

# Hedges & edges: Spatially targeting woodland creation in fragmented landscapes

Samuel Mark Hughes

University of Leeds School of Biological Sciences

Submitted in accordance with the requirements for the degree of Doctor of  
Philosophy

June 2023

The candidate confirms that the work submitted is his own, except where work which has formed part of jointly authored publications has been included. The contribution of the candidate and the other authors to this work has been explicitly indicated below. The candidate confirms that appropriate credit has been given within the thesis where reference has been made to the work of others.

#### Chapter 2:

Hughes, S., Kunin, W., Watts, K. and Ziv, G., 2023. New woodlands created adjacent to existing woodlands grow faster, taller and have higher structural diversity than isolated counterparts. *Restoration Ecology*, p.e13889.

The study was initially conceived by SH after the pandemic prevented field work. All authors contributed to study design. SH collected and analysed the data. SH wrote the manuscript but all authors contributed to manuscript drafts.

#### Chapter 3:

Hughes, S., Kunin, W., Ziv, G., Watts, K., 2023. The effects of spatially targeted woodland creation on the colonisation credit of understory woodland plants. This manuscript is currently in its second round of reviewer comments at *Ecological solutions and evidence*.

The study was initially conceived by SH and KW on a trip to the Isle of Wight to scope potential sites. All authors contributed to study design. SH collected and analysed the data. SH wrote the manuscript but all authors contributed to manuscript drafts.



This copy has been supplied on the understanding that it is copyright material and that no quotation from the thesis may be published without proper acknowledgement.

The right of Samuel Mark Hughes to be identified as Author of this work has been asserted by Samuel Mark Hughes in accordance with the Copyright, Designs and Patents Act 1988.

© 2016 The University of Leeds and Samuel Mark Hughes.

## Acknowledgements

First, I would like to acknowledge my three supervisors, Bill Kunin, Guy Ziv, and Kevin Watts. They made weekly meetings a source of excitement thanks to their enthusiasm for good science and general support and encouragement. Without this team the present thesis could not have been completed and I owe them all a great deal for guiding me through this process.

I would also like to thank Forestry England, particularly the Hampshire office for touring us around the Isle of Wight to look at potential study sites for chapters two and three. Angus Clarke was especially helpful here, as he was so proactive in getting us in touch with landowners to seek permission to access sites, and was in general very supportive of our project.

The LUES group at Forest Research have also played a part in the completion of this thesis. By offering me three months work mid-way through this programme I was able to gain valuable experience from a scientific organisation that has direct impacts on woodland restoration policy. This short-term role also gave me a much needed step back from my PhD work, which motivated me and gave me a better long term perspective.

While doing this PhD I have found some fantastic friends who made the whole process very enjoyable and provided the moral support that makes undertaking a task like this possible. My partner especially has made the mental load of the final year a lot easier to handle, and has also provided some much needed motivation and advice regarding the write up of this thesis.

I certainly could not have even started this endeavour without the constant support and encouragement of my family. I am very lucky to have a stable foundation for whenever things might have been a bit overwhelming. They have always been there to offer advice and guidance, and really this thesis should be dedicated to them.

## Abstract

We are in a time of global restoration efforts to defragment and restore degraded woodland landscapes. However, this needs to be balanced with other important habitat types and economically productive land, which leaves limited space for woodland creation. This thesis unpicks how the spatial targeting of woodland creation can enhance the benefits obtained from new woodlands. It does this using a range of methods to assess multiple restoration success metrics. Chapter Two uses LiDAR data to assess how targeting woodland creation to enhance connectivity can increase the speed at which woodlands develop. Here, it finds that creating woodlands adjacent to mature stands increases their growth, and also leads to greater structural complexity. Chapter Three attempts to quantify the long ecological time-lags between creating woodlands and species colonisation. It shows that colonisation credit can take decades to fulfil, and that spatially targeting woodland creation can help to ameliorate this. Chapter Four assesses how different spatial targeting strategies can influence population dynamics of individual species at the landscape-scale, it then observes how the presence of ecological corridors modify the efficacy of these different strategies. This chapter shows that in the fragmented landscapes of the UK, extending existing woodland patches is generally the best strategy to increase population sizes and connect woodland fragments. However, the presence of hedgerows improves the performance of isolated stepping-stone habitats, and thus these must be utilised where woodland is created in an isolated setting. These results show that creating

woodlands adjacent to mature existing woodlands should be a priority. This will speed up the development of new woodlands, reduce local ecological time-lags, and improve population persistence across landscapes.

## Abbreviations

AGB - Above Ground Biomass

AIC - Akaike Information Criterion

CWM L - Community Weighted Mean Ellenberg L

CWM N - Community Weighted Mean Ellenberg N

CWM pH - Community Weighted Mean Ellenberg pH

DTM - Digital Terrain Model

ED - Edge Density

FHD - Foliage Height Diversity

GEDI - Global Ecosystems Dynamics Investigation

GLMM - Generalized Linear Mixed Model

IBM - Individual Based Model

LiDAR - Light Detection And Ranging

LMM - Linear Mixed Model

NFI - National Forest Inventory

NLP - National LiDAR programme

RH90 - Relative height at the 90th percentile of LiDAR returns

SRS - Savannah River Site

TIN - Triangulated Irregular Network

WGS - Woodland Grant Scheme

WrEN - Woodland Restoration and Ecological Networks

# Table of contents

<b>1</b>	<b>Introduction</b>	<b>1</b>
1.1	Woodland habitat loss . . . . .	2
1.1.1	Woodland restoration initiatives . . . . .	5
1.2	Where we create woodland matters . . . . .	6
1.3	Approaches to studying woodland restoration . . . . .	8
1.3.1	Natural experiments . . . . .	9
1.3.2	Remote sensing . . . . .	10
1.3.3	Simulation modelling . . . . .	11
1.4	Knowledge gaps . . . . .	12
1.5	Thesis structure . . . . .	15
<b>2</b>	<b>New woodlands created adjacent to existing woodlands grow faster, taller and have higher structural diversity than isolated counterparts</b>	<b>17</b>
2.1	Abstract . . . . .	17
2.2	Introduction . . . . .	18
2.3	Methods . . . . .	21
2.3.1	Study area and sample design . . . . .	21
2.3.2	LiDAR processing . . . . .	26
2.3.3	Statistical analysis . . . . .	27
2.4	Results . . . . .	29
2.5	Discussion . . . . .	30
<b>3</b>	<b>Spatial targeting of woodland creation can reduce the colonisation</b>	



<b>credit of woodland plants</b>	<b>40</b>
3.1 Abstract . . . . .	40
3.2 Introduction . . . . .	41
3.3 Methods . . . . .	45
3.3.1 Study region and site selection . . . . .	45
3.3.2 Field surveys . . . . .	48
3.3.3 Colonisation credit . . . . .	49
3.3.4 Community weighted mean Trait value . . . . .	49
3.4 Results . . . . .	50
3.5 Discussion . . . . .	54
3.6 Conclusions . . . . .	61
<b>4 How do ecological corridors modify habitat creation strategies?</b>	<b>63</b>
4.1 Abstract . . . . .	63
4.2 Introduction . . . . .	64
4.2.1 Aims and objectives . . . . .	69
4.3 Methods . . . . .	70
4.3.1 Landscape selection . . . . .	70
4.3.2 Conceptual Species . . . . .	75
4.3.3 Simulations . . . . .	76
4.3.4 Extracted metrics . . . . .	80
4.3.5 Statistical analysis . . . . .	80
4.4 Results . . . . .	82
4.4.1 Null Models . . . . .	82

4.4.2	Habitat creation models . . . . .	86
4.5	Discussion . . . . .	95
4.6	Conclusion . . . . .	100
<b>5</b>	<b>Conclusions</b>	<b>102</b>
5.1	Discussion and synthesis . . . . .	103
5.1.1	Woodland structural development . . . . .	103
5.1.2	Benefits to understory plant communities . . . . .	103
5.1.3	Population persistence across landscapes . . . . .	104
5.1.4	Connecting isolated woodlands with hedgerows . . . . .	105
5.1.5	Findings across spatial scales . . . . .	106
5.1.6	Context dependency . . . . .	107
5.1.7	Time lags associated with woodland creation . . . . .	108
5.2	Implications for woodland creation schemes . . . . .	108
5.2.1	Connecting created woodlands . . . . .	109
5.2.2	Connecting woodlands with hedgerows . . . . .	111
5.2.3	Carbon sequestration benefits . . . . .	112
5.2.4	Management interventions . . . . .	113
5.3	Future research . . . . .	114
5.3.1	Range shifting with climate change . . . . .	114
5.3.2	The influence of spatial scale . . . . .	115
5.3.3	Mychorrhizae . . . . .	116
5.3.4	Negative effects of ecological corridors . . . . .	117
5.4	Final remarks . . . . .	117

## List of Figures

- 1 A map showing the study region within the Isle of Wight. Mature created woodlands were created between the years 1970 and 1990, where young created woodlands were created between the years 1995 and 2005. The presence of an adjacent mature neighbor is denoted by color. All woodland plots used in the study were below 1 ha in area. . . . . 25
- 2 Two examples of recently created woodland connected to adjacent older neighboring woodlands. On the left the recently created woodland is connected to a closed canopy woodland, where on the right the recently created woodland is connected to a strip of mature trees. These more linear strips of trees were considered as adjacent neighboring woodlands as long as they ran parallel to the created woodland as in the picture. . . . . 28
- 3 A boxplot showing how the 90th percentile of canopy height (m) is affected by woodland age ( $p < 0.01$ ,  $t = -5.55$ ,  $df = 55$ ) and adjacency to mature neighboring woodlands ( $p < 0.05$ ,  $t = 2.3$ ,  $df = 55$ ). This index was measured from woodlands in the Isle of Wight using discrete return LiDAR data collected in the winter of 2021. . . . . 32

- 4 A boxplot showing how foliage height diversity is affected by woodland age ( $p < 0.01$ ,  $t = -5.32$ ,  $df = 55$ ) and adjacency to older neighboring woodlands ( $p < 0.05$ ,  $t = 3.2$ ,  $df = 55$ ). This index was measured from woodlands in the Isle of Wight using discrete return LiDAR data collected in the winter of 2021 and calculated using a modified version of Shannon’s evenness. . . . . 33
- 5 Examples of two young created woodlands, one (on the top row) planted adjacent to an older strip of woodland, and the other (on the bottom row) planted in isolation. The left column shows a cross-section of each woodland, for the young woodland planted adjacent to an older woodland, this older woodland is included in the cross-section. The right column is a bird’s eye view of each woodland, the adjacent older neighbor for the top woodland is colored darker. Both created woodlands are roughly the same age. This helps visualize how the woodland created adjacent to an older neighbor has grown taller. . . . . 34

6	A boxplot showing the effects of woodland age and adjacency to a mature woodland neighbor on the percentage growth between 2011 and 2021. Adjacency did not significantly affect growth rates, however on average young woodlands with adjacent neighbors grow more than their isolated counterparts. As LiDAR data collected in 2011 will had a different sampling protocol to that collected in 2021 it is important not to take this percentage change as raw growth, but instead consider it relative to other woodlands. . . . .	37
7	Map of the 23 study sites in the Isle of Wight made up of 8 ancient woodlands and 15 recent woodlands. These are organised into 8 blocks. Mature woodlands first appeared on maps between 1940 and 1970, where young woodlands first appeared around the start of the new millennium (1999-2005). The base map is provided by the OS zoomstack, where dark green patches represent other woodland. . . . .	47
8	Sum abundances of woodland plant species found across recent woodlands separated by age and the degree of isolation. This plot also shows the dominance of <i>Hedera helix</i> in more mature woodlands. Species marked with an asterisk are considered woodland specialists and not just woodland plants as characterised by Ellenberg values and functional traits (Kirby et al. 2012). . . . .	52

- 9 Pairwise colonisation credit between recent woodlands planted adjacent to an ancient woodland and those planted in isolation. These were separated into mature (50-80 years old) and young (16-22 years old) as denoted by shape. Numbers left of the forward slash are the amount of woodland plant species available in the nearby ancient woodland, where numbers right of the forward slash are the amount of these species that have made it to the created woodland. Adjacent woodlands had a significantly lower colonisation credit than isolated woodlands. These were separated into dispersal types also, mammals and birds, ants, wind and unspecialised. . . . . 53
- 10 The community weighted mean Ellenberg L value of woodlands grouped by age (Young, Mature and Ancient) and whether they were created adjacent to an ancient woodland or isolated from existing older woodland. Young woodlands are between 15 and 21 years of age, mature woodlands are 50-80 years of age, and ancient woodlands are believed to have existed since the 1600s. 55
- 11 The community weighted mean Ellenberg N value of woodlands grouped by age (Young, Mature and Ancient) and whether they were created adjacent to an ancient woodland or isolated from existing older woodland. Young woodlands are between 15 and 21 years of age, mature woodlands are 50-80 years of age, and ancient woodlands are believed to have existed since the 1600s. 56

12 The community weighted mean Ellenberg pH value of woodlands grouped by age (Young, Mature and Ancient) and whether they were created adjacent to an ancient woodland or isolated from existing older woodland. Young woodlands are between 15 and 21 years of age, mature woodlands are 50-80 years of age, and ancient woodlands are believed to have existed since the 1600s. 57

13 A map showing the 2125km<sup>2</sup> area covering part of the midlands in the UK. Red squares indicate the final 18 landscapes selected as model inputs. . . . . 73

14 The 18 landscapes chosen to independently vary in woodland percentage cover, woodland edge density and hedgerow area. The percentage woodland cover increases along the x axis where edge density increases along the y axis. . . . . 74

15 A diagram explaining the four conceptual species, the 18 original landscapes, and the habitat creation scenarios applied for the present study. Null models were run on the 18 original landscapes with hedgerow corridors and without, where habitat creation models were run on landscapes modified using the habitat creation scenarios, again with and without hedgerow corridors. . . . . 79

- 16 A scatter plot showing the mean population of null landscapes, with no habitat creation, and how this is effected by ED, the percentage woodland cover and the presence of hedgerow corridors. Population sizes were averaged over the last 50 years of simulations, and across 5 replicates for each landscape with and without hedgerow corridors. Rows are separated by species, and columns are separated as a categorical variable for percentage woodland cover so that any interactions between predictive variables can be viewed. The data for corridors present for Species 3 and Species 4 is not visible as these species were able to survive in all small habitat patches, meaning that the presence of corridors had little effect on their populations. . . . 84



17 A scatter plot showing the mean percentage of woodland patches occupied in null landscapes, with no habitat creation, and how this is effected by ED, the percentage woodland cover and the presence of hedgerow corridors. Occupancy percentages were averaged over the last 50 years of simulations, and across 5 replicates for each landscape with and without hedgerow corridors. Rows are separated by species, and columns are separated as a categorical variable for percentage woodland cover so that any interactions between predictive variables can be viewed. Species 3 and 4 are able to maintain populations in all small habitat patches, meaning that their occupancy does not change over time. As such they are removed from this plot . . . 85

18 A Boxplot showing how the presence of hedgerow corridors interacts with the different habitat creation scenarios (create adjacent and create isolated) to affect the percentage increase in populations for four different species. The plot is faceted by the percentage woodland cover of original landscapes. . . . . 87

19 Showing how the presence of hedgerow corridors interacts with the different habitat creation scenarios (create adjacent and create isolated) to affect the percentage increase in populations for four different species. The plot is faceted by ED of original landscapes. 88

20	A boxplot showing how the presence of hedgerow corridors interacts with the effectiveness of different habitat creation scenarios (create adjacent and create isolated) in increasing the occupancy of original habitat patches for four different species. The plot is faceted by how much woodland cover there was in the original landscape. . . . .	89
21	A boxplot showing how the presence of hedgerow corridors interacts with the effectiveness of different habitat creation scenarios (create adjacent and create isolated) to effect the population of newly created patches for four different species. The plot is faceted by how much woodland cover was in the original landscape. . . . .	91
22	A boxplot showing how the presence of hedgerow corridors interacts with the effectiveness of different habitat creation scenarios (create adjacent and create isolated) to effect the population of newly created patches for four different species. The plot is faceted by the ED of the original landscape. . . . .	92
23	A boxplot showing how the presence of hedgerow corridors interacts with the effectiveness of different habitat creation scenarios (create adjacent and create isolated) to effect the percentage occupancy of newly created patches by four different species. The plot is faceted by how much woodland cover there was in the original landscape. . . . .	93

24	A boxplot showing how the presence of hedgerow corridors interacts with the effectiveness of different habitat creation scenarios (create adjacent and create isolated) to effect the percentage occupancy of newly created patches by four different species. The plot is faceted by the ED of the original landscape.	94
A1	Height profiles of each individual created woodland calculated as the proportion of LiDAR returns in each 1m height bin. The top set (a) of figures are young created woodlands, where the bottom (b) set of figures are mature created woodlands. Bars filled with colours were created using LiDAR data from 2021, where transparent were created using LiDAR data from 2011. Red = those with adjacent neighbours, Blue = those planted in isolation . . . . .	170
A2	Bar graphs showing results of the sensitivity analysis. This explored how key parameters affect model outcomes by increasing or decreasing their values by 10%. Bars display the mean population outcomes after 5 model iterations, and error bars show the full range of population outcomes after 5 model iterations. Dispersal distance in SMS species ( , ) is controlled by the step mortality parameter. Mortality rate is not included for x or x as it is built into the fecundity parameter . . . . .	171

## List of Tables

1	Showing the distribution of plants across different age and isolation categories. Plants are also subset into woodland plants. Young woodlands were created between 1995 and 2001, where mature woodlands were created between 1940 and 1970. Adjacent woodlands were created adjacent to an ancient woodland, where isolated woodlands were not. . . . .	51
A1	Displaying how woodland samples are spread across ages, adjacent or isolated and geology. . . . .	143
A2	The results of 3 linear models assuming Gaussian error structures: the first predicting canopy height in the form of Relative Height at the 90th percentile, the second predicting the foliage height diversity, and the third predicting change in canopy height between 2011 and 2021. *= P between 0.01 and 0.05, **= P< 0.01 and - = non-significant. Substrate compared to Argillaceous rock and year planted compared to mature woodlands planted before 1980 . . . . .	144
A3	Full parameters used in Rangeshifter for all 4 conceptual species	145
A4	Results of statistical models predicting the populations and proportional occupation of 4 conceptual species across simulated landscapes . . . . .	146

# 1 Introduction

Habitat loss and fragmentation have had detrimental effects on biodiversity globally (IPBES 2019). This is particularly true for woodland, a complex habitat type that has been reduced over millenia (Laurance 2014). There are now efforts to reverse biodiversity decline by restoring fragmented and degraded ecosystems. For example, resources are being provided to create millions of hectares of woodland across the globe (Government of Canada 2020; HM Treasury 2020; European Commission 2021). However, where we create this new woodland will be constrained by other important habitats, competing economic interests and resource availability (Holl and Brancalion 2020; Hua et al. 2022). Thus, it is important for land managers to know how to spatially target woodland creation to accrue the most biodiversity benefits with limited space and resources.

Ecological theory alongside the study of historically fragmented landscapes can provide some guidance on how to spatially target new woodland. However, empirical evidence from restoration actions is also needed, as restored woodlands are functionally different to old-growth remnants and the way that woodland species utilise these two habitat types will vary (Peterken and Game 1984). This thesis aims to provide such evidence in a UK context by using a range of approaches to test how spatially targeting woodland creation can enhance biodiversity benefits. It does this first by using remotely sensed Light Detection and Radar (LiDAR) to assess woodland structure, then by quantifying the colonisation credit of recent woodlands and assessing what might be holding

this back, and finally by modelling different habitat creation strategies at the landscape scale.

This first chapter provides the theoretical framework for the following thesis and consists of 5 sections. The first section reviews the detrimental effects that habitat loss has on woodland biodiversity and the current aims to counter this by creating new woodland. The second section discusses how fundamental ecological theory, and evidence attained from fragmented landscapes show that where we create new woodland matters. The third and fourth sections review current approaches to evidencing woodland restoration strategies, and discuss some of the meaningful knowledge gaps still to fill. Finally, the fifth section sets out the empirical chapters of the thesis, presenting how these use a full range of restoration success criteria to assess the benefits of spatially targeting woodland creation.

## **1.1 Woodland habitat loss**

Habitat transformation is considered to be the greatest current threat to global biodiversity (IPBES 2019). Historically this has taken place to make room for farmland and the extraction of natural resources, and increasing agricultural and economic pressures could see this problem exacerbated in the near future (Habel et al. 2019). Woodlands are a prime example of reduced and fragmented habitat: 70% of global forested land is now within 1km of a woodland edge (Haddad et al. 2015). This is not just the product of recent history, as deforestation has been occurring globally throughout the Holocene, largely driven by anthropogenic land conversion for agriculture (Rackham 1980; Bhagwat et al. 2014). To take

England as an example, woodland conversion began in the Neolithic era and increased upon the Roman invasion, before continuing until total woodland cover was reduced to around 15% in the high middle-ages. Further, these remaining fragments did not resemble the original post-glacial woodlands, as centuries of management had significantly altered them (Rackham 1980). Between 1920 and 1980 this clearing process continued, alongside the conversion of ecologically important ancient woodland (Box 1) into timber plantations (Peterken 2000), bringing the native woodland cover of England to a historic low.

**Box 1:**

Ancient woodlands are defined in England as having been continuously wooded since 1600AD. These areas are assumed to be primary woodland with direct lineage from the original trees that colonised England following the last ice-age. Due to their long ecological continuity and unique management through history these woodlands are important to a range of woodland specialist species and communities.

Under habitat transformation the dual processes of habitat loss and fragmentation lead to reduced patch sizes and increased isolation across spatial scales, often leaving small patches of woodland isolated in a matrix of inhospitable land-use. Originally the term “fragmentation” was thought to capture all the necessary negative processes behind habitat transformation (Banks-Leite et al. 2020). However, habitat loss and habitat fragmentation have more recently been recognised as two different, but often interlinked, phenomena. Habitat loss per

se is simply the removal of habitat, where fragmentation is the splitting apart of habitat with no necessary habitat loss (Fahrig 2017a; Banks-Leite et al. 2020).

A reduction of patch size leads to a reduction in species diversity primarily due to the species area curve; as patch size reduces so does the number of species (Cain 1938). There are multiple hypothesized drivers of this curve, including equilibrium theory, where smaller patch sizes suppress populations and increase extinctions (MacArthur and Wilson 1967); and the habitat diversity hypothesis, where a larger area of habitat has more niches (Kallimanis et al. 2008). Species richness can also be reduced by a habitat loss event per se, by immediate local extinctions (Hooftman et al. 2016), extinction debts (Vellend et al. 2006) and reduced genetic diversity (Honnay and Jacquemyn 2007; Aavik et al. 2019). Fragmentation alongside habitat reduction leads to increased distance between habitat patches. This in turn hinders species abilities to disperse to new patches (Staude et al. 2020). If habitat patches become too isolated, their local populations will not be supplemented by nearby sources, leading to local extinction risks (Chase et al. 2020).

Increased fragmentation also leads to an increase in woodland edge density leading to a higher proportion of transition habitats (woodland into matrix) across woodland landscapes. An increase in woodland edges has profound effects on biodiversity because woodland edge habitats are fundamentally different to woodland interior habitats, and host compositionally distinct species communities (Hansson 2000; Watson et al. 2004). For example, woodland plants are specially adapted to compete in low shade and lower nutrient environments;



higher nitrogen and light availability along woodland edges has been shown to result in a higher proportion of generalist species and declines in woodland specialist species relative to woodland interiors (Willi et al. 2005).

### **1.1.1 Woodland restoration initiatives**

To counter-act centuries of woodland decline and ameliorate the resulting negative effects, there are now global initiatives to restore degraded wooded landscapes. The UK plans to plant 30000ha of trees a year by 2025 (HM Treasury 2020), the European Union plans to plant 3 billion trees before 2030 (European Commission 2021), Canada has pledged to plant 2 billion trees over 10 years (Government of Canada 2020), and the Bonn Challenge is a global pledge to restore 150m ha of woodland.

There are some concerns regarding the feasibility of global pledges to increase woodland cover. Fagan et al. (2020) calculated risk indicators for countries that had made commitments to the Bonn Challenge (Bonn Challenge 2019). These indicators were calculated using a range of metrics, such as historical efficiency and target feasibility. When looking at progress reported to the Bonn Challenge, the authors found that countries with higher risk indicator scores were already failing targets. There are also inherent issues with woodland habitat that makes reaching - even well-intentioned - biodiversity targets difficult. Woodlands are very slow to develop and take decades to become structurally mature (Fuentes-Montemayor et al. 2021). Their specialist species are also very slow colonisers and take decades to reach new patches (Honnay et al. 2002a). This leads to long

ecological time lags that last longer than most targeted time frames (Watts et al. 2020).

It is not just unrealistic pledges that cause concern; it is also the inclination to treat tree planting as a panacea. Holl and Brancalion (2020) argue that tree planting is not a simple solution, and cite examples where treating it as such can lead to detrimental outcomes. These include creating mono-cultures that harbour little biodiversity value, and replacing other important habitats. Further, there are trade-offs to be made between creating woodlands for biodiversity benefits and creating woodlands to enhance ecosystem services. Global woodland restoration for the purposes of timber production looks very different to woodland restoration for the purpose of biodiversity benefits; uniform plantations favour the former where native structurally complex stands favour the latter (Hua et al. 2022). Land managers need to navigate these trade-offs to meet a range of restoration targets, which leaves limited space to create woodlands for biodiversity benefits. As such, woodland creation needs to be targeted in a way that enhances biodiversity with limited space and resources.

## **1.2 Where we create woodland matters**

Fundamental ecological theory tells us that where we target woodland creation matters. Island biogeography dictates that larger islands closer to mainland source communities will hold a higher species richness than smaller more isolated islands (MacArthur and Wilson 1967). This is because larger area allows for larger populations, which reduces the risk of local extinctions. Further,

any local extinctions that do occur can be readily counteracted by immigrants from the nearby source population, meaning that larger less isolated patches equilibrate at higher species richness. In woodland landscapes, remnant old growth woodlands would act as the mainland where newly created patches would act as islands; thus creating larger new woodlands near to existing patches would theoretically accrue the highest local. Meta-population ecology is the theory that multiple local populations interact with each other to form a larger regional population. Thus the reduction of a local population can be counter-acted by immigrants from nearby communities (Hanski and Gaggiotti 1999). This would suggest that increasing connectivity between existing woodland fragments will increase the viability of their populations.

To summarise, ecological theory suggests that woodland creation should be targeted to increase contiguous habitat areas and increase the connectivity between existing patches. This is not just theoretically sound but also has a strong empirical foundation. Peterken and Game (1984) showed that woodland area positively correlates with the species richness of specialist woodland plants in remnant patches. The authors also found that secondary woodland spatially connected to ancient woodland held a higher number of woodland plant species. More recently Honnay et al. (2005) have found that herbaceous plant populations in small isolated patches are less viable than in larger well connected patches due to genetic drift and inbreeding depression. These results have also been mirrored across a range of taxa (Humphrey et al. 2015) demonstrating the importance of woodland size and connectivity.

It may be useful to consider connectivity in the form of habitat networks as described by Lawton et al (2010) in the influential “Making Space for Nature” report. This report concluded that England’s protected areas need to be bigger, better, and more joined up, which echoes the ecological theory and evidence discussed above. Here, a habitat network is made up of core habitat patches that are connected by corridor features and stepping stones. In the woodland study system, connected networks consist of remnant old-growth patches of woodlands connected by ecological corridors (e.g. hedgerows), recent woodland patches and trees outside of woodland. Evidence is needed to inform land managers on how best to enhance these habitat networks (Isaac et al. 2018).

### **1.3 Approaches to studying woodland restoration**

There are a range of approaches to provide evidence on how to target woodland restoration. However, evidence is best provided by studies on restoration actions, rather than extrapolating from fragmented landscapes (Watts et al. 2016). This is because the processes of habitat fragmentation and habitat restoration are not necessarily symmetrical due to functional groups responding differently to each process. To take woodland plants as an example: these species will persist for centuries in fragmented habitats (Naaf and Kolk 2015), leading us to believe that habitat quality is more important to their biodiversity than connectivity. However they are also poor dispersers (Honnay et al. 2005), meaning that they will not take advantage of newly created habitat unless it is well connected. Here I will discuss the current approaches to evidencing restoration strategies, from natural

experiments through to remote sensing and finally to simulation modelling.

### **1.3.1 Natural experiments**

Natural field experiments have recently been employed to specifically study woodland restoration strategies and the importance of connectivity. For example the Savannah River Site (SRS) corridor project in South Carolina created replicates of restored woodland patches with different connectivity treatments in the form of corridors (Haddad 1997). This was performed by clearing patches of productive pine plantations to allow the native long-leaf pine savannah to regenerate. Strips of cleared conifer forest were also used as corridors between restored patches, and each replicate block contained some connected patches and some isolated patches. This large-scale natural experiment has since found that corridors increase species richness and reduce local extinctions in restored woodlands (Damschen et al. 2019). Natural experiments such as this are important and provide unique insights into woodland restoration. However, these are resource intensive and can take decades to produce results due to ecological time lags (Watts et al. 2020).

More recently the Woodland creation & Ecological Networks (WrEN) project in the UK has taken a different approach to large scale restoration experiments (Watts et al. 2016). Here, recent woodland patches were selected to maximise variation in area and isolation, where site age was ascertained using historical maps. This project takes advantage of previously created woodlands and coerces them into a natural experiment framework. This means that results can be

produced immediately and ecological lag times are not a factor. Recently the WREN project has demonstrated the importance of local habitat heterogeneity alongside landscape connectivity to moth (Fuentes-Montemayor et al. 2022) and mammal (Fuentes-Montemayor et al. 2020) species.

The WREN project has also been used to demonstrate the extreme ecological time-lags associated with created woodlands. After creation, temperate woodlands seem to follow a predictable development pattern. The first 30 years are considered the stand initiation phase, where there is a thicket of even aged saplings; for the next 50 years some trees die-off where others grow taller shading out ground vegetation; it is not until 80 years on-wards that understory regeneration initiates (Fuentes-Montemayor et al. 2021). These long development stages are partly responsible for the long colonisation lags of new woodlands (Naaf and Kolk 2015), and the reason that biodiversity benefits are slow to accrue (Watts et al. 2020).

### **1.3.2 Remote sensing**

It is often important to monitor restoration outcomes over broad spatial and temporal scales. Remote sensing has been increasingly utilised to do this in a cost effective way (Camarretta et al. 2020). LiDAR has become particularly important to monitoring the structure of restored woodlands, which is itself a proxy for biodiversity (MacArthur and MacArthur 1961). LiDAR is an active remote sensing technique, where high frequency laser pulses are emitted from a remote instrument and reflected back off of foliage in a woodland. The time

it takes pulses to return is measured and used to model the structure of target woodlands in the form of point clouds. This is often done from space, for example the global ecosystem dynamics investigation (GEDI) (University of Maryland 2023) or from aircraft, for example the UK's National Lidar Programme (Environment Agency 2021). There have been many applications of LiDAR to monitor restoration actions. For example, in Brazil Almeida et al. (2019a) have used LiDAR to show how intensive seed planting and weed management can increase above ground biomass (AGB) in restored tropical woodlands. Further, Wiggins et al. (2019) have used LiDAR to create reference models of different woodland types. These models were calculated for a variety of different previous land-uses so that land managers can compare their restoration efforts to accurate reference stands.

### **1.3.3 Simulation modelling**

Due to the long time-lags associated with woodland creation and the difficulty of coercing existing woodland creation sites into an experimental design, simulation modelling has become an important tool for understanding the role of connectivity in woodland restoration. With increasing computational power, spatially explicit individual based models (IBMs) have been used to understand the processes behind ecological connectivity rather than simply the patterns it produces (Synes et al. 2016). These models simulate the movement of a population of individuals - each with their own traits and behaviours - across cellular landscapes with different habitat configurations. There has been some

modelling work to explore how best to target woodland habitat creation to increase landscape scale connectivity (Synes et al. 2020). The results of this approach have demonstrated that targeting woodland creation adjacent to existing patches accrues the most biodiversity benefits over time at the landscape scale. Similar work has shown the importance of trees outside of woodlands acting as ecological stepping stones (Plenderleith et al. 2022). This work simulated the removal of these trees and found that this incurred a reduction in invertebrate dispersal.

#### **1.4 Knowledge gaps**

Despite these efforts, the field of restoration ecology is still young and there are still many meaningful knowledge gaps regarding how to spatially target woodland creation effectively. These knowledge gaps are particularly important in the UK where there is a limited supply of appropriate planting materials, resources, and space (Whittet et al. 2016). As discussed, modelling work has shown that targeting woodland creation adjacent to existing sites may be the best way to increase population sizes and landscape permeability in the UK context (Huxel and Hastings 1999; Synes et al. 2020). However, these models only account for species populations and do not account for the full range of restoration targets related to woodland creation. Here I discuss three important knowledge gaps: (1) How spatially targeting woodland creation impacts woodland structural development; (2) how it also impacts the long ecological time-lags associated with woodland biodiversity; and (3) how matrix features such as ecological



corridors impact the efficacy of different spatial targeting strategies.

Habitat structure is fundamental to biodiversity in mature woodlands, as increased structural complexity offers more niche spaces to be filled and more suitable habitat for woodland species (MacArthur and MacArthur 1961; Menge et al. 2023). However, woodland structure is known to take decades to develop which partly contributes to long colonisation lags associated with new woodlands (Fuentes-Montemayor et al. 2021). Despite its increasing use in monitoring woodland structure, LiDAR has so far not been used to assess how ecological connectivity impacts structural metrics in created woodlands. The wind protection provided by connected woodlands alongside increased colonisation from nearby populations may increase the rate of structural development in recently created woodlands. This would in turn speed up the rate that biodiversity benefits are realised by increasing habitat suitability and structural complexity. With an increase in woodland creation over the past few decades, and widely available LiDAR data, it is now possible to test how spatially targeting woodland creation could speed up the rate of woodland structural development.

As stated, time-lags are a big issue for woodland creation and are partly responsible for our failure to meet short-term biodiversity targets (Watts et al. 2020). Colonisation credit is defined as the number of species to colonise a new habitat taken from the potential number of species that could colonise the same habitat (Jackson and Sax 2010). Colonisation credit is known to last decades in created woodlands representing a long ecological time lag (Brunet 2007). Thus, it is important to understand how spatially targeting woodland creation

can reduce these lags. Recent work from Brunet et al. (2021) has suggested that woodlands created adjacent to mature source patches fulfill colonisation credit faster than isolated patches. However, even after 80 years there was still credit remaining in these well-connected patches. As this study used species richness as a performance metric and did not inspect the presence or absence of individual functional groups, it is hard to tease apart what might be holding even well connected-woodlands back. A more detailed approach is needed so that early milestones of restoration success can be identified, and management recommendations made.

Where colonisation credit is concerned with the local scale biodiversity of recently created woodlands, the modelling work described above from Huxel and Hastings (1999) and Synes et al. (2020) was concerned with how spatial targeting strategies affect populations at the landscape scale. However, these works miss an important component of landscape-scale population dynamics: ecological corridors. In the woodland landscapes of the UK, corridors take the form of hedgerows. Hedgerows have long been considered habitat for woodland specialists (Pollard 1971), and have more recently been shown to fulfill a corridor function for a range of woodland species (Pelletier-Guittier et al. 2020; Lenoir et al. 2021). Corridors in the form of hedgerows are likely to increase the viability of isolated woodlands more so than woodlands adjacent to existing patches. However we do not know if the presence of hedgerows can make isolated patches as effective a strategy as creating adjacent patches. Thus, more work is needed that tests how the presence of hedgerow corridors interacts with different habitat

creation strategies.

## **1.5 Thesis structure**

This thesis attempts to fill these knowledge gaps to contribute a full picture of how spatially targeting woodland creation can enhance biodiversity benefits in the UK woodland landscape. It does this by evaluating a range of restoration success metrics and uses a range of methods to do so. This thesis also takes advantage of a Woodland Grant Scheme (WGS) premium offered in the Isle of White, which incentivised landowners to create woodlands adjacent to existing patches (Quine and Watts 2009). This, alongside spatially isolated woodland creation on the island approximates a robust experimental design which allows for the comparison of different spatial targeting strategies.

Chapter Two explores how spatially targeting woodland creation adjacent to existing patches contributes to variation in woodland height and height diversity. It explicitly tests the hypothesis that woodlands created adjacent to mature woodland patches grow taller, faster, and have greater structural diversity than isolated counterparts. Chapter Three is concerned with local biodiversity, and attempts to quantify how spatial connectivity can reduce the long colonisation lags in recently created woodlands. By identifying specific species that are struggling to reach new woodlands this chapter unpicks the local habitat conditions that may hold back well connected woodlands from fulfilling their colonisation credit and recommends management interventions. Chapter Four looks at species populations at the landscape scale by following a similar

framework to Synes et al. (2020). Here an individual based model (IBM) is used to test how the presence of hedgerows in the landscape affects the populations of conceptual species under different habitat creation strategies. Finally the results of these three data chapters are synthesised and the implications to UK woodland creation will be evaluated.

## **2 New woodlands created adjacent to existing woodlands grow faster, taller and have higher structural diversity than isolated counterparts**

### **2.1 Abstract**

Creating native woodland is a policy goal globally, and one strategy to maximise woodland creation benefits in limited space is to target efforts to extend existing woodlands. There is evidence to support spatially targeting habitat creation for biodiversity, however, there is little evidence of how this affects a habitat's structural development. Here, a space-for-time study using LiDAR (Light Detection and Ranging) data assesses how the structure of recently created woodlands are affected by the presence of an adjacent older woodland. Recently created native woodlands were identified across the Isle of Wight UK using historical maps and satellite imagery. Canopy height and foliage height diversity were derived for all woodlands from LiDAR data collected at two different time points (2011 and 2021), and linear models were used to test for any differences in these structural metrics between sites with an adjacent older woodland, and those without. The percentage change in woodland height between the two time points was also tested. In woodlands created adjacent to older woodlands, canopy height was found to be higher by an average of nearly 2m, and foliage height diversity was found to be on average 4.7% higher, using the 2021 data. Growth rates between 2011 and 2021 were not significantly different between

the groups, although young adjacent woodlands grew the most on average. This research shows that creating woodlands adjacent to existing older woodlands reduces the time taken to create tall and to a lesser extent structurally diverse habitat, which may lead to early biodiversity benefits.

## **2.2 Introduction**

Across the world attempts are being made to reverse centuries of deforestation by creating and restoring native woodland (Keenan et al. 2015; Davies 2017; European Commission 2021). The reasons for this afforestation are multifaceted, including carbon sequestration to combat climate change (Bastin et al. 2019; Holl and Brancalion 2020), restoring and protecting biodiversity, and providing cultural/recreational benefits (Di Sacco et al. 2021). More recently, it has been argued that planting trees should not be considered a panacea, and that treating it as such can lead to unintended negative results, such as the destruction of other important habitats or the displacement of productive farmland (Holl and Brancalion 2020). However ambitious targets remain, for example the UK government has pledged to plant 30,000 ha of trees a year by 2025 (HM Treasury 2020), the European Union plans to plant 3 billion trees by 2030 (European Commission 2021), and Canada has embarked on a 2 billion trees commitment (Government of Canada 2020). Evidence is needed to inform decisions regarding where to spatially target woodland creation and restoration in ways which maximise benefits in limited space.

Tree planting decisions are often influenced by a need to decrease fragmentation

and increase ecological connectivity among native woodlands (Peterken 2000; Humphrey 2003; Melles et al. 2011). This is exemplified by Haddad et al. (2015) who demonstrated that global woodlands are small and fragmented with 70% of them being within 1km of a woodland edge. One strategy which has been shown to successfully combat this is to extend existing mature woodlands (Quine and Watts 2009). There is evidence showing that targeting woodland creation this way benefits biodiversity by increasing the colonisation rate for a range of woodland specialist species (Opdam et al. 1984; Dunning Jr et al. 1995; Brunet et al. 2021). Synes et al. (2020) have also used individual-based models and simple land cover change scenarios to show that targeting habitat creation adjacent to existing habitat is potentially one of the most effective strategies to conserve biodiversity in a changing climate. However, many such studies assume that the recently created habitat is instantly suitable for species to colonise and fail to account for the considerable temporal lag in structural development (Jackson and Sax 2010; Lira et al. 2019; Watts et al. 2020).

There are many reasons why it is important to consider structural metrics when planning woodland creation, not least for ecosystem services such as carbon storage and timber production (Vashum and Jayakumar 2012; Felipe-Lucia et al. 2018; Lutz et al. 2018). Woodland structure is also known to have strong effects on biodiversity (Smith et al. 2007): woodlands that reach canopy closure sooner are likely to provide refuge for woodland specialist species more quickly (Harmer et al. 2001; Brunet et al. 2011), and woodlands with greater structural diversity have been shown to increase species richness (MacArthur and MacArthur 1961;

Dracup et al. 2015; Fuller et al. 2018).

Monitoring woodland height and structure across large spatial extents can be achieved using LiDAR (Light Detection and Ranging), a technology that allows for the recording of three-dimensional woodland structure. Recently, LiDAR has been used specifically in restoration ecology across the globe: in Brazil, drone-borne LiDAR was used to compare two different planting densities and two different management types in restored woodlands (Almeida et al. 2019a), other studies in the region have shown it to be accurate at estimating many metrics pertinent to restoration success, such as above ground biomass (AGB) and tree species diversity (Almeida et al. 2019b), work in Mexico has used LiDAR to create high resolution reference models for woodlands on different landform types (Wiggins et al. 2019), and a study in Oregon used LiDAR to assess fuel accumulation in restored woodlands to combat wildfires (Olszewski and Bailey 2022).

The present study uses discrete return LiDAR data from two points in time (winter 2011 and winter 2021) to look at how canopy height and foliage height diversity (FHD) of recently created woodlands is affected by the presence of adjacent, older woodland neighbours, which were mature and well-established at the time of the recent woodland's creation. Although light availability can be a limiting factor in plant growth (Shirley 1929), we expect that LiDAR data will show trees planted adjacent to an existing woodland have increased growth in height, because older trees compete for light causing planted saplings to grow taller and avoid shade (Craine and Dybzinski 2013). Older adjacent neighbours may also buffer the



target woodlands from wind effects reducing mechanical stress, and plants are known to increase growth when mechanical stress is reduced (Liu et al. 2007). We predict that older adjacent woodlands will also lead to an increase in FHD (a metric of structural diversity), by providing additional propagules resulting in more rapid understory development.

## **2.3 Methods**

### **2.3.1 Study area and sample design**

The Isle of Wight was chosen as an ideal study region for two reasons: (1) there have been recent efforts to create new native woodlands adjacent to mature and often ancient woodlands (existing since 1600), thereby reducing fragmentation (Quine and Watts 2009); and (2) there are no populations of deer or grey squirrels on the island which means there are no complex interactions between woodland growth and grazing pressure (Spake et al. 2020). As deer fencing is now funded as an option within the current woodland creation grant in England (Rural Payments Agency 2021), this means woodlands created on the Isle of Wight will be representative of future woodlands created across the rest of the country. The Island has a maritime climate with an average summer temperature between 13°C and 20°C, an average winter temperature between 3°C and 9°C and average precipitation of around 870mm (Met Office 2020). The climate is consistent across the island and thus elevation (increasing up to 240m above sea level) is expected to control for any variation in temperature.

The UK National LiDAR Programme provided data for the year 2021 (Environment Agency 2021), where data from 2011 were downloaded from Defra (Department of Environment Food & Rural Affairs). 2011 was chosen as this was the previous year with the most coverage over the island and a gap of ten years should leave enough time for growth rate observations (Fuentes-Montemayor et al. 2022). Both products are aircraft-based LiDAR data collected by the UK Environment Agency during winter, they were both tested against ground control samples to ensure that the absolute height error is less than +/- 15cm. The mean point cloud densities were 1.17 per m<sup>2</sup> and 1.56 per m<sup>2</sup> for 2011 and 2021 respectively and both products are discrete return LiDAR with 4 returns per pulse. Using two different sets of LiDAR data has risks as they may result from different collection and post-processing protocols. However, these were both collected in winter by the same agency and were both tested for errors against ground surveys, thus we cautiously use them to compare which woodlands grew more than others, but will not use them to infer absolute growth rates.

Sample woodlands (n = 63) were selected from the National woodland Inventory (NFI) 2015 (Forestry Commission 2015), after removing all ancient and non-broadleaved woodlands, and then filtering out all plots larger than 1ha or which were not covered by the LiDAR data (Figure 1). We focused on small plots as these are more likely to be affected by an adjacent woodland. Woodland ages were identified using historical Ordnance Survey maps (EDINA 2020), and historical satellite imagery, accessed on Google Earth Pro version 7.3 (Google.inc 2020). Woodlands planted in 2005 or later were not included, as not enough

time has passed between their creation and the available LiDAR data. Woodland creation dates ranged between 1970 and 2000 although few woodlands were found originating in the 1980s, and so these were pooled with woodlands created in the 1970s. From now on, woodlands created between 1970 and 1989 will be referred to as “mature created woodlands”, and woodlands created between 1995 and 2005 will be referred to as “young created woodlands” (Figure 1). There were no woodlands in our sample originating between 1989 and 1995.

The historical records were also used to determine whether woodlands were adjacent to or isolated from an existing older woodland at their creation. Adjacent woodlands were defined as closed canopy woodlands (at least 20 years old) which border the adjacent created woodland, but we also considered lines of mature trees to be adjacent older woodlands if they ran parallel and not perpendicular to the adjacent created woodland (Figure 2). All but two adjacent created woodlands shared at least a quarter of their edge with an adjacent older woodland. The lowest percentage edge in common between adjacent woodlands was 10%. Geological information was also extracted to each woodland using the ‘DiGMapGB-50 Rock Unit’ product (EDINA 2008). Created woodlands were 0.65ha on average, and their spread across age groups, adjacency and geology is displayed in Table A1.

Tree species information is not included in the NFI dataset, meaning that any differences in height between woodlands could be caused by the specific species occupying each woodland. To eliminate this possibility, we visited a subset of publicly accessible woodlands from our sample (13 adjacent, 17 isolated).

On these visits the two most dominant tree species were visually identified to see if tree species were evenly spread between adjacent and isolated created woodlands. Most sites were dominated by *Fraxinus excelsior* and *Quercus robur*, with 12 isolated and 13 adjacent woodlands including one or both in their two most dominant species. Other less common species include *Acer campestre*, *Crataegus monogyna* and *Corylus avellana*. One woodland was dominated by *Alder glutinosa*, and one other had been invaded by *Salix* species. The vast majority of this subset represent typical native broadleaved woodlands which are encouraged in a UK context, and therefore we are confident that the species mix is not confounding results.

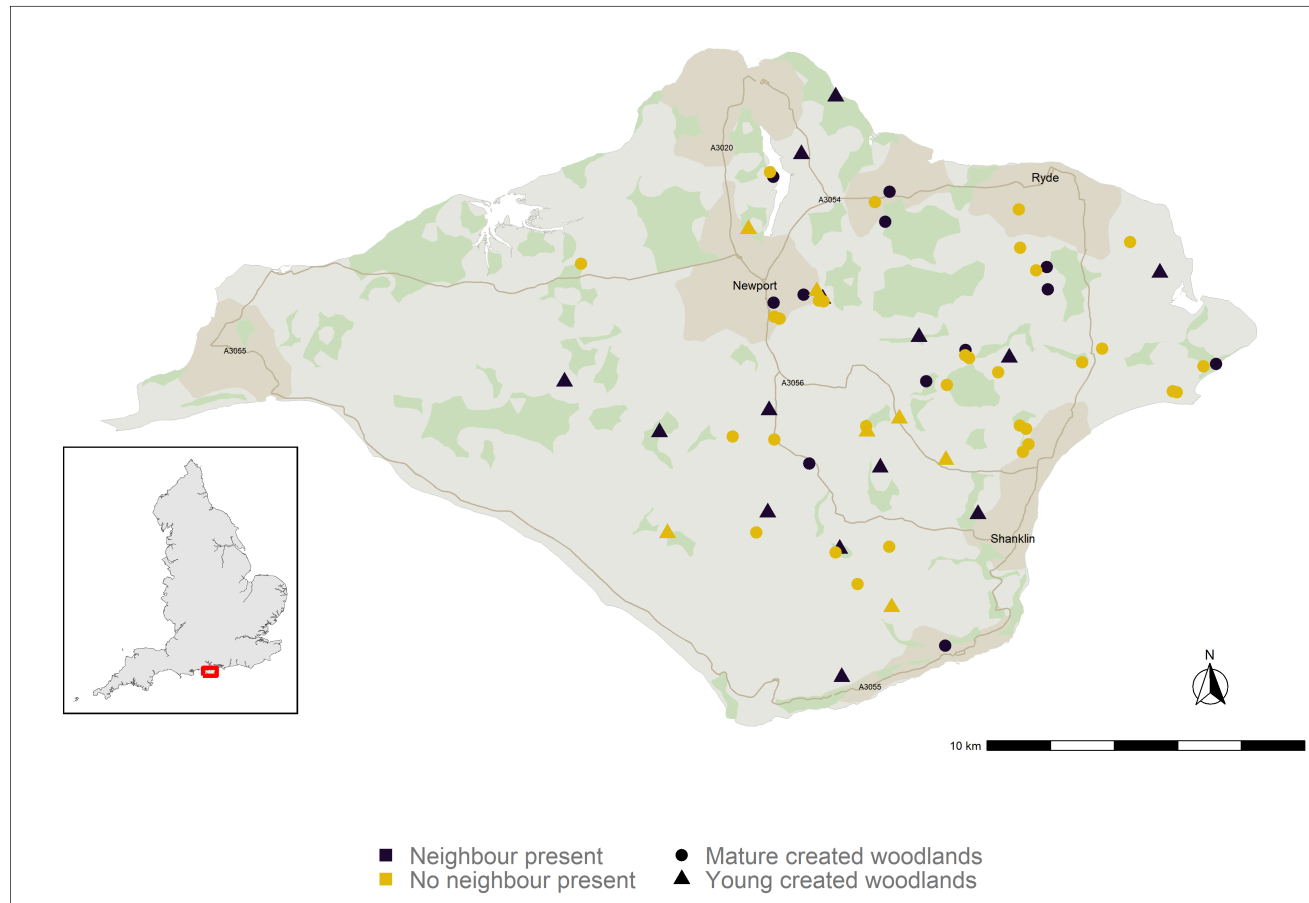


Figure 1: A map showing the study region within the Isle of Wight. Mature created woodlands were created between the years 1970 and 1990, where young created woodlands were created between the years 1995 and 2005. The presence of an adjacent mature neighbor is denoted by color. All woodland plots used in the study were below 1 ha in area.

### 2.3.2 LiDAR processing

LiDAR point clouds were processed using R version 4.0.3 (R core team 2022), using the packages LidR (Roussel et al. 2020), and Raster (Jacob van Etten 2012). All the following steps were completed for both the 2021 and 2011 LiDAR data.

Point clouds were first checked for noise using the “noise\_ivf” function from the LidR package, which showed there to be very little noise in the data overall. The point-clouds for each woodland had their ground returns classified using a progressive morphological filter (Zhang et al. 2003), and a Digital Terrain Model (DTM) was then produced at a 1m grain size using a Triangulated Irregular Network (TIN). Visually inspecting cross sections of our point clouds showed very few omission or commission errors, and any commission errors tended to occur below 1<sup>m</sup> in height, and points this low were excluded from the analysis. The classified point-clouds were normalised by computing the difference between points and the DTM so that every point represents the height relative to the ground.

From these point clouds canopy height was extracted as the relative height at the 90th percentile (RH90) of returns and Foliage Height Diversity (FHD) was extracted using the entropy function from the LidR package. This function modifies Shannon’s evenness index (DeJong 1975) by assuming that maximum diversity would include evenly distributed foliage in all 1m height bins below the max canopy height, whereas Shannon’s evenness index would normalise the corresponding diversity index using only the height bins occupied by foliage. The proportion of LiDAR returns in each height bin for each woodland can be

viewed in Figure A1. It is possible to set a uniform maximum canopy height for all woodlands to normalise Shannon's diversity index (Ewijk et al. 2011). However, for this study the maximum height of each respective woodland was used instead as setting a uniform maximum height would penalize shorter woodlands simply for being short. Height is an important component of FHD, but it is measured already by the RH90 metric.

Other factors which could potentially affect woodland height and thus confound results were also obtained. Topographic metrics including elevation, slope and aspect were computed from the DTMs using the 'Terrain' function from the Raster package. Aspect was then converted to a 'Northness' variable which ranged between -1 (due south) and 1 (due north) and calculated by taking the cosine of the aspect radians. Each derived metric was extracted to the relevant woodland using area summarizing statistics. Canopy Height was extracted as RH90, FHD was extracted as the index calculated by the entropy function whereas elevation, slope, and Northness were extracted as averages.

### **2.3.3 Statistical analysis**

Three linear models assuming Gaussian errors were used to analyse the data. The first model tested whether being planted next to an adjacent older neighbour had a significant effect on the height of a created woodland, using the RH90 variable from the 2021 data only. The second model tested for significant effects of an adjacent neighbour on structural diversity using FHD, again this only looked at the most recent 2021 data. The final model tested for the effects of adjacency on



Figure 2: Two examples of recently created woodland connected to adjacent older neighboring woodlands. On the left the recently created woodland is connected to a closed canopy woodland, where on the right the recently created woodland is connected to a strip of mature trees. These more linear strips of trees were considered as adjacent neighboring woodlands as long as they ran parallel to the created woodland as in the picture.



the percentage change in RH90 between 2011 and 2021, by dividing the difference in RH90 between the two years by the RH90 in 2021 and multiplying this by 100.

All models included variables of adjacency, woodland age categorised as young or mature woodlands, underlying geology, mean elevation, and aspect (Northness). The significance of each variable was tested using a t test. Slope was not included in any model as it is strongly correlated with elevation and replacing elevation with slope did not improve or greatly worsen model fits. Residual plots were checked to ensure they fit a Gaussian distribution and variance inflation factors were checked to ensure no multicollinearity was affecting results.

## **2.4 Results**

The presence of an adjacent mature neighbour significantly increased the RH90 of the created woodlands in 2021 (Figure 3) by an average of 1.99m ( $p < 0.05$ ,  $t = 2.3$ ,  $df = 55$ ,  $R^2 = 0.47$ ) (Table A2) and increased the FHD (Figure 4), by an average of 4.7% ( $p < 0.05$ ,  $t = 3.2$ ,  $df = 55$ ,  $R^2 = 0.4$ ) (Table A2). Examples of these differences can be viewed in Figure 5 which are the plotted point clouds of one adjacent created woodland and one isolated created woodland. The percentage change in height between 2011 and 2021 was not significantly affected by adjacency, however, Figure 6 shows that woodlands with the greatest average increase in height were young woodlands adjacent to older neighbours. It is important to note that this change in height should not be considered as an accurate absolute change but must only be considered to see if certain woodlands grew more or less than others, as the two sets of LiDAR data may have small differences in sampling

protocols.

Individual height profiles for each woodland are shown in Figure A1. These plots show the proportion of LiDAR returns in each height bin of a woodland, from which the overall FHD is calculated. These show that any difference in height or FHD between created woodlands is not because some simply fail to establish. They are also useful to visualise how height profiles have changed between the 2011 and 2021 data.

Unsurprisingly woodland age significantly affected both its height (Figure 3) and its FHD (Figure 4), on average young created woodlands were 5m shorter ( $p < 0.01$ ,  $t = -5.32$ ,  $df = 55$ ,  $R^2 = 0.47$ ) (Table A2) and had an 11% lower FHD value ( $p < 0.01$ ,  $t = -5.55$ ,  $df = 55$ ,  $R^2 = 0.4$ ) (Table A2) than mature created woodlands. The underlying geology did not significantly affect either height or height diversity. Elevation did negatively affect woodland height ( $p = < 0.05$ ,  $t = -2.13$ ,  $df = 55$ ,  $R^2 = 0.47$ ) and FHD ( $p < 0.01$ ,  $t = -2.06$ ,  $df = 55$ ,  $R^2 = 0.4$ ) (Table A2) although the effect sizes were small with a 2cm decrease in height and a  $< 0.001$  decrease in FHD for each metre increase in elevation. Other topographic variables did not significantly affect woodland height or FHD (Table A2).

## **2.5 Discussion**

The present study adds to the evidence base informing where to plant and restore native woodlands, not by focusing on biodiversity directly, but by evaluating structural metrics that have the potential to enhance it. The results show that

woodlands planted adjacent to older woodland neighbours grow taller and to a lesser extent become more structurally diverse than their isolated counterparts. This effect was smaller in mature created woodlands than it was in younger created woodlands, and when looking at the percentage change in height between 2011 and 2021, young created woodlands planted adjacent to older neighbouring stands grew more on average than their older or isolated counterparts, although not significantly. This suggests that the difference in height and structural diversity may begin to even out with age. Other studies have found trees at higher elevations to be shorter (Uzoh and Oliver 2006; Messaoud and Chen 2011), we also found this here although the effect sizes were very small possibly due to the low range in elevation across the study area (0- 240m).

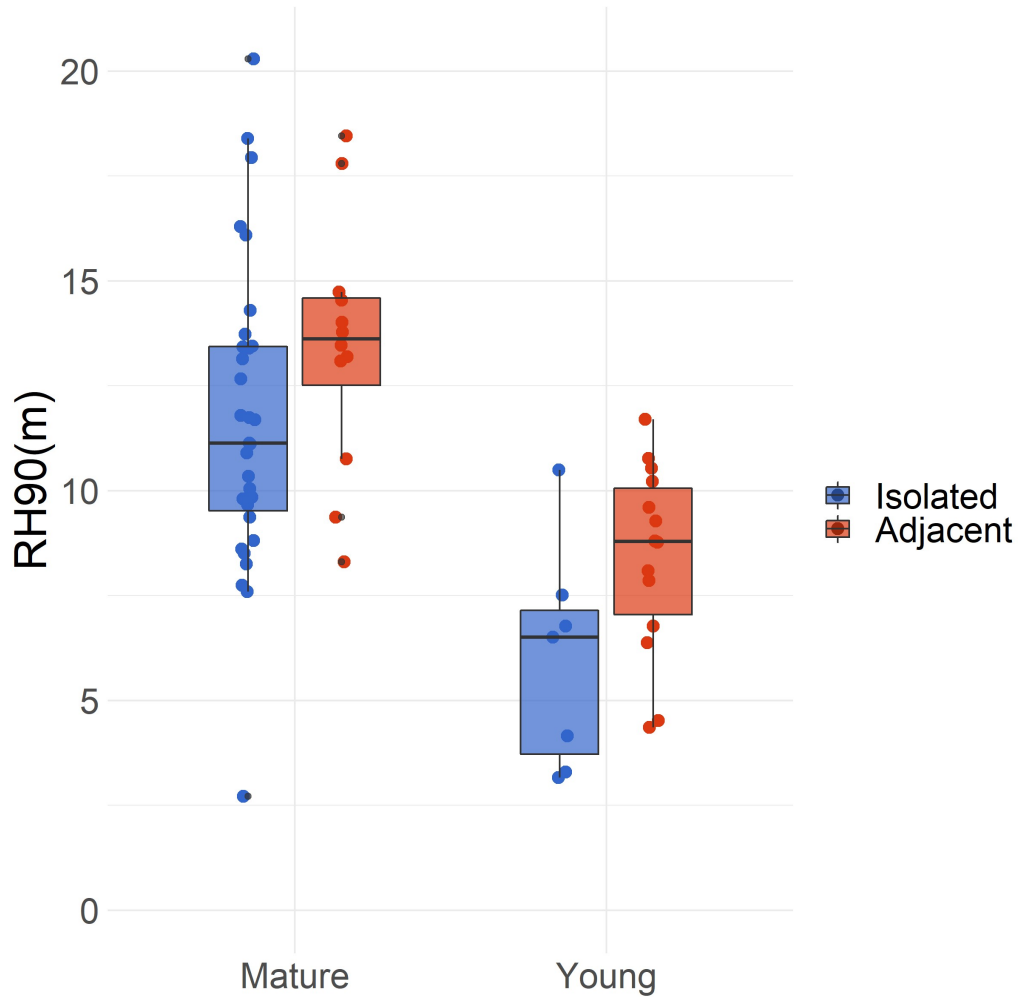


Figure 3: A boxplot showing how the 90th percentile of canopy height (m) is affected by woodland age ( $p < 0.01$ ,  $t = -5.55$ ,  $df = 55$ ) and adjacency to mature neighboring woodlands ( $p < 0.05$ ,  $t = 2.3$ ,  $df = 55$ ). This index was measured from woodlands in the Isle of Wight using discrete return LiDAR data collected in the winter of 2021.

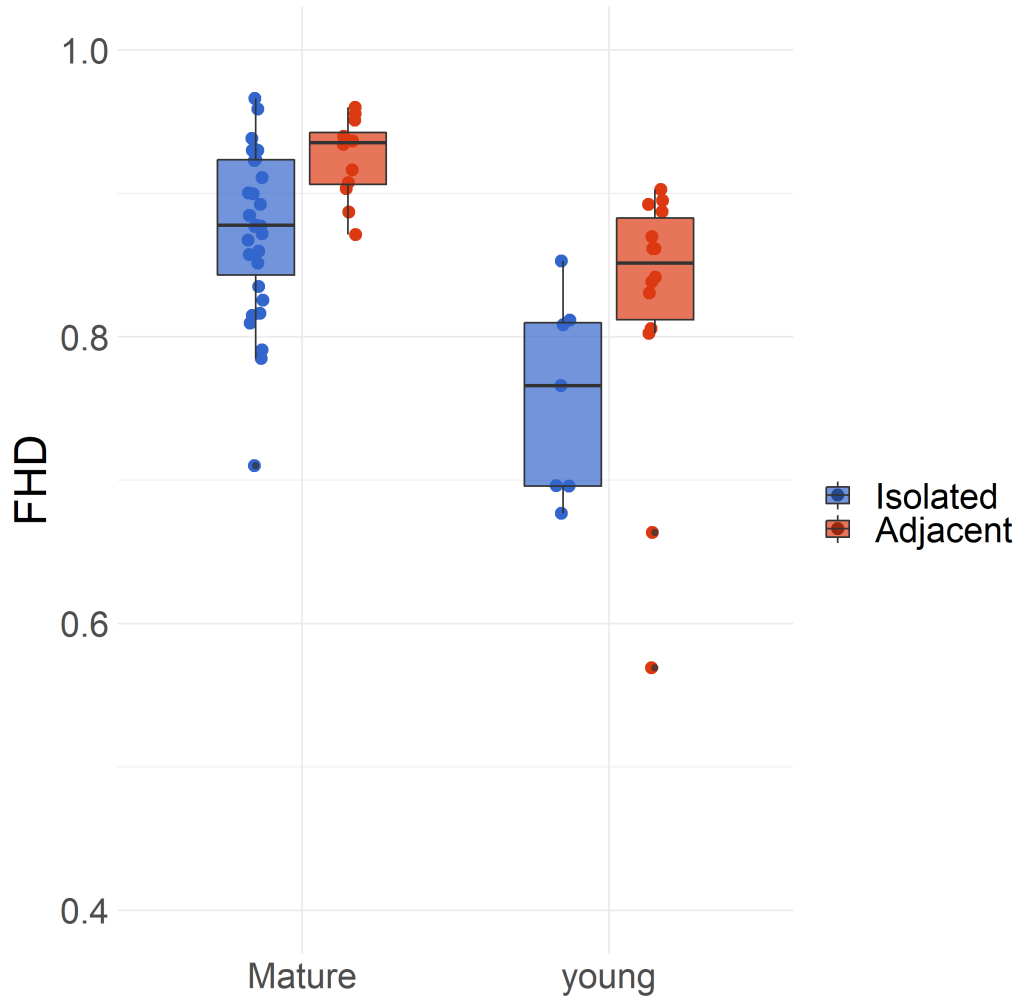


Figure 4: A boxplot showing how foliage height diversity is affected by woodland age ( $p < 0.01$ ,  $t = -5.32$ ,  $df = 55$ ) and adjacency to older neighboring woodlands ( $p < 0.05$ ,  $t = 3.2$ ,  $df = 55$ ). This index was measured from woodlands in the Isle of Wight using discrete return LiDAR data collected in the winter of 2021 and calculated using a modified version of Shannon's evenness.

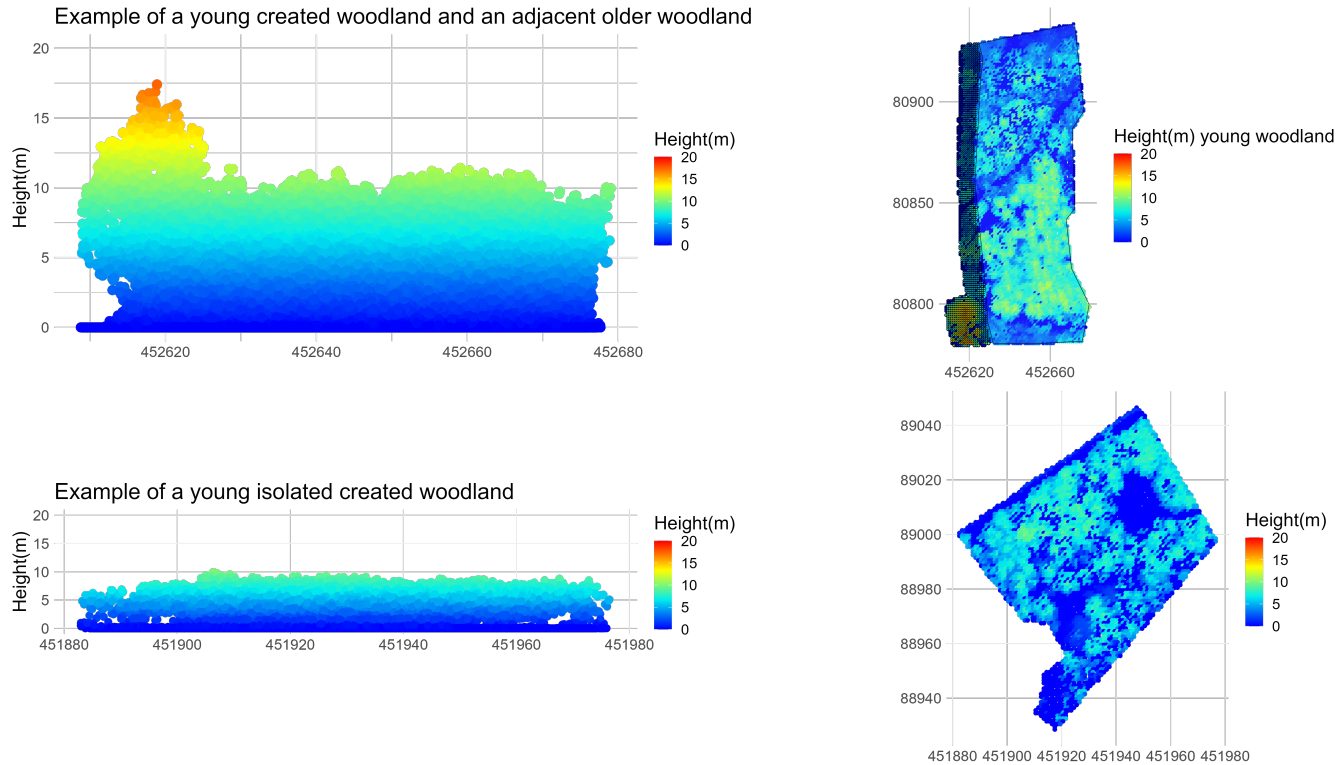


Figure 5: Examples of two young created woodlands, one (on the top row) planted adjacent to an older strip of woodland, and the other (on the bottom row) planted in isolation. The left column shows a cross-section of each woodland, for the young woodland planted adjacent to an older woodland, this older woodland is included in the cross-section. The right column is a bird's eye view of each woodland, the adjacent older neighbor for the top woodland is colored darker. Both created woodlands are roughly the same age. This helps visualize how the woodland created adjacent to an older neighbor has grown taller.

There are a few possible mechanistic explanations for the significant increase in height caused by adjacent older neighbours, the first involving light competition, which provides a reason for trees to grow tall despite maintenance trade-offs (Iwasa et al. 1985). Taller neighbours would cast shade on saplings encouraging them to grow taller and reach sunlight. A second explanation for this phenomenon is to do with wind buffering and the removal of edge effects. A study from Meng et al. (2006) experimented with tethering trees to see how this affected their growth; the authors found that tethered trees had lower bending moments allowing them to expend less energy anchoring themselves and more energy growing taller. This relates to the present study, as an established adjacent neighbour would act as a wind buffer for recent woodlands. A study with greater statistical power could attempt to further detect this effect by including a parameter of aspect relative to neighbour. Here it would be expected that woodlands buffered in the direction of prevailing winds would grow taller than those buffered from different directions. By including the direction of shade cast from a mature woodland the effects of wind and light competition could also be disentangled.

The effect of an adjacent older woodland on the FHD of target woodlands was much smaller than the effect on height, however there was still a significant difference. Woodland height itself is known to be a key determinant of FHD (Aber 1979), which would explain the increased FHD in woodlands growing adjacent to older neighbours. This is because as woodlands get taller there is simply a larger range of possible foliage heights (Müller et al. 2018). However, this study normalised FHD by maximum tree height within each site to measure

FHD per se. As woodlands reach older successional stages their vertical complexity increases due to canopy closure and natural rejuvenation in the understory (Ewijk et al. 2011). If the presence of an adjacent woodland increases tree growth to match that of an older woodland then it may cause vertical complexity to increase quicker. Mature neighbours may also be acting as seed sources (Pereira et al. 2013) promoting an increased density of foliage below the canopy in the form of saplings, potentially well before newly planted trees are mature enough to reproduce. A more likely explanation is that trees nearer the adjacent neighbour grow taller, but this effect reduces with distance across the site, making for a more varied canopy height.

This study took place in temperate western Europe, and the nature of small target woodlands created adjacent to remnant patches of older woodland is very typical of this region. However, the question of how to enhance structure in restored woodland is important globally (Stanturf et al. 2014), especially as we enter the UN Decade of Ecosystem Restoration (UNEP 2022). In the tropics for example, there are many restoration techniques being tested to not only improve biodiversity outcomes but to quickly create structurally diverse woodland. Natural colonisation, applied nucleation, and direct seeding have all been proposed as ways to obtain a more natural stand structure (Freitas et al. 2019; Holl et al. 2020). The present results may be able to further enhance these techniques, especially as they require nearby seed sources for success, which would be provided by adjacent older neighbouring woodlands.

An important point to note about these results is that the Isle of Wight lacks any



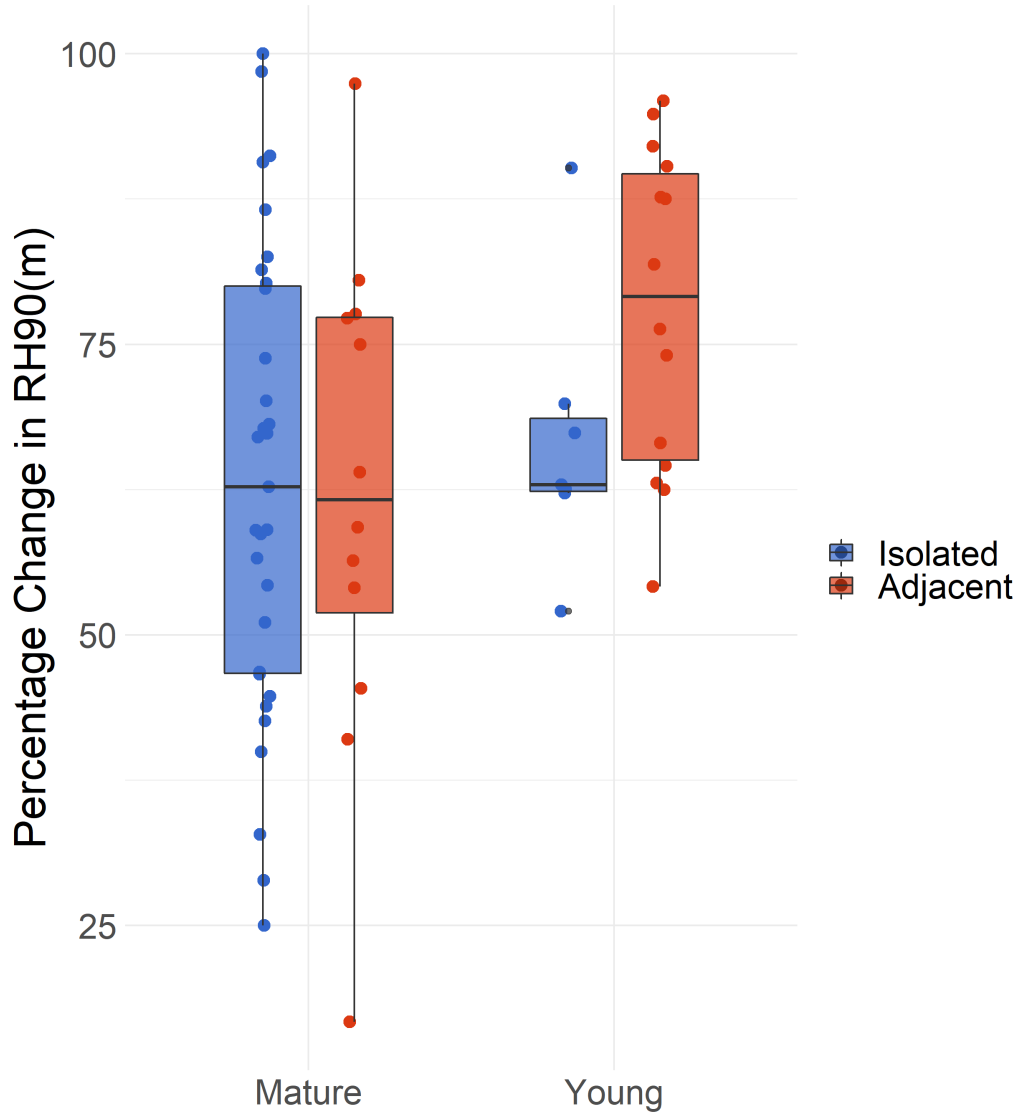


Figure 6: A boxplot showing the effects of woodland age and adjacency to a mature woodland neighbor on the percentage growth between 2011 and 2021. Adjacency did not significantly affect growth rates, however on average young woodlands with adjacent neighbors grow more than their isolated counterparts. As LiDAR data collected in 2011 will had a different sampling protocol to that collected in 2021 it is important not to take this percentage change as raw growth, but instead consider it relative to other woodlands.

wild deer population. Deer are known to reduce the sapling density and height of regenerated or planted woodlands (Gill and Beardall 2001). It would be easy to assume that the presence of deer would lead to uniformly shorter woodlands, however recent work has shown this may not be the case. Spake et al. (2020) have found that woodland cover in the surrounding landscape can increase the likelihood of deer damage, though this is also dependant on climate and matrix composition. If this is the case then then we could expect the results to be modulated by the presence of deer. An interesting future study could compare recent woodlands on the Isle of Wight with those in mainland Britain situated in similar conditions. This could also test between fenced and non-fenced plots in landscapes where deer are present, considering that future woodland creation schemes will have deer control (Forestry Commission 2020). Another factor which could be important to these findings is that of woodland patch size. We controlled for this by focusing on smaller woodlands, so we did not need to account for it in statistical models. Larger woodlands with a lower percentage of their edge bordering an adjacent older neighbour may not be as strongly affected by this neighbour as the smaller woodlands in our study. Future work could address this.

The policy and management implications of these findings will pertain to the targeting of woodland creation and the potential benefits for biodiversity and ecosystem services. There is much evidence showing that ecological connectivity increases colonisation rates (Opdam et al. 1984; Peterken and Game 1984; Petit et al. 2004), and recent research has shown that habitat creation should target

the extension of existing habitat (Synes et al. 2020). However, it has also been argued that woodland restored in small fragments will also be beneficial to biodiversity by creating greater landscape heterogeneity and providing stepping-stones between existing fragments (Hodgson et al. 2012; Arroyo-Rodríguez et al. 2020). The present study adds a new dynamic to this decision-making process by showing that woodland habitat reaches structural maturity quicker, with potentially greater biodiversity benefits, when planted adjacent to older woodland neighbours. Depending on management objectives this may present a more palatable strategy than creating fragmented patches of woodland.

We are in a time where conservation actions increasingly need to be targeted in the most cost-effective way (Rappaport et al. 2015; Synes et al. 2020), and the results of this study present an often unconsidered factor in restoration planning which could benefit biodiversity.

### **3 Spatial targeting of woodland creation can reduce the colonisation credit of woodland plants**

#### **3.1 Abstract**

Colonisation credit refers to the temporal lag between positive conservation actions and species' colonisation and may be one of the reasons we fail to meet short-term conservation targets. This is particularly evident in woodlands which take decades to develop and harbour slow colonising species. Given global objectives to increase woodland cover, it is important to know the timeframe within which colonisation credit will be fulfilled. The colonisation of woodland plants was examined in recent woodlands, created between 15 and 80 years ago, and located adjacent or isolated from existing ancient woodlands. Colonisation credit was calculated as the proportion of understory woodland plant species in the nearest ancient woodland which had not colonised recent woodlands. Looking at individual species traits also allowed us to tease apart their impact on the species colonisation and establishment ability. Spatial adjacency between created and ancient woodland reduced colonisation credit by an average of 28%, and more mature created woodlands (50-80 years old) had fulfilled 24% more of their colonisation credit on average than younger created woodlands (15-21 years old). However, mature woodlands created adjacent to ancient woodlands had still only been colonised by an average of 72% of the available species pool. Plants which had reached adjacent created woodlands were dispersed by a range of mechanisms, where those that had reached more isolated sites were

largely dispersed by birds or mammals. Low community weighted mean shade tolerance, high community weighted nutrient affiliation, and the dominance of *Hedera helix* suggest that competition from dominant natives may be preventing certain species establishing in new woodlands. This research demonstrates the need to account for appropriate time-lags when setting biodiversity targets, with most sites still displaying colonisation credit decades after they were created. The results also indicate that spatially targeting woodland creation adjacent to species-rich mature woodlands should be prioritised. Still, poor local habitat conditions may lead to the dominance of specific competitors which prevent a range of other species from establishing. Local management interventions such as translocations and tree thinning may ameliorate this, but further research is needed.

## **3.2 Introduction**

Ecological time-lags – the delays in ecological responses to landscape change - have been observed globally across a range of ecosystems (Kuussaari et al. 2009; Jackson and Sax 2010; Lira et al. 2019). Colonisation credit refers to the temporal lag between positive conservation action, such as habitat creation and restoration, and species' response (Jackson and Sax 2010). This credit has been observed in a wide range of species and ecosystems, and found to operate over a broad range of spatial and temporal scales (Lira et al. 2019). Colonisation credit is driven by a range of mechanisms, but is especially evident in small populations of specialist species which struggle to reach slow developing habitat (Lira et al. 2019).

Woodland (used here as a synonym for forest) is a habitat particularly affected by long time-lags, especially colonisation credit. This is because trees take decades to develop structurally (Fuentes-Montemayor et al. 2021), and woodland specialist species are particularly slow colonisers (Honnay et al. 1999a; Brouwers and Newton 2009). There are global efforts to create and restore woodland habitat (Bonn Challenge 2019), however, due to the slow development of woodland and the isolated nature of remnant woodland patches (Haddad et al. 2015), long time-lags between woodland creation and biodiversity benefits should be expected.

Woodland understory herbaceous plants are an interesting case study in this regard. Due to their adaptations of shade tolerance, long life, and large seeds (Whigham 2004), these plants rely on woodlands to out-compete landscape generalists which would otherwise dominate. Woodland plant species are also exceptionally slow colonisers of newly created woodlands, as diaspores struggle to reach isolated patches (Honnay et al. 2002b). Further, initial biodiversity increases in plant communities after woodland creation may represent different communities to those resulting after decades of woodland development. After woodland creation, light demanding landscape generalists have been shown to quickly colonise. However, it is expected that these will slowly be outcompeted by shade tolerant woodland specialist plants before dying out and being completely replaced (Harmer et al. 2001). This means that any short-term biodiversity increases may not persist in the long term, and also may not signal any later colonisation by woodland specialist plants. It has been suggested that

colonisation credit could be masking our ability to observe progress towards conservation success (Watts et al. 2020). Thus, a greater understanding of the drivers of colonisation credit will give us an opportunity to account for future species' responses and to intervene to reduce these temporal lags and speed up the realisation of biodiversity benefits.

There is a rich history of study looking at how specialist plants colonise recently created woodlands (Peterken and Game 1984; Brunet and Von Oheimb 1998; Honnay et al. 2002b; Kolk et al. 2017), and more recently colonisation credit has been explicitly considered (Naaf and Kolk 2015; Brunet et al. 2021). Calculating the colonisation credit of woodland understory plants could be done in many ways, including comparing the observed species richness to that of nearby suitable habitat, or by modelling species richness against past and present landscape patterns (Lira et al. 2019). Naaf and Kolk (2015) inferred from recent woodlands in Germany that some colonisation credit in isolated woodlands remained after centuries, when compared to similar ancient woodlands in the area. Recently, Brunet et al. (2021) showed how this process is sped up in recent woodlands contiguous to ancient neighbours, although after 80 years colonisation credit was still not fulfilled. As these studies were large scale, they compared the species richness of recent woodlands to a baseline species richness of nearby ancient woodlands. Thus, woodlands were deemed to have fulfilled their colonisation credit if they had an equal species richness to their older neighbouring woodlands, although species identities and community composition could be different.

The present research attempts to further unpick the colonisation credit of recent woodlands by focusing on species identity and whether the species present in ancient woodlands have either succeeded or failed to colonise nearby recent woodlands. The dispersal mechanisms and habitat requirements of these plants are then further explored. From this we can identify which traits may be limiting species colonising and establishing in more or less isolated recent woodlands. We used an approach aligned with a natural experiment design by using paired blocks of planted woodlands within the Isle of Wight, each containing an “adjacent created woodland” and an “isolated created woodland”. Adjacent created woodlands were recent woodlands created adjacent to an ancient woodland (in existence since the year 1600) (Spencer and Kirby 1992), where isolated created woodlands were recent woodlands created at least 100m away from any ancient woodland. Adjacent and isolated created woodlands were always of similar age within blocks but varied in age between blocks with a range of 15 and 80 years. This allowed us to observe how quickly colonisation credit can be fulfilled, and how the spatial proximity of adjacent ancient woodlands might speed this up. We expected the colonisation credit of recent woodlands to take decades to fulfil due to the slow colonisation time of most woodland plants and the length of time it takes new woodlands to develop. We were not sure if connecting newly created woodlands to existing source woodlands would ameliorate this fully, but we did expect colonisation credit to be higher in younger isolated created woodlands and lower in older adjacent created woodlands. Lastly, we expected the colonisation of woodland plants in isolated woodlands to be driven by mammals and birds



as their primary dispersal vector, where adjacent created woodlands may have been colonised by plants with a range of long and shorter distance dispersal mechanisms.

### **3.3 Methods**

#### **3.3.1 Study region and site selection**

The study took place on the Isle of Wight in the south of England where there have been recent efforts to extend ancient existing woodland (Quine and Watts 2009) along with ongoing planting programmes with no such spatial targeting rule. Taken together these approximate an experimental design: with approximately equal areas of woodland planted either adjacent to or isolated from ancient woodland sites. There is also no wild deer population on the Isle of Wight, which significantly reduces the grazing pressure on recently planted woodlands. Woodlands were planted with native broadleaf species similar to those found in the nearby ancient woodlands. Planted species included *Fraxinus excelsior*, *Fagus sylvatica*, *Acer campestre*, *Quercus robur* and *Corylus avellana*. Many of the woodlands had subsequently been colonised by *Salix viminalis* and *Crataegus monogyna*.

Woodlands were selected in blocks of three, with each block including one ancient ‘source’ woodland, one recent woodland planted adjacent to the source woodland, and a second recent woodland of a similar age and size planted in isolation (on average 494m from the source woodland, range: 129m - 887m).

The ages of recent woodlands were discerned using historical maps and ranged between 80 - 15 years old, where their sizes ranged between 0.2ha and 2ha. In total, 8 blocks were identified (Figure 7) although one (“America”) only included a source woodland and an adjacent created woodland, as the isolated counterpart was not found to be wooded on arrival. Due to proximity, the source woodland of “Great park a” was used as the counterpart to the isolated woodland of “Great park b” (Figure 7). Recent woodlands were separated into two age categories; mature created woodlands were those planted between 1940 and 1970 (50-80 years old), whereas young created woodlands were those planted between 1999 and 2005 (15-21 years old). Relatively few woodlands were planted between 1970 and 1999 and so these are not represented here. The study sites ranged between 2 and 87m above sea level, with an average summer temperature between 13°C and 20°C, an average winter temperature between 3°C and 9°C and average precipitation of around 870mm (Met Office 2020). The northern half of the island is largely made up of clays where the southern half is made up of sandstones.

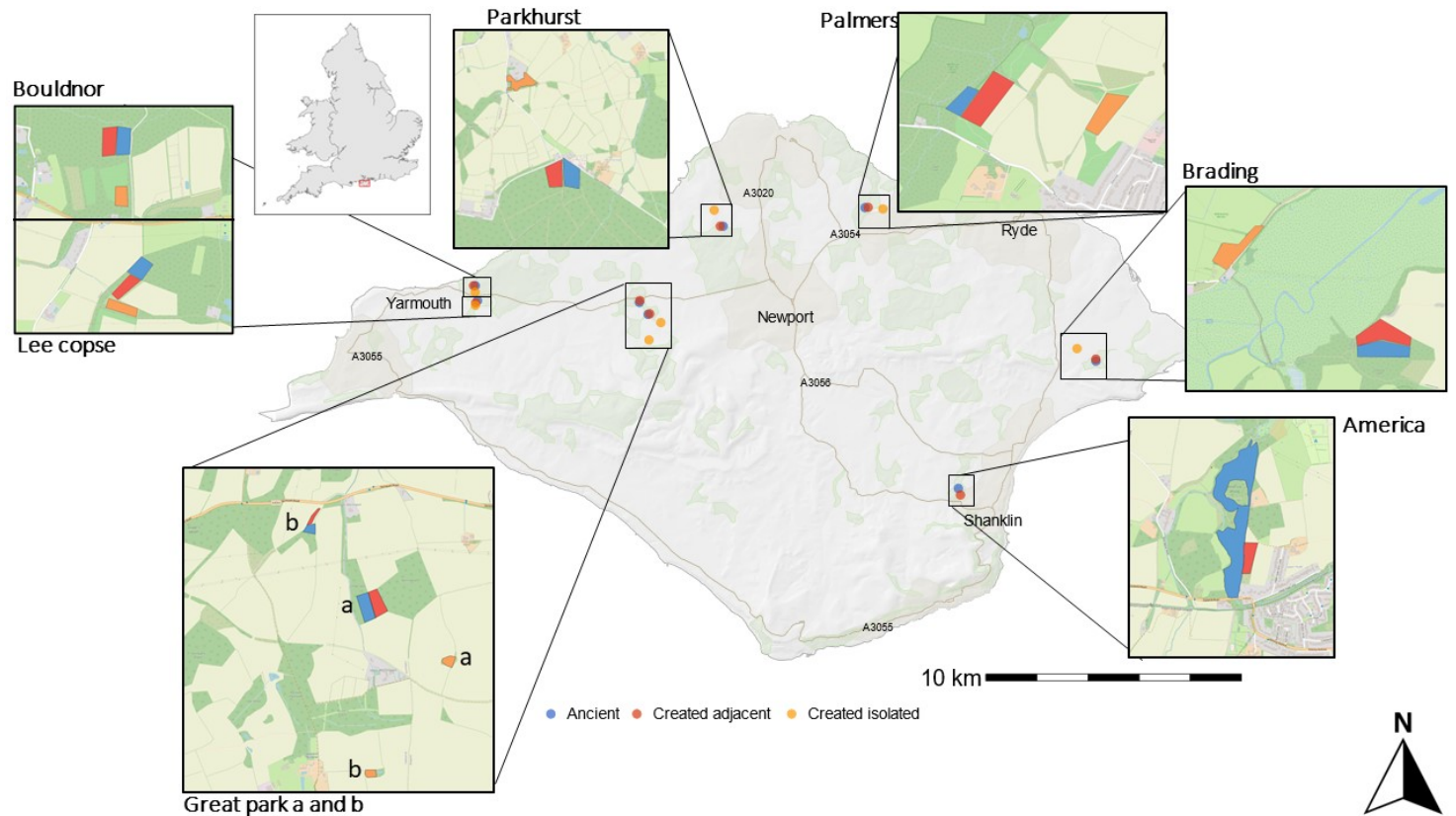


Figure 7: Map of the 23 study sites in the Isle of Wight made up of 8 ancient woodlands and 15 recent woodlands. These are organised into 8 blocks. Mature woodlands first appeared on maps between 1940 and 1970, where young woodlands first appeared around the start of the new millennium (1999-2005). The base map is provided by the OS zoomstack, where dark green patches represent other woodland.

### 3.3.2 Field surveys

Field surveys were carried out in July 2021. All woodlands were sampled systematically using six 1m<sup>2</sup> quadrats. In adjacent created woodlands, two quadrats were placed at 25% and 75% of the length of the edge adjacent to the source woodland 15m in towards the centre, two were placed 20m either side of the woodland centroid, parallel to the adjacent edge, and two were placed 15m in from the far edge opposite the quadrats near the adjacent woodland. In isolated created woodlands the same pattern was used mimicking the orientation of the adjacent created woodland. Where source woodlands were significantly bigger than the adjacent created woodland, far quadrats in the source woodland were placed equidistant to the far quadrats in the adjacent created woodland. Within each quadrat all vascular non-woody plants were recorded along with their percentage cover, estimated subjectively by dividing the quadrat into 20cm<sup>2</sup> cells to aid the observer. Docks and brambles were aggregated into *Rumex* and *Rubus spp.* respectively. Plant species were separated into woodland plants or non-woodland plants and assigned an Ellenberg Light (L) Nitrogen (N) and pH value based on their habitat preferences as defined by PLANTATT (Hill et al. 2004). The mean seed weight and dispersal strategy of each plant was also recorded from the EcoFlora database (Fitter and Peat 1994).

Data were analysed using R version 4.1.0 (R core team 2022). Woodland level analyses were performed by aggregating the quadrats of each plot, and Linear Mixed Models (LMs) were constructed using the lme4 package (Bates et al. 2014) with block as a random effect.

### **3.3.3 Colonisation credit**

Colonisation credit was analysed using a GLMM assuming a binomial error distribution. Here, the number of plants available in the ancient woodland acted as the number of trials, and the number of plants shared between the recent woodland and the ancient woodland acted as successful colonisations. This model included the age of the recent woodland as a categorical predictor variable including young created woodlands and mature created woodlands (described above), and whether the recent woodland was created adjacent to the ancient woodland or isolated from the ancient woodland as a second categorical predictor variable. An interaction term between the two predictor variables (age and distance) was also tested. The isolated woodland of the block “Great park b” was paired with the ancient woodland of “Great park a” due to it being closer to this than the ancient woodland of “Great park b”.

### **3.3.4 Community weighted mean Trait value**

The Community Weighted Mean (CWM) L, N and pH values were calculated for each created woodland to test how plant communities vary in functional diversity. These values were calculated using all understory plant species to get a picture of local habitat conditions that may be preventing the establishment of understory woodland plant species. The methods of Garnier et al. (2004) were followed to calculate these values, by summing the proportional cover of all species multiplied by their respective trait value. LMMs were then built with binary predictor of adjacency to an ancient woodland and a categorical predictor

of woodland age (young or mature). Ancient woodlands were not included in the statistical analysis, although they are included in the result plots for reference. The CWM seed weight (mg) value was calculated for just woodland understory plants in the recent woodlands, this was to assess if heavier seeds were limiting the dispersal of certain woodland species. This was tested using an LMM with the same predictor variables as described above (adjacency and age).

### 3.4 Results

In total, 48 understory plant species were found; of these 28 were recorded in source woodlands, 28 were recorded in created adjacent woodlands and 23 were recorded in created isolated woodlands. There were 19 woodland plant species found; 17 of these were recorded in ancient woodlands, 13 were recorded in recent adjacent woodlands and 8 were recorded in recent isolated woodlands. There was an average of 5.25 woodland plant species in ancient woodlands and 2.8 in created woodlands. Species numbers are summarised across adjacency status and age groups in Table 1. Many of the recent sites were dominated by ivy (*Hedera helix*), but other more specialist woodland plants such as *Hyacinthoides non-scripta* had also colonised at lower rates (Figure 8).

There was no significant interaction between the age of woodlands and their adjacency to ancient woodlands when predicting colonisation credit, and so this term was removed from the model. Mature created woodlands had fulfilled 24% more of their colonisation credit than young created woodlands ( $p= 0.05$ ,  $SE= 0.49$ ,  $z= 1.9$ ). However, mature created woodlands had still only fulfilled 58%

Table 1: Showing the distribution of plants across different age and isolation categories. Plants are also subset into woodland plants. Young woodlands were created between 1995 and 2001, where mature woodlands were created between 1940 and 1970. Adjacent woodlands were created adjacent to an ancient woodland, where isolated woodlands were not.

	Ancient woodland	Mature created adjacent woodland	Young created adjacent woodland	Mature created isolated woodland	Young created isolated woodland
Total plant species richness	28	22	27	12	23
Woodland plant species richness	17	10	6	6	5

of their colonisation credit on average. Colonisation credit was significantly reduced by adjacency on average by 28% (Figure 9), however this was only significant at the 10% level ( $p= 0.06$ ,  $SE= 0.48$ ,  $z= 1.86$ ). Even mature adjacent created woodlands had only fulfilled 72% of their colonisation credit on average. One mature adjacent created woodland did have no remaining colonisation credit, although this resided next to a particularly depauperate ancient woodland. Of the 19 woodland plant species used in this analysis, 7 were dispersed by mammals and/or birds, 2 were dispersed by ants, 4 by wind and 6 were unspecialised. Of the 13 species found in adjacent recent woodlands only 6 were dispersed by animals, the others were either self-dispersed, carried by wind or carried by ants. In contrast, six out of the eight species found in isolated woodlands were dispersed by mammals or birds.

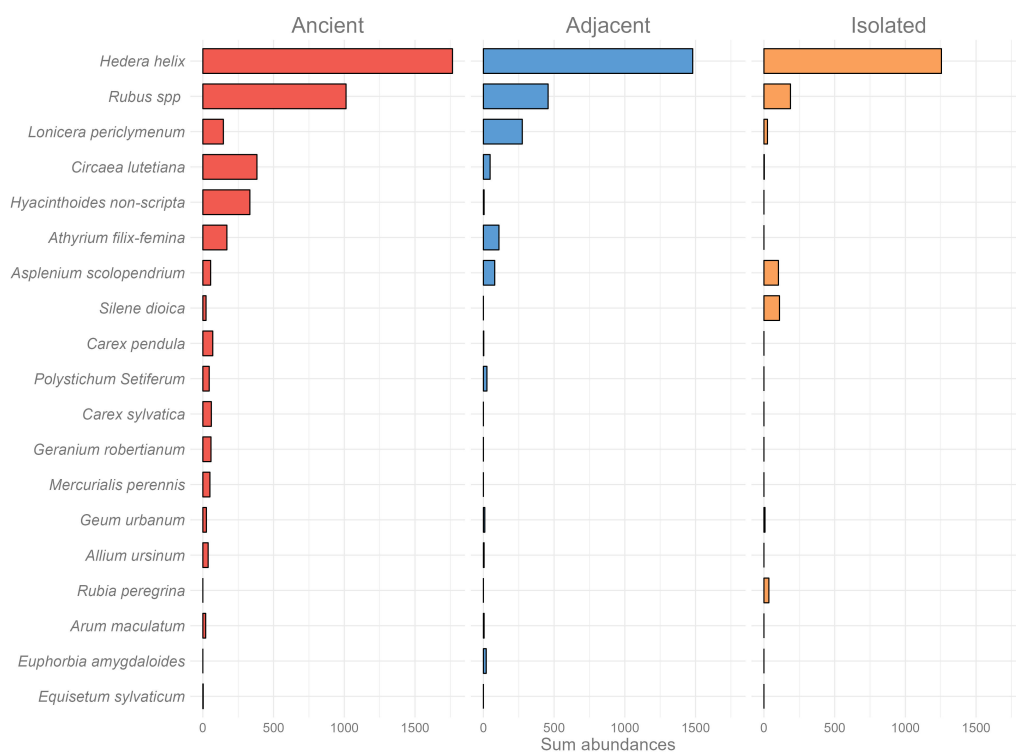


Figure 8: Sum abundances of woodland plant species found across recent woodlands separated by age and the degree of isolation. This plot also shows the dominance of *Hedera helix* in more mature woodlands. Species marked with an asterisk are considered woodland specialists and not just woodland plants as characterised by Ellenberg values and functional traits (Kirby et al. 2012).



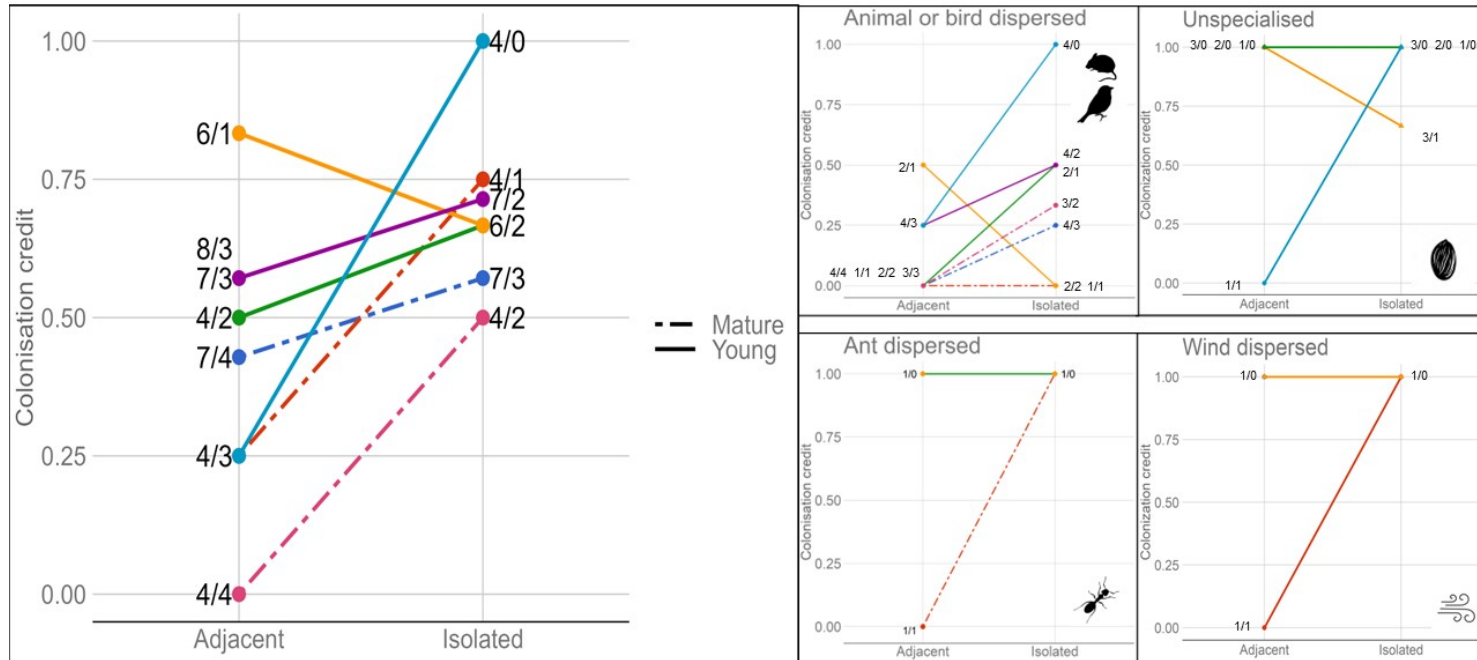


Figure 9: Pairwise colonisation credit between recent woodlands planted adjacent to an ancient woodland and those planted in isolation. These were separated into mature (50-80 years old) and young (16-22 years old) as denoted by shape. Numbers left of the forward slash are the amount of woodland plant species available in the nearby ancient woodland, where numbers right of the forward slash are the amount of these species that have made it to the created woodland. Adjacent woodlands had a significantly lower colonisation credit than isolated woodlands. These were separated into dispersal types also, mammals and birds, ants, wind and unspecialised.

The community weighted mean L value was not significantly affected by adjacency ( $p= 0.87$ ,  $t= 0.16$ ,  $df= 8.59$ ) or age ( $p= 0.21$ ,  $t= -1.61$ ,  $df= 7.60$ ). Interestingly, young adjacent created woodlands had a lower CWM L value than young isolated created woodlands, where mature adjacent created woodlands had a higher CWM L value than mature isolated created woodlands, although this interaction was not significant (Figure 10). CWM N and pH values were significantly affected by adjacency but not woodland age. Woodlands created adjacent to ancient woodlands had lower N values ( $p= 0.008$ ,  $t= -3.63$ ,  $ddf = 6.8$ ) (Figure 11) and lower pH values ( $p= 0.01$ ,  $t= -3.45$ ,  $ddf = 5.8$ ) (Figure 12). CWM seed weight (mg) was not significantly affected by age or adjacency.

### **3.5 Discussion**

Using the approach of a natural experiment design, this study has shown that the colonisation credit of woodland plants remains up to 80 years after woodland creation. Creating woodlands adjacent to ancient woodland sources does speed up this process (although only significant at the 10% level) but is not enough to completely fulfill colonisation credit within a meaningful time frame. These results concur with other work looking at ecological time lags in temperate woodlands: Vellend et al. (2006) found that extinction debt remains 100 years after woodlands have been fragmented and Naaf and Kolk (2015) found that colonisation credit could last centuries. This extended colonisation credit is a testament to the importance of considering ecological lags when judging conservation outcomes (Watts et al. 2020), and means that other markers of

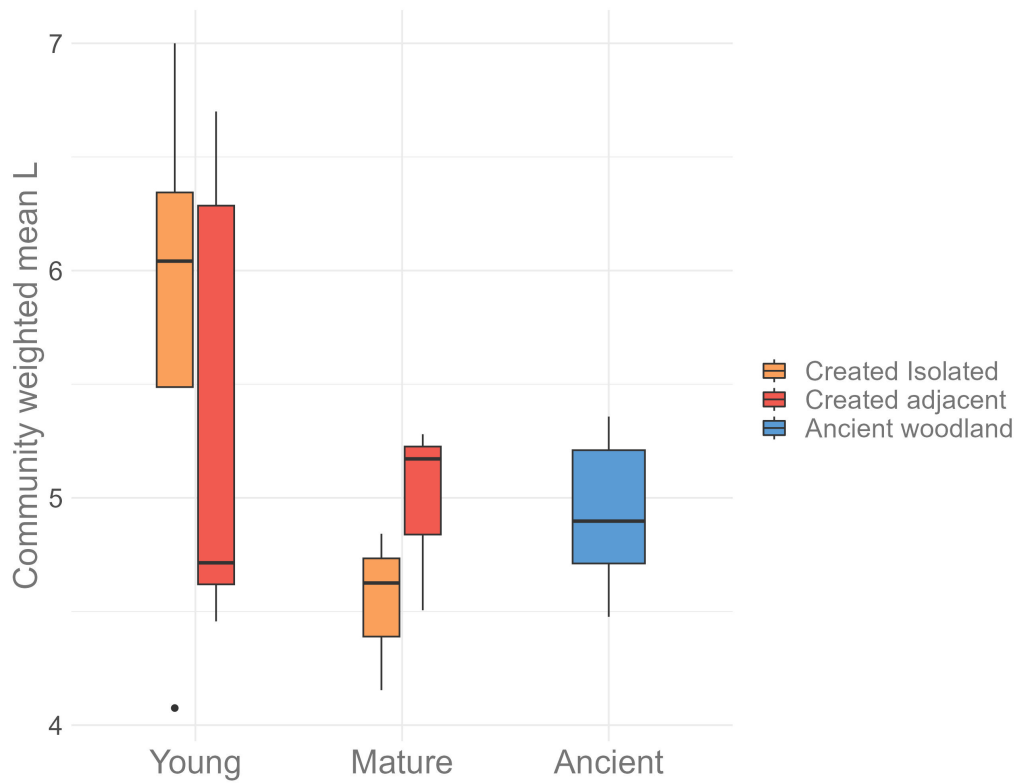


Figure 10: The community weighted mean Ellenberg L value of woodlands grouped by age (Young, Mature and Ancient) and whether they were created adjacent to an ancient woodland or isolated from existing older woodland. Young woodlands are between 15 and 21 years of age, mature woodlands are 50-80 years of age, and ancient woodlands are believed to have existed since the 1600s.

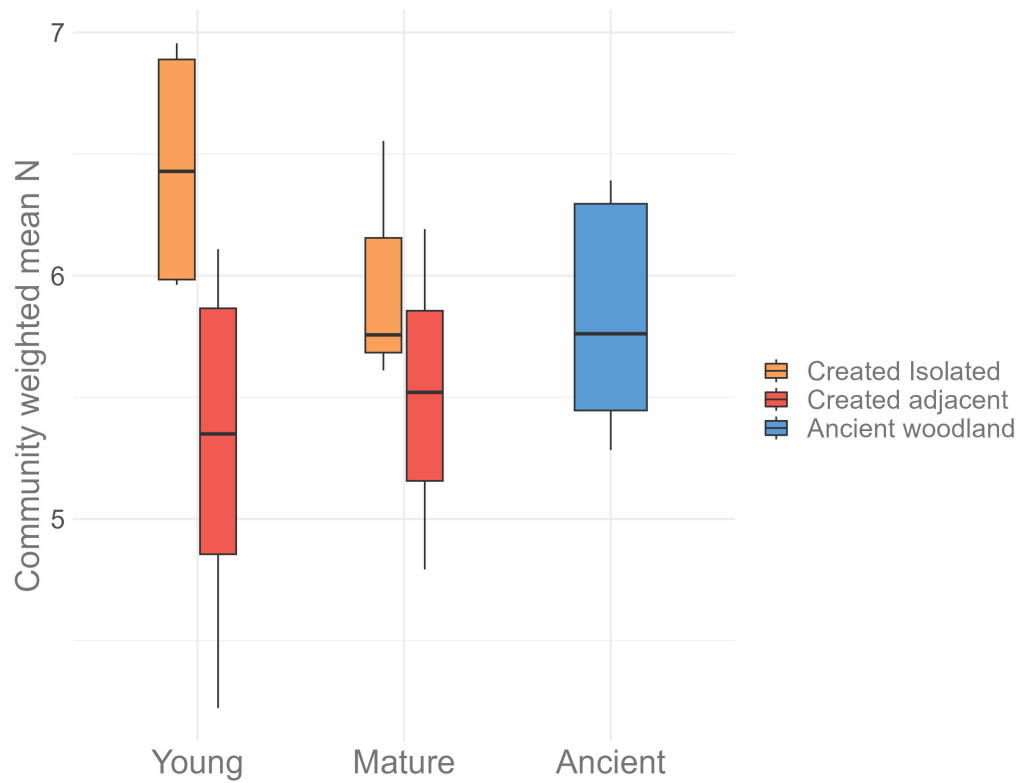


Figure 11: The community weighted mean Ellenberg N value of woodlands grouped by age (Young, Mature and Ancient) and whether they were created adjacent to an ancient woodland or isolated from existing older woodland. Young woodlands are between 15 and 21 years of age, mature woodlands are 50-80 years of age, and ancient woodlands are believed to have existed since the 1600s.

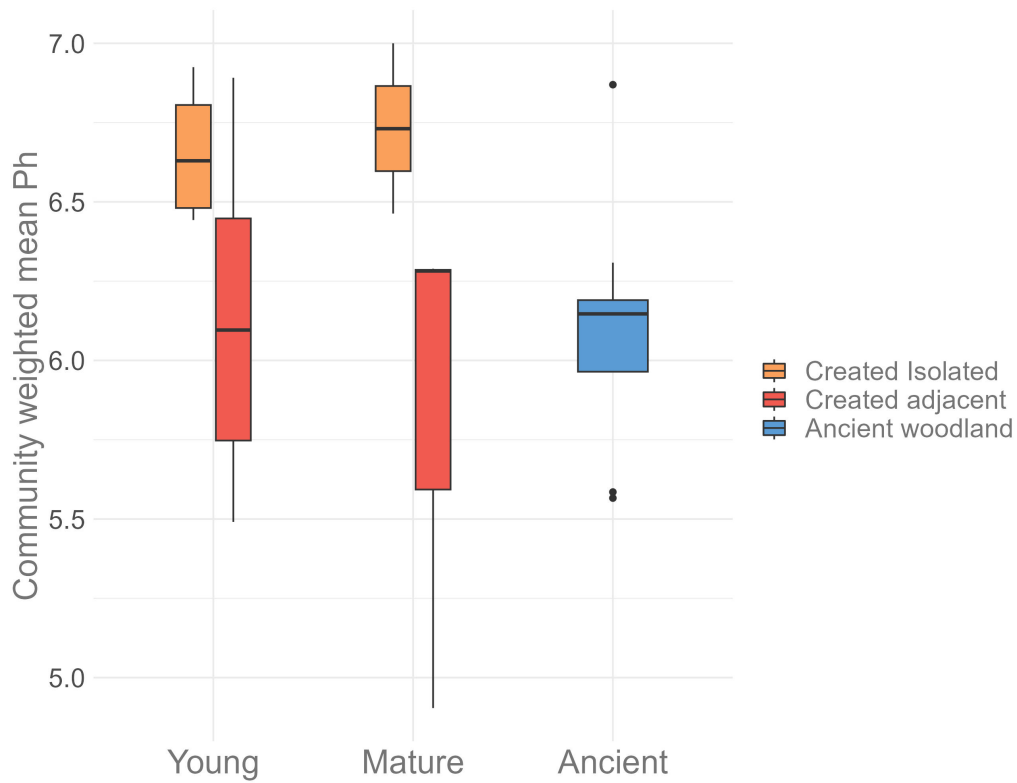


Figure 12: The community weighted mean Ellenberg pH value of woodlands grouped by age (Young, Mature and Ancient) and whether they were created adjacent to an ancient woodland or isolated from existing older woodland. Young woodlands are between 15 and 21 years of age, mature woodlands are 50-80 years of age, and ancient woodlands are believed to have existed since the 1600s.

success may be needed to judge whether management interventions will be necessary in the long-term.

The colonisation of woodland plants into recently created woodlands could be limited by two factors: (1) habitat suitability, and (2) dispersal distances. Woodlands take decades to develop structurally and young created woodlands often have higher stem densities and provide more shade than ancient woodland counterparts (Fuentes-Montemayor et al. 2021). Woodland plants need the shade provided by woodland canopies to outcompete landscape generalists (Whigham 2004), however too much shade can lead to overcrowding by native dominants such as *Hedera helix* (Marrs et al. 2013). Woodland plants are also extremely slow to disperse (Honnay et al. 2002a; Whigham 2004) and dispersal limitations are likely to cause the slow colonisation of recent woodlands. General principles suggest that woodlands closer to ancient woodland sources would fulfill their colonisation credit faster than those planted in isolation. However, even in mature adjacent created woodlands there was still a substantial colonisation credit. This, alongside the dominance of *Salix viminalis* suggests that habitat quality in recent woodlands limits their colonisation credit being fulfilled.

The dominance of a particularly shade-tolerant species that outcompetes other potential woodland species could be considered a negative milestone in restoration timelines. Many of the recent woodlands in this study had been completely dominated by *Salix viminalis* which blocked out almost all light. As a result ivy (*Hedera helix*) dominated the ground of most recent woodlands. This is supported by the low CWM L values of the more mature created woodlands

where ivy was often ubiquitous across the ground. Creating woodlands adjacent to existing source woodlands did counteract this slightly by providing more plant species to compete against the ivy. This explains why the CWM L values in mature created woodlands were higher if they were created adjacent to an existing ancient woodland. Young adjacent created woodlands had a lower CWM L value than their isolated counterparts. This was expected because the adjacent source woodland was providing shade over the recent woodland (Harmer et al. 2001). It has been shown that traditional management techniques such as coppicing significantly increase the abundance and richness of woodland plant species in the understory (Barkham 1992; Fuller and Warren 1993; Kirby et al. 2017). Some of the woodlands in this study are too young to be coppiced, however thinning to counteract the overshading of *Salix viminalis* could increase the biodiversity of ground flora by allowing a more diverse range of plants to compete with the ivy (Kirby and Thomas 2017).

The high CWM N and pH values of isolated woodlands also point to more generalist plant species outcompeting woodland specialists. Woodland plants have been shown to favour medium nutrient levels and neutral pH conditions (Hermy et al. 1999). This is also demonstrated by the CWM N and pH values of ancient woodlands in this study. In isolated woodlands the presence of nitrophilous competitors such as *Urtica dioica* alongside the low abundance of specialist woodland plants leads to higher CWM N and pH values. These values may be lower in adjacent created woodlands as more woodland plants are able to reach them to compete against landscape generalists.

Plants dispersed by mammals and birds were routinely reaching adjacent and isolated created sites, where plants dispersed by wind, ants or their own mechanisms tended to only reach adjacent sites. This suggests that dispersal mechanisms also limit the fulfillment of colonisation credit, because mammals and birds can disperse seeds a lot further than ants or unsepecialised mechanisms (Brunet and Von Oheimb 1998). Watts et al. (2020) suggest the use of “milestone species” to assess whether a restoration action is on course to fulfill its potential. In the case of new woodlands initial milestone species could be those with longer ranged dispersal mechanisms as these are expected to reach new habitat sooner. Later, and perhaps more important, milestone species’ would be those dispersed by short range dispersal mechanisms. If after some years these have not made it to a newly created site, it is likely that the site is too isolated. In this case further management interventions may be needed. These could take the form of translocations or seed sowing, which have been shown to increase the establishment of native plant species in restored sites (Orrock et al. 2023; Paraskevopoulos et al. 2023).

The source woodlands included in this study happened to be relatively species poor. This could either be a result of the lack of recent management that has shaped ancient woodlands over the centuries, or the small size of these isolated fragments (Rackham 2008). The species pool available to colonise new habitat patches is known to play an important role in how a focal site is colonised (Cornell and Harrison 2014). Catano et al. (2021) found that seeding a restored site with a larger species pool steepens the species area curve due



the spatial aggregation of new species. This further supports the use of seeding or translocation interventions when recent woodlands are not being colonised. If the cause of this is not the isolation of the new woodland but in fact a poor available species pool then management interventions may be the only way to increase diversity in a recent woodland.

### **3.6 Conclusions**

The colonisation credit of specialist plants in recently created woodlands takes decades to fulfil and remains up to 80 years after creation. Spatially targeting woodland creation adjacent to existing ancient woodlands does reduce colonisation credit faster but does not fulfil it in a meaningful time frame. The use of a natural experimental design allowed us to focus in on which species are driving these long time-lags after woodland creation. Early signs of success after creating a new woodland may be the arrival of specialist plants which are dispersed by long-range mechanisms. These species should make it to more isolated sites as they are less dispersal limited. What would limit these species is poor local habitat conditions. Over-shading may cause more shade tolerant species to dominate the woodland floor, and under-shading may mean that landscape generalists move in and out-compete woodland species. If there are conditions such as these, extra management interventions may be needed such a thinning or supplementary tree planting. The arrival of species dispersed over shorter distances may be an appropriate second milestone with which to judge woodland creation by. If these species arrive and establish it would suggest that

dispersal distance is not a limiting factor in fulfilling colonisation credit. If these species do not start to arrive when habitat conditions are suitable it may suggest the need for management interventions such as translocations.

Ecological time-lags in woodland ecosystems are exceptionally long these must be considered when planning restoration projects, and success needs to be judged over appropriate timeframes or by identifiable early milestones.

Warning: package 'knitr' was built under R version 4.2.3

Warning: package 'flextable' was built under R version 4.2.3

## **4 How do ecological corridors modify habitat creation strategies?**

### **4.1 Abstract**

Spatially targeting habitat creation has been shown to improve landscape scale biodiversity. Despite the fact that ecological corridors enhance species' populations across fragmented landscapes, they are rarely considered when assessing evidence on how best to target habitat creation at the landscape scale. Here, an individual based modelling framework was applied to real landscape scenarios to test how the presence of hedgerow corridors affects species' population dynamics in fragmented woodland landscapes both before and after habitat creation. I compared two habitat creation strategies; one where woodland was created adjacent to existing patches, and another where woodland was created isolated from existing patches. I simulated population dynamics of four species with distinct functional traits across these landscapes and assessed their responses to landscape configuration in terms of mean population size and mean patch occupancy. In landscapes pre-habitat creation, higher edge densities were associated with higher populations, indicating that the creation of isolated 'stepping stone' habitats should be prioritised. Further, the presence

of hedgerows had little effect on populations pre-habitat creation. However, under habitat creation scenarios, I found that the creation of adjacent woodlands provides the best outcomes across all metrics considered. The benefits of hedgerