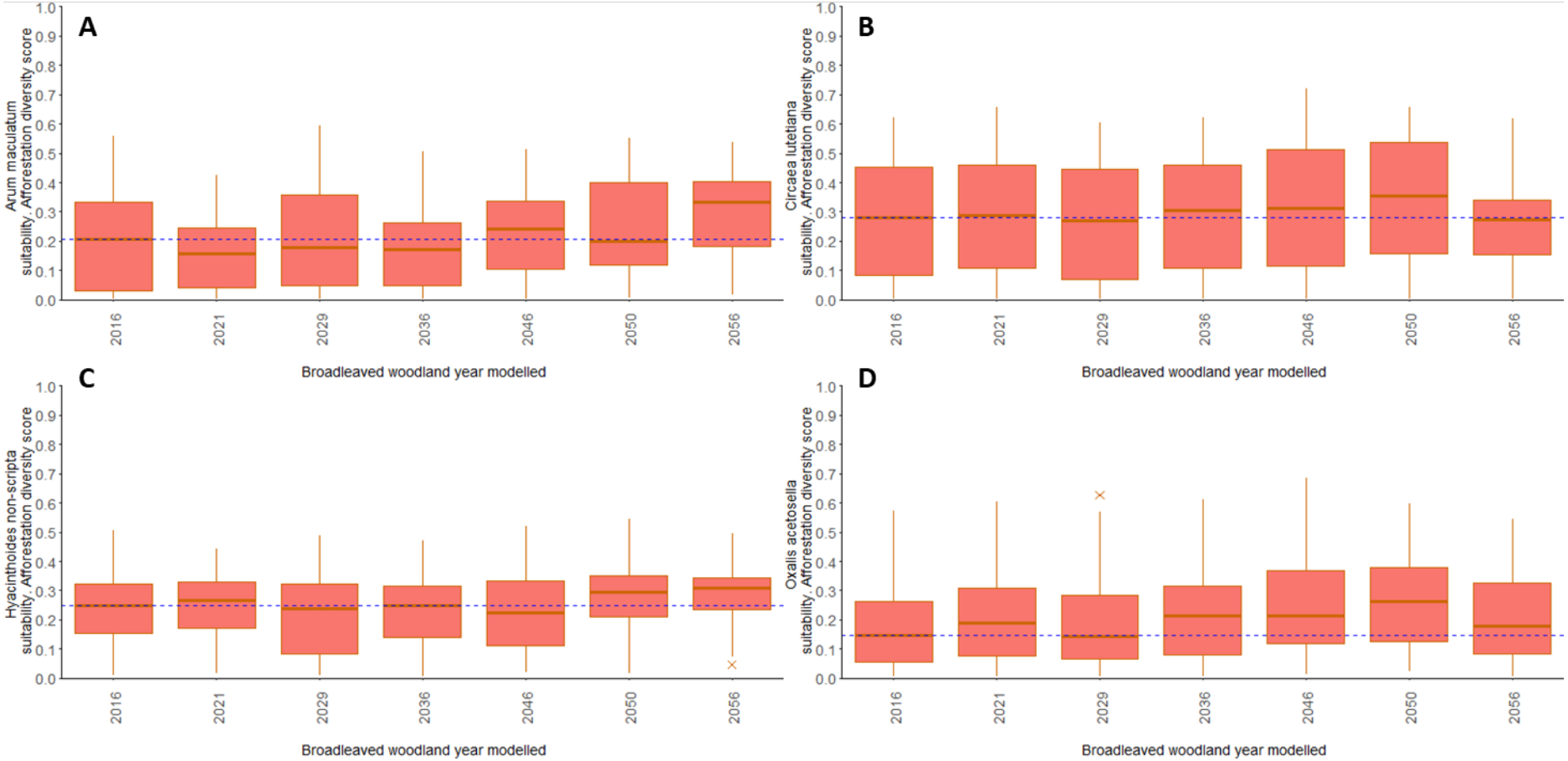

Figure B.3. Boxplots of *Arum maculatum*(A), *Circaea lutetiana*(B), *Hyacinthoides non-scripta*(C), and *Oxalis acetosella*(D), MutliMOVE output results. Data represents broadleaved woodland at baseline in 2016 from Glastir Monitoring and Evaluation Program data under predicted climate data (UKCP18).

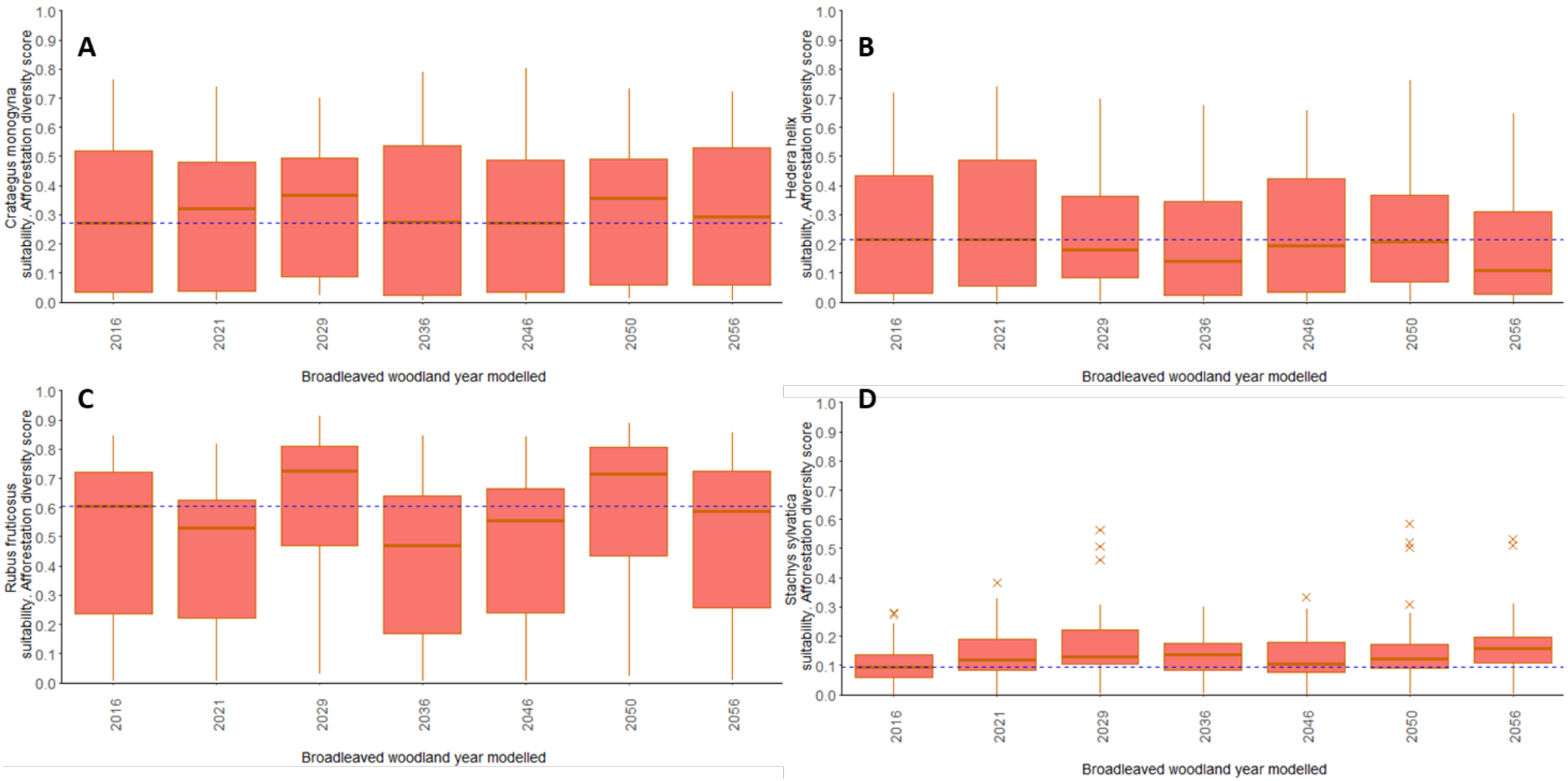

Figure B.4. Boxplots of *Crataegus monogyna*(A), *Hedera helix*(B), *Rubus fruticosus*(C), and *Stachys sylvatica*(D), MutliMOVE output results. Data represents broadleaved woodland at baseline in 2016 from Glastir Monitoring and Evaluation Program data under predicted climate data (UKCP18).

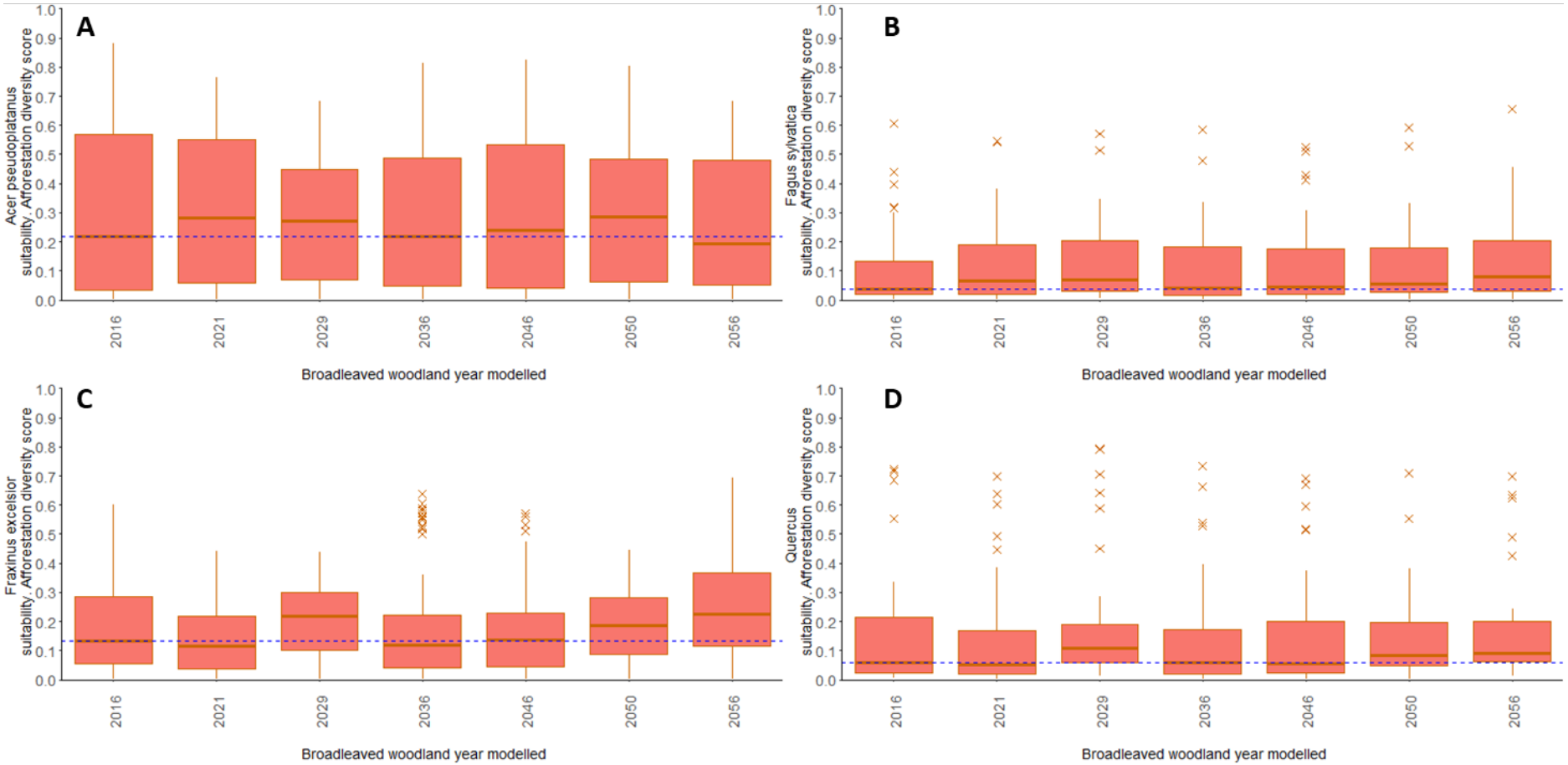

Figure B.5. Boxplots of *Acer pseudoplatanus*(A), *Fagus sylvatica*(B), *Fraxinus excelsior*(C) and *Quercus Sp.* (D), MutliMOVE output results. Data represents broadleaved woodland at baseline in 2016 from Glastir Monitoring and Evaluation Program data under predicted climate data (UKCP18).

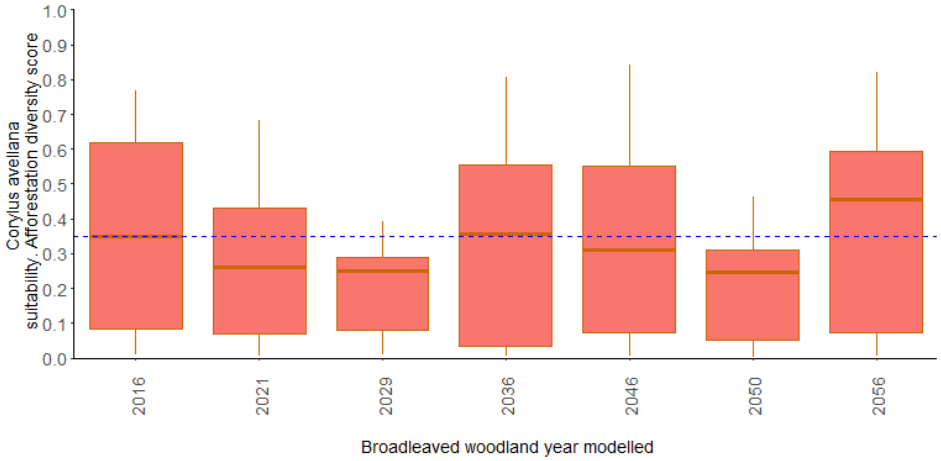

Figure B.6. Boxplots of *Corylus avellana*, MutliMOVE output results. Data represents broadleaved woodland at baseline in 2016 from Glastir Monitoring and Evaluation Program data under predicted climate data (UKCP18).

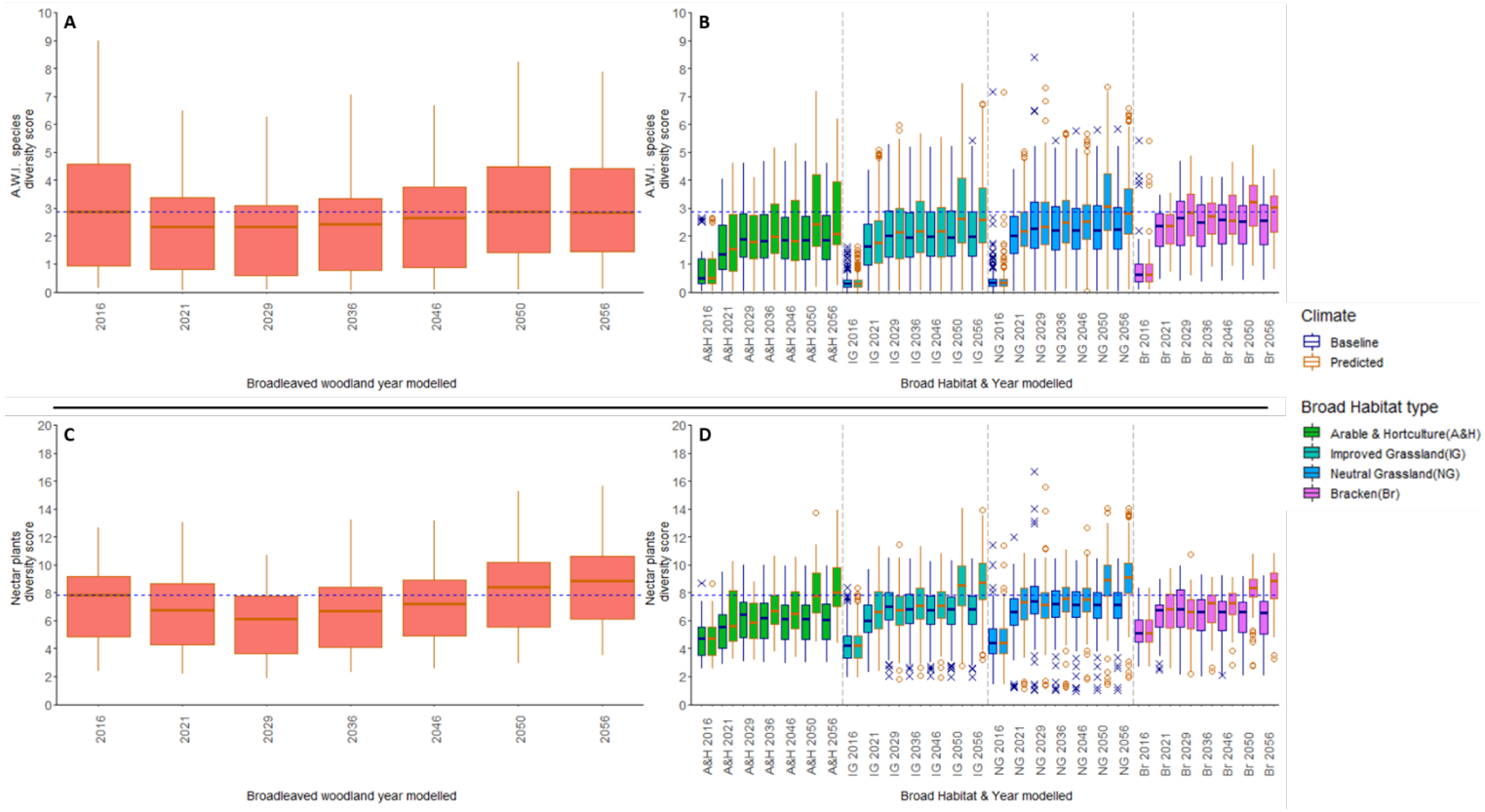

Figure B.7. Boxplots of species group diversity scores: **A**, Broadleaved woodland habitat ancient woodland indicator (A.W.I.) species at baseline in 2016 and later years with predicted climate; **B**, the four habitats A.W.I. species scores at baseline and modelled as being planted broadleaf in subsequent years, with baseline and predicted climate; **D** Broadleaved woodland habitat nectar producing (N.P.) species at baseline in 2016 and later years with predicted climate; **C** the four habitats N.P. species scores at baseline and modelled as being planted broadleaf in subsequent years, with baseline and predicted climate. The **dashed blue line** represents the median A.W.I. score for broadleaved woodland at baseline in A&B and the same N.P. mean for D&C. The data used to create these boxplots was generated using an ecological niche model MultiMOVE, inputs were altered to represent baseline (1981-2016) and future climates using downscale UKCP18 climate data, incremental increase of cover weighted canopy height representing tree growth and generalised linear mixed effect models of soil variable change under broadleaved plantation.

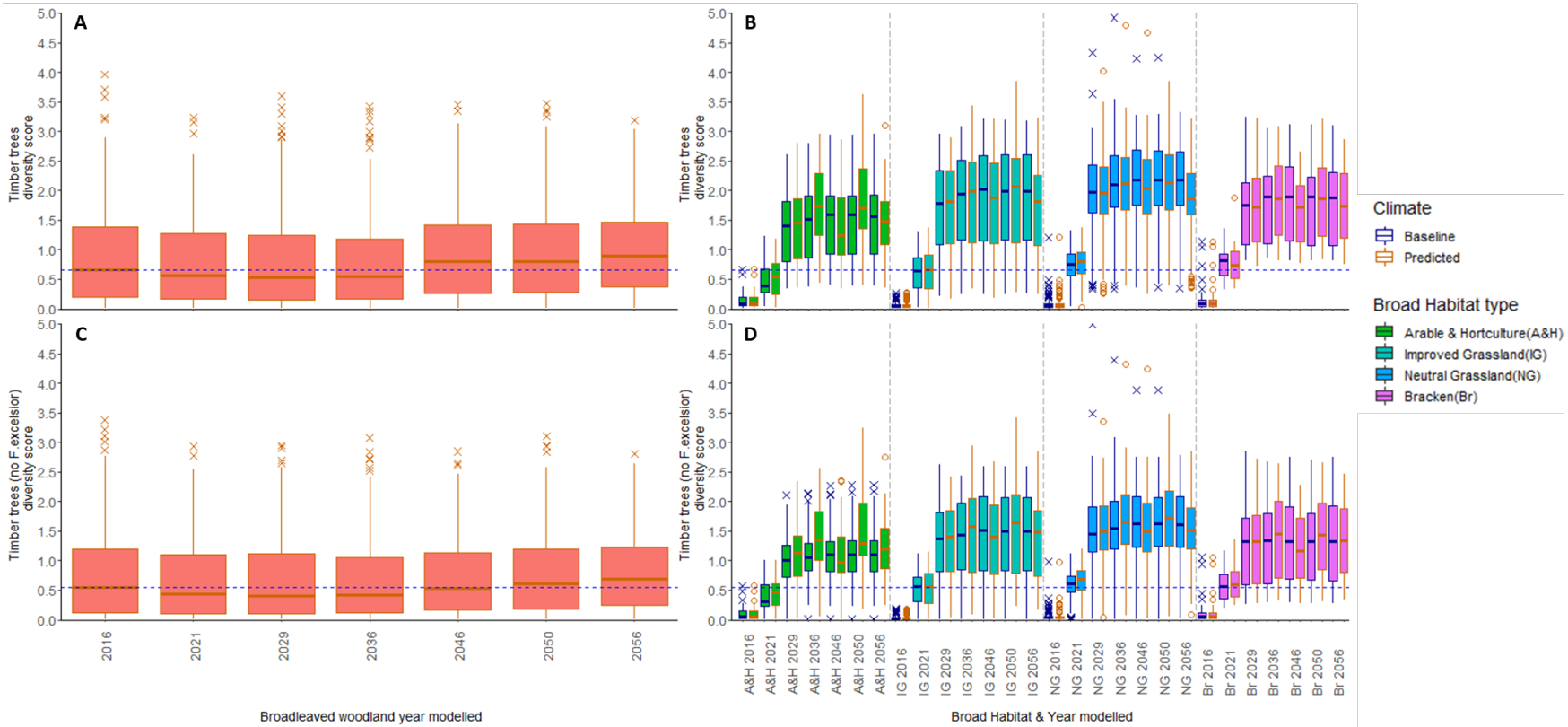

Figure B.8. Boxplots of diversity scores of timber species group diversity (TSGD): **A**, Broadleaved woodland habitat TSGD at baseline in 2016 and later years with predicted climate; **B**, the four habitats at baseline and modelled as being planted broadleaf TSGD in subsequent years, with baseline and predicted climate; **D** is the same as A but with *Fraxinus excelsior* removed; **C** is the same as B with *Fraxinus excelsior* removed. The **dashed blue line** represents the mean TSGD for broadleaved woodland at baseline in A&B and the mean TSGD without *F. excelsior* for broadleaved woodland at baseline for D&C. The data used to create these boxplots was generated using an ecological niche model MultiMOVE, inputs were altered to represent baseline (1981-2016) and future climates using downscale UKCP18 climate data, incremental increase of cover weighted canopy height representing tree growth and generalised linear mixed effect models of soil variable change under broadleaved plantation.

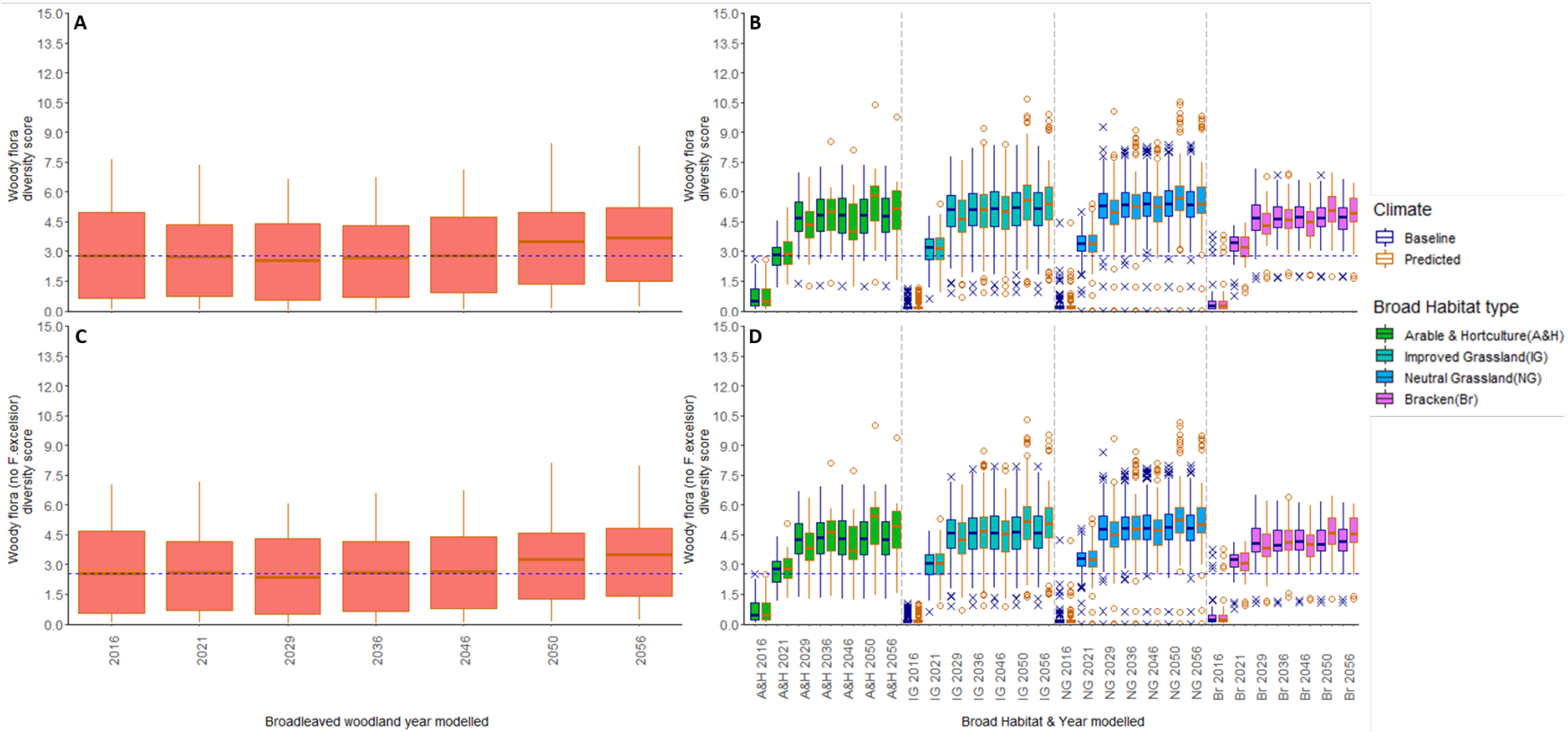

Figure B.9. Boxplots of diversity scores of woody flora (WFD): **A**, Broadleaved woodland habitat WFD at baseline in 2016 and later years with predicted climate; **B**, the four habitats at baseline and modelled as being planted broadleaf WFD in subsequent years, with baseline and predicted climate; **D** is the same as A but with *Fraxinus excelsior* removed; **C** is the same as B with *Fraxinus excelsior* removed. The **dashed blue line** represents the median WFD for broadleaved woodland at baseline in A&B and the median WFD without *F. excelsior* for broadleaved woodland at baseline for D&C. The data used to create these boxplots was generated using an ecological niche model MultiMOVE, inputs were altered to represent baseline (1981-2016) and future climates using downscale UKCP18 climate data, incremental increase of cover weighted canopy height representing tree growth and generalised linear mixed effect models of soil variable change under broadleaved plantation.

B.4 | Climatic variables

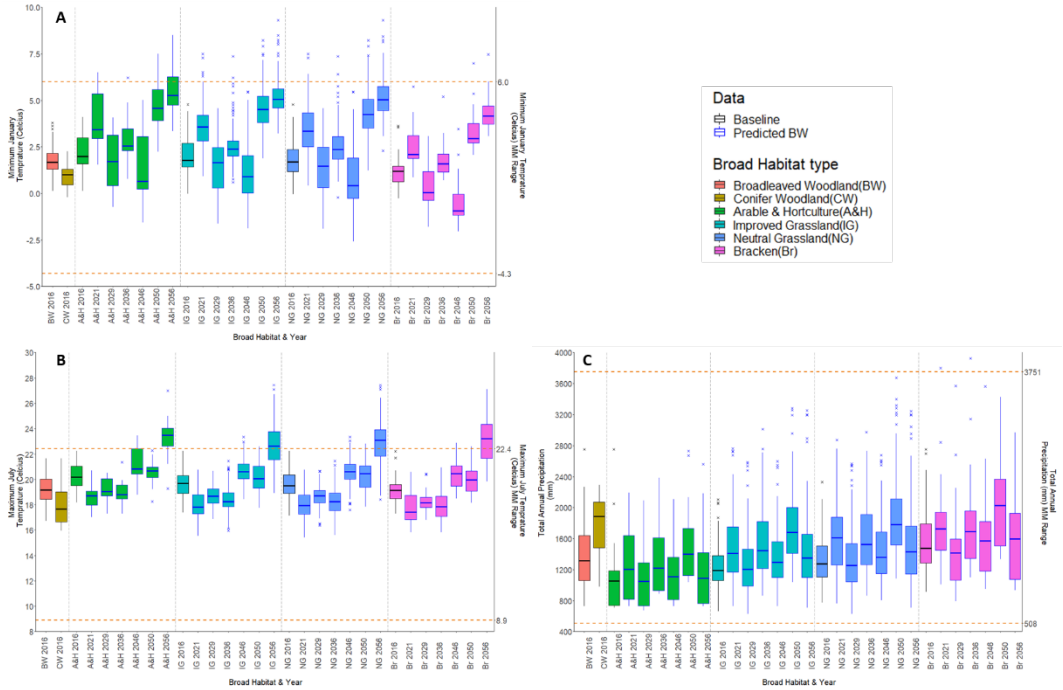

Figure B.10. Boxplots showing Glastir Environmental Monitoring Program X-plot climate data from UKCP18 at 1 km square scale from 2016 (averaged from 1981 to 2016 as a baseline) through subsequent predicted years up to 2056. Observed (2016, black edged box plots) data was sourced from Met Office HadUK-Grid, 1 km climate data and averaged. Predictions data (blue edged box plots) from the UKCP18 high emissions scenario, RCP8.5, UK regional 12 km scale probabilistic data, was downscaled to 1km. **A. Total annual precipitation** in mm, **B. minimum January temperature** in °C and **C. Maximum July temperature** in °C; georeferenced to the 1 km square each X-plot was within. Left hand Y-axes shows variable ranges to derive boxplot values from (**black observed average for 2016; blue beyond 2016 predicted**). The **dashed orange lines** show the top and bottom of ranges the R package MultiMOVE was constructed within. X-axis labels show the X-plot groups of year and board habitat type: **A&H = arable and horticulture; I.G. = improved grassland; N.G. = neutral grassland; Br = Bracken.**

C | Appendix C. Supporting information and data for Chapter four

C.1 | Description of grassland Broad Habitat Types

The three broad habitats, improved grassland, neutral grassland and acid grassland are described in Jackson (2000). During the baseline Glastir Monitoring and Evaluation Programme (GMEP) survey areas of land were assigned to these three broad habitats among others using a vegetation key available online at: http://nora.nerc.ac.uk/id/eprint/5194/1/N005194CR.pdf.

The top 10 most common species in quadrats surveyed in GMEP and assigned to each broad habitat were as follows:

- **Improved grassland:** *Lolium perenne, Trifolium repens, Ranunculus repens, Holcus lanatus, Cerastium fontanum, Taraxacum agg., Poa trivialis, Agrostis capillaris, Poa annua, Rumex obtusifolius*
  Management: Regular fertiliser application and possibly manure too with cutting and grazing.
- **Neutral grassland:** *Holcus lanatus, Agrostis capillaris, Trifolium repens, Lolium perenne, Ranunculus repens, Cerastium fontanum, Anthoxanthum odoratum, Taraxacum agg., Cynosurus cristatus, Rumex acetosa*
  Management: Regular grazing possible with cutting with little to no fertiliser application or manure.
- **Acid grassland:** *Rhytidiadelphus squarrosus, Galium saxatile, Anthoxanthum odoratum, Festuca ovina, Agrostis capillaris, Potentilla erecta, Deschampsia flexuosa, Pleurozium schreberi, Vaccinium myrtillus, Hylocomium splendens*
  Management: Grazing with rarely if ever occurring fertiliser application and cutting.

C.1 | References

Jackson, D. L. (2000). Guidance on the interpretation of the Biodiversity Broad Habitat Classification (terrestrial and freshwater types): Definitions and the relationship with other habitat classifications. Joint Nature Conservation Committee, Peterborough, UK.

C.2 | Appendix C. Species pool for modelling

The species group lists below can be found in the table included with this document:

- Nitrogen fixers (Smart *et al.*, 2017); 21 species; N_fixers in **Table C.1**.
- Nitrophiles (Rowe *et al.*, 2016; Smart *et al.*, 2017); 68 species; Nitrophilous_Sp. in **Table C.1**.
- Nitrophobes (Rowe *et al.*, 2016; Smart *et al.*, 2017); 273 species; Nitrophobous_Sp. in **Table C.1**.
- Species with leaf N content data from the TRY plant functional trait database (Kattge *et al.*, 2020); 148 species; N_holders in **Table C.1**.

The species list can be found within the .csv file:

Table C.1.*Appendix C.2.* N_Sp._groups.csv
listed with this document but available at the DOI:
http://dx.doi.org/10.13140/RG.2.2.10410.90560.

C.2 | References

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Tautenhahn, S., Werner, G. D. A., Aakala, T., & Abedi, M. (2020). TRY plant trait database–enhanced coverage and open access. *Global Change Biology*, *26*(1), 119–188.

Rowe, E. C., Ford, A. E. S., Smart, S. M., Henrys, P. A., & Ashmore, M. R. (2016). Using qualitative and quantitative methods to choose a habitat quality metric for air pollution policy evaluation. *PloS One*, *11*(8), e0161085.

Smart, S. M., Henrys, P. A., Norton, L. R., Wallace, H., Wood, C. M., Williams, B., & Bunce, R. G. H. (2017). Changes in the frequency of common plant species across linear features in Wales from 1990 to 2016: implications for potential delivery of ecosystem services. *New Journal of Botany*, *7*(2–3), 112–124. https://doi.org/10.1080/20423489.2017.1408190

C.3 | Appendix C. Modelling change in soil variables with N use

Determining how soils change in response to management was achieved via constructing generalized linear mixed-effects models trained on data gathered from literature review where the effects of N use on soil variables had been measured over time. The use of biogeochemistry models to dynamically process the impact of management change was not adopted because the necessary soil measurements do not exist for each modelled location. Using average inputs coarsely resolved to larger grid squares and dominant soil type would have greatly decreased the accuracy and realism of the modelling process removing the benefit of filtering the observed plant species composition at our very high resolution sampling sites.

The three soil variables (C, N, pH) were also modelled independently of each other as no study measured all these variables together over long enough time periods. Hence, our results are strongly dependent on the representativeness of the studies selected from literature review and the realism of the modelled change in each variable.

Readers can inspect the underlying data and assess the representativeness of the observations and the robustness of the estimated soil changes via review of the below.

C.3 | Literature sources

Care was taken to closely match the methods of each study found during literature review to the CS methods or ensure data values could be converted to match. Non-UK studies were omitted. This search resulted in datasets of varying size as requests were made to study authors to provide full datasets but not always yielded, and also including relevant open access data; these are:

1. Project supplementary material from grassland restoration from arable (Pywell *et al.*, 2007)
2. UK Department for Environment, Food and Rural Affairs (Defra) report (Wagner *et al.*, 2014)
3. Defra project on managing grassland diversity (Defra, 2015)
4. Sheep grazing removal experiment, full data set provided by author (Marrs *et al.*, 2018)
5. Project on restoration from farmland (Pywell, Webb and Putwain, 1994)
6. Upland long term environmental change experiment, summary data (Mcgovern *et al.*, 2013)
7. A 12-year fertiliser and lime experiment, supplementary material from (Kirkham *et al.*, 2011)
8. Soil organic carbon stocks in upland grasslands (Eze, Palmer and Chapman, 2018)
9. Changes in soil C and N stoichiometry 21 years after land use change (Baddeley, Edwards and Watson, 2017)
10. Effects of long-term grassland management on the carbon and nitrogen pools (Egan, Crawley and Fornara, 2018)
11. Species-rich grasslands response to long-term simulated nitrogen deposition (Horswill *et al.*, 2008)
12. Improved grassland, 19 years of restoration management effects on soil and vegetation (Pavlů, Pavlů and Fraser, 2021)
13. Grassland 120 years of fertiliser addition impacts (Kidd *et al.*, 2017)
14. Elan Valley grasslands report (Hayes and Lowther, 2014)
15. Rothamsted Research, Park Grass long-term experiment data, full data set provided (Rothamsted Research, 2016)

This data was then used as described in the main text to created generalised linear mixed effect models for soil pH, total soil C%, and total soil N%. The data can be found within the .csv:

Table C.2. Appendix C.3. Soil N use data.csv
listed with this document but available at the DOI:
http://dx.doi.org/10.13140/RG.2.2.10410.90560.

C.3 | References

Baddeley, J. A., Edwards, A. C., & Watson, C. A. (2017). Changes in soil C and N stocks and C: N stoichiometry 21 years after land use change on an arable mineral topsoil. *Geoderma*, *303*, 19–26.

Defra. (2015). *Managing grassland diversity for multiple ecosystem services*. http://sciencesearch.defra.gov.uk/Default.aspx?Menu=Menu&Module=More&Location=None&Completed=0&ProjectID=17251

Egan, G., Crawley, M. J., & Fornara, D. A. (2018). Effects of long-term grassland management on the carbon and nitrogen pools of different soil aggregate fractions. *Science of the Total Environment*, *613*, 810–819.

Eze, S., Palmer, S. M., & Chapman, P. J. (2018). Soil organic carbon stock and fractional distribution in upland grasslands. *Geoderma*, *314*, 175–183.

Hayes, M. J., & Lowther, R. A. (2014). *Conservation management of species-rich grasslands in the Elan Valley, Radnorshire*. https://www.elanvalley.org.uk/sites/default/files/fileman/Hayes__Lowther_2014_-_Conservation_management_of_species-rich_grasslands_in_the_Elan_Valley_Radnorshire_-_Evidence_report_8.pdf

Horswill, P., O'Sullivan, O., Phoenix, G. K., Lee, J. A., & Leake, J. R. (2008). Base cation depletion, eutrophication and acidification of species-rich grasslands in response to long-term simulated nitrogen deposition. *Environmental Pollution*, *155*(2), 336–349.

Kidd, J., Manning, P., Simkin, J., Peacock, S., & Stockdale, E. (2017). Impacts of 120 years of fertilizer addition on a temperate grassland ecosystem. *PLoS One*, *12*(3), e0174632.

Kirkham, F., Dunn, R., Tallowin, J., Bhogal, A., & Chambers, B. (2011). *BD1468 Appendix 2, Are inputs of fertilizer and lime compatible with the restoration of species diversity to hay meadows? Evidence from a 12 year fertilizer and lime experiment*. Department for Environment, Food and Rural Affairs (Defra), Nobel House, 17 Smith Square, London SW1P 3JR helpline@defra.gsi.gov.uk. http://sciencesearch.defra.gov.uk/Default.aspx?Module=More&Location=None&ProjectID=16130

Marrs, R., Sánchez, R., Connor, L., Blackbird, S., Rasal, J., & Rose, R. (2018). Effects of removing sheep grazing on soil chemistry, plant nutrition and forage digestibility: Lessons for rewilding the British uplands. *Annals of Applied Biology*, *173*. https://doi.org/10.1111/aab.12462

Mcgovern, S., Evans, C. D., Dennis, P., Walmsley, C., Turner, A., & Mcdonald, M. A. (2013). Resilience of upland soils to long term environmental changes. *Geoderma*, *s 197–198*, 36–42. https://doi.org/10.1016/j.geoderma.2012.12.018

Pavlů, L., Pavlů, V. V, & Fraser, M. D. (2021). What is the effect of 19 years of restoration managements on soil and vegetation on formerly improved upland grassland? *Science of the Total Environment*, *755*, 142469.

Pywell, R. F., Bullock, J. M., Tallowin, J. B., Walker, K. J., Warman, E. A., & Masters, G. (2007). Enhancing diversity of species-poor grasslands: An experimental assessment of multiple constraints. *Journal of Applied Ecology*, *44*(1), 81–94. https://doi.org/10.1111/j.1365-2664.2006.01260.x

Pywell, R. F., Webb, N. R., & Putwain, P. D. (1994). Soil fertility and its implications for the restoration of heathland on farmland in southern Britain. *Biological Conservation*, *70*(2), 169–181.

Rothamsted Research. (2016). *Park Grass soil pH*. https://doi.org/10.23637/KeyRefOAPGsoilpH

Wagner, M. ., Bullock, J. M. ., Hulmes, S. ., Hulmes, L. ., Peyton, J. ., Amy, S. ., Savage, J. ., Dos Santos Pereira, G. ., Tallowin, J. R. B. ., Dunn, R. M. ., & Pywell, R. F. (2014). *BD1459: Techniques to enhance the establishment and persistence of poor-performing species in grassland restoration - RP00199*. http://publications.naturalengland.org.uk/publication/5700071847886848?category=513173

C.4 | Appendix C. Workflow output graphical plots.

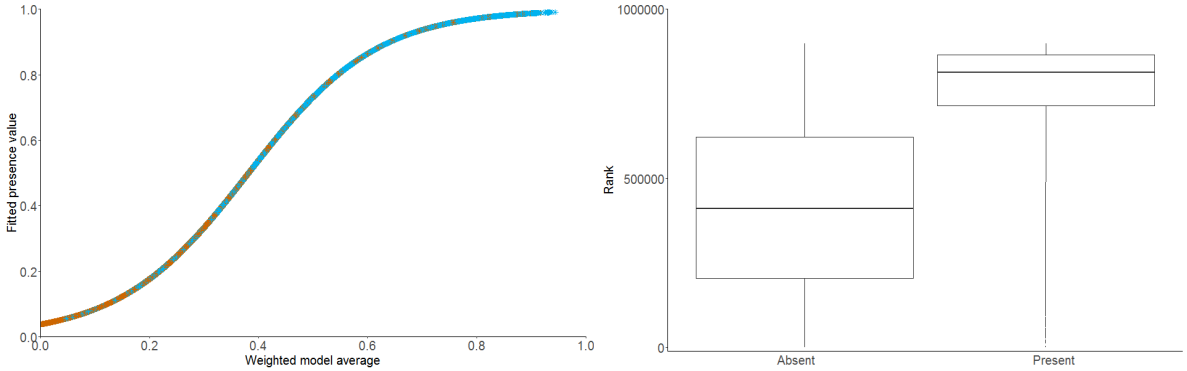

Figure C.1. Results of testing the species ecological niche model MultiMOVE outputs against the observed 2007 baseline. **Left,** Logistic regression (LR) of weighted model averages (WMA, or habitat suitability) of species per X-plot observed as present (**light blue**) or not present (**brown**). A species within a plot having a WMA of 0.386 or over according to the LR is more likely to be observed as present (fitted presence of 0.51) than absent within the input data (logistical regression WMA model coefficients P-value <0.001). **Right,** Boxplots with median rank of WMA values shown as the central thicker horizontal line, central hinges and out whiskers represent the 1st, 2nd & 3rd Interquartile ranges from bottom to top.

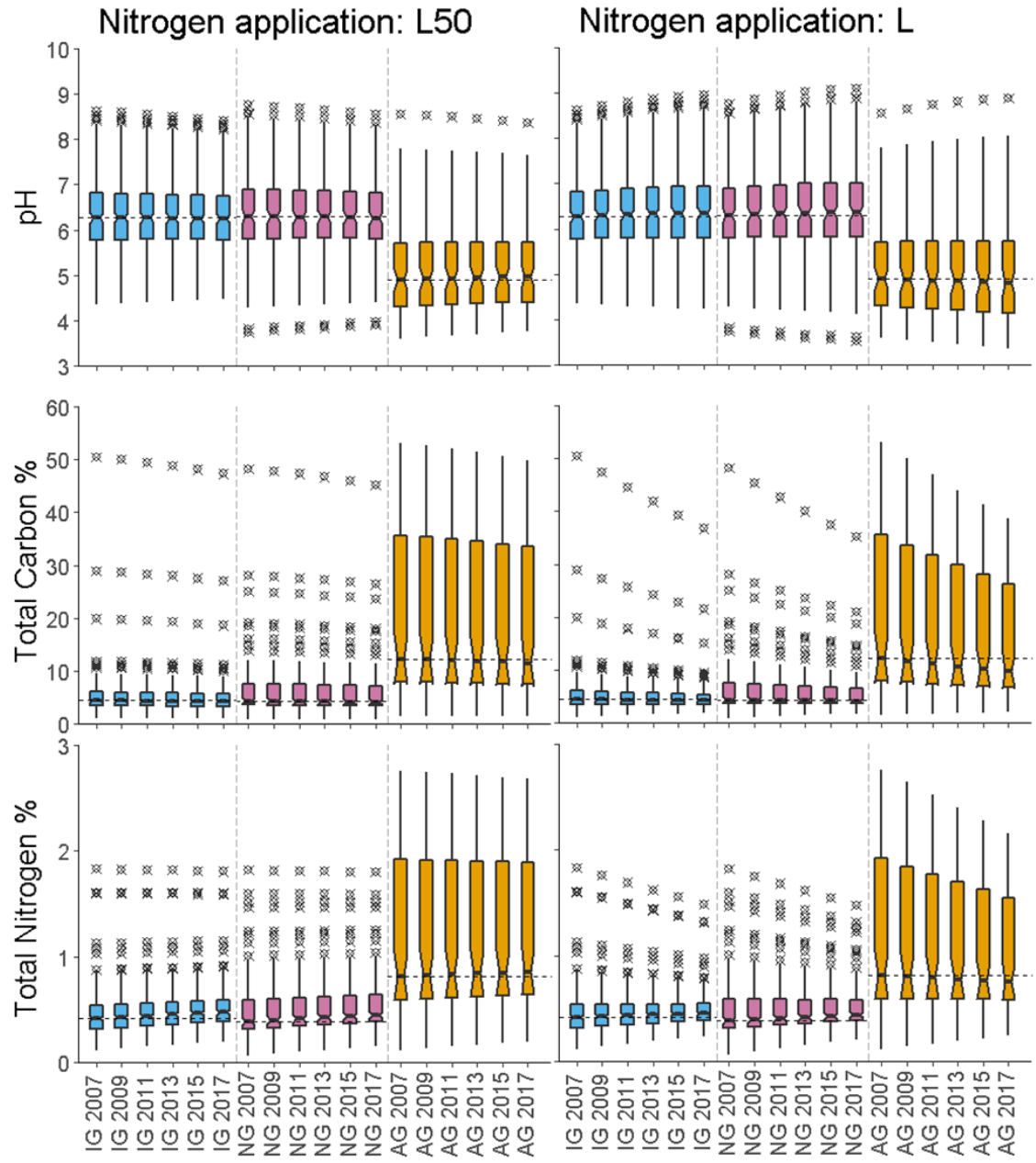

Figure C.2. Boxplots show soil pH (top row); total soil carbon% (middle row); total soil nitrogen% (bottom row) under each scenario, board habitat and year. Columns are nitrogen fertiliser application scenarios: L50 = Application of less than 50 kg ha^{-1} yr^{-1} of N; L = Low level application of N, 50-100 kg ha^{-1} yr^{-1}. All values are driven by soil variable (pH;C%;N%) generalised linear mixed effect models of different categorised levels of fertiliser applications. X-axis = Broad Habitats (BH): IG = Improved grassland (blue); NG = Neutral grassland (pink); AG = Acid grassland (orange); the dashed line in each part of each plot represents the BH's 2007 median value.

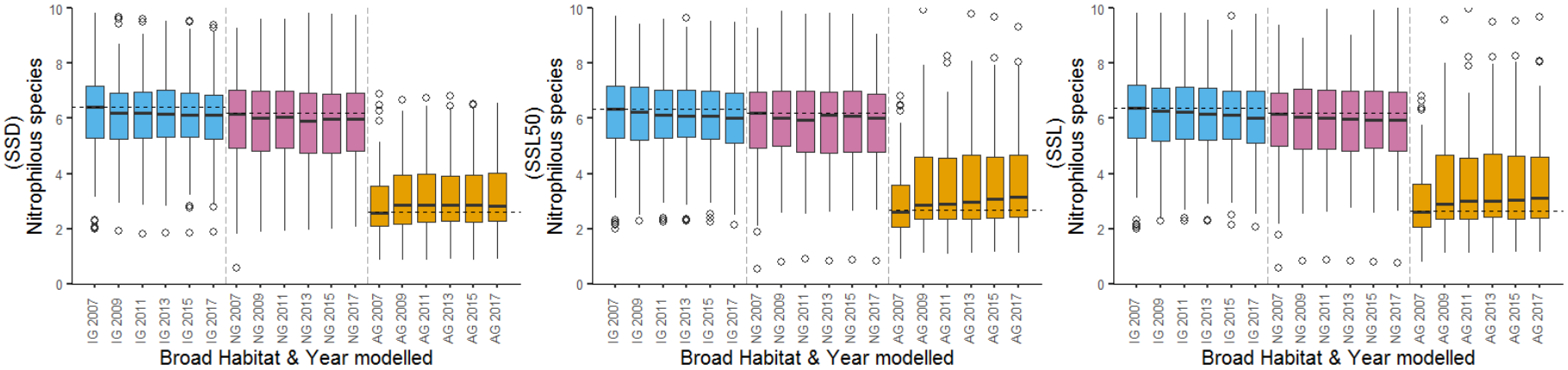

Figure C.3. Boxplots show the Nitrophilous species group diversity score under each scenario, board habitat and year. Scenarios bracketed beside the Y-axis are: SSD = Nitrogen deposition (Ndep) from Bayesian modelling N deposition effects on Ellenberg N and a recovery from acidification increment applied to pH before generating Ellenberg R from soil variables (field moisture %, pH, C%, N%); SSL50 = Application of less than 50 kg ha^{-1} yr^{-1} of N; SSL = Low level application of N, 50-100 kg ha^{-1} yr^{-1}. SSL50 & SSL values are driven by soil variable (pH;C%;N%) generalised linear mixed effect models of different categorised levels of fertiliser applications. X-axis = Broad Habitats (BH): IG = Improved grassland (blue); NG = Neutral grassland (pink); AG = Acid grassland (orange); the dashed line in each part of each plot represents the BH's 2007 median value.

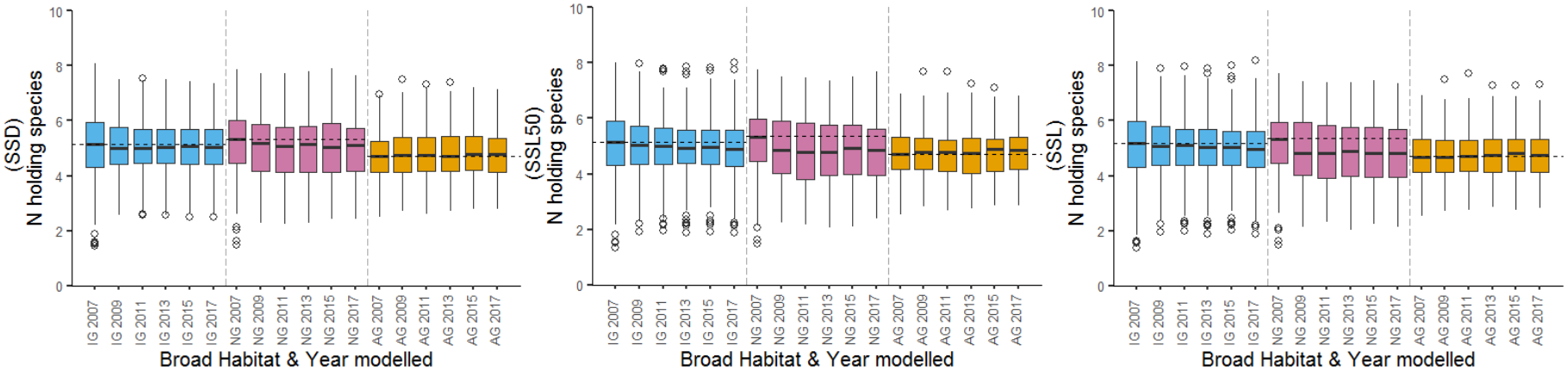

Figure C.4. Boxplots show the species group diversity score of species with Leaf nitrogen content data from TRY (Kattge *et al.*, 2020) under each scenario, board habitat and year. Scenarios bracketed beside the Y-axis are: SSD = Nitrogen deposition (Ndep) from Bayesian modelling N deposition effects on Ellenberg N and a recovery from acidification increment applied to pH before generating Ellenberg R from soil variables (field moisture %, pH, C%, N%); SSL50 = Application of less than 50 kg ha-1 yr-1 of N; SSL = Low level application of N, 50-100 kg ha-1 yr-1. SSL50 & SSL values are driven by soil variable (pH;C%;N%) generalised linear mixed effect models of different categorised levels of fertiliser applications. X-axis = Broad Habitats (BH): IG = Improved grassland (blue); NG = Neutral grassland (pink); AG = Acid grassland (orange); the dashed line in each part of each plot represents the BH's 2007 median value.

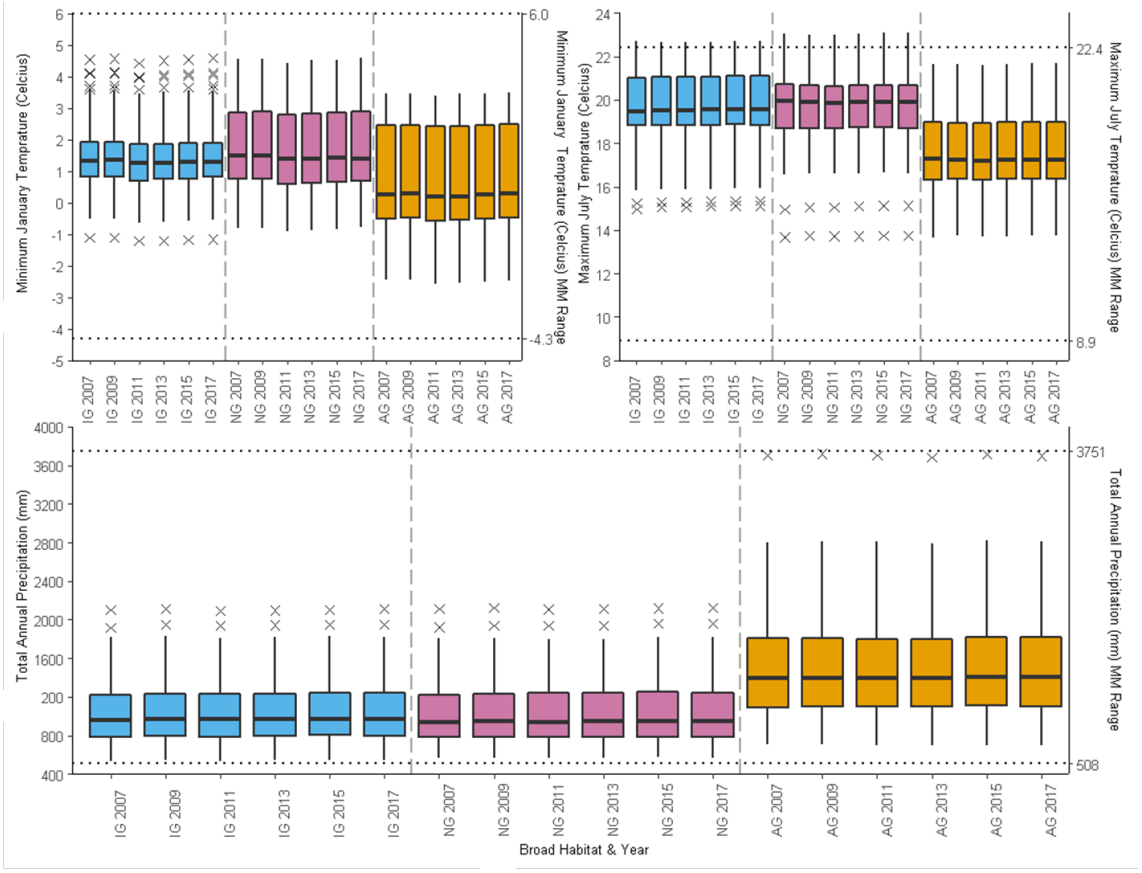

Figure C.5. Boxplots show the climate data from UKCP18 at 1 km square scale for each board habitat and year in the scenarios (climate data is the same for all scenarios). The right hand Y-axes with associated horizontal lines shows the operating space of the ecological niche model MultiMOVE reflective of the range of its training data. Broad Habitats (BH): IG = Improved grassland (blue); NG = Neutral grassland (pink); AG = Acid grassland (orange).

D | Appendix D. Supporting information and data for Chapter five

D.1 | Appendix D. Comparison of modelled and observed data for validation

The table below (**Table D.1**) shows the comparison of the scenarios constructed within *Chapter 4* with the observed baseline Glastir Monitoring and Evaluation Program data (Emmett *et al.*, 2017).

Table D.1. Significant differences comparing variables from modelled scenarios using Countryside Survey data with observed data from the Glastir Monitoring and Evaluation Program (GMEP). The data here considers only one year, 2016 as this is the year the GMEP surveying completed. The comparison was determined using an unpaired t-test with significance indicated by: **NS** = Not significant; ***** = p-value<0.05; **-** = Not applicable. Variables: **EbN** = Ellenberg nutrient score; **EbR** = Ellenberg reactivity score; **pH** = soil pH; **C%** = total soil carbon content by percentage; **N%** = total soil nitrogen content by percentage. Scenarios: **Ndep** = Background Nitrogen deposition; **L<50** = Management representative of livestock grazing with N applications of less than 50 kg ha^{-1} yr^{-1}; **L** = Management representative of livestock grazing with N applications of 50-100 kg ha^{-1} yr^{-1}. The increasing shading represents from light to dark and increase in N abundance change within the scenarios. Scenarios **L** & **L<50** represent levels of Nitrogen use based on the Soil Nitrogen Supply status for Long-term grass found in the RB209 Nutrient Management Guide (AHDB, 2021).

Scenario	Countryside Survey Plots	GMEP Plots	Year	Grassland Habitat	Significant difference of predictions versus (GMEP) observations				
					EbR	EbN	pH	C%	N%
N dep	44	22	2016	Improved	*	*	-	-	-
N dep	12	8	2016	Neutral	*	*	-	-	-
N dep	6	4	2016	Acid	*	*	-	-	-
L<50	44	22	2016	Improved	*	*	*	NS	NS
L<50	12	8	2016	Neutral	*	*	NS	*	*
L<50	6	4	2016	Acid	*	*	NS	NS	NS
L	44	22	2016	Improved	*	*	*	NS	NS
L	12	8	2016	Neutral	*	*	NS	*	*
L	6	4	2016	Acid	*	*	NS	NS	NS

This comparison was explored to validate the predictions from the three scenarios within *Chapter 4* , however a robust comparison was not possible. This is because data measuring the real amount of N deposition or fertiliser applied within the GMEP data is not available, so it is unknown if the data (**Table D.1**) is a robust like-for-like comparison. The number of occurrences of significant differences between the modelled data and the observed data suggests it is not, like-for-like.

D.1 | References

AHDB. (2021). *Section 3 Grass and forage crops Nutrient Management Guide (RB209) 2: Vol. Section 3*. Agriculture and Horticulture Development Board. https://projectblue.blob.core.windows.net/media/Default/Imported Publication Docs/RB209 2021/RB209_Section3_2021_210208_WEB.pdf

Emmett, B. A., Abdalla, M., Anthony, S., Astbury, S., & August, T. (2017). Glastir Monitoring & Evaluation Programme. Final report. In *Final Report to Welsh Government*. https://doi.org/10.13140/RG.2.2.25314.02243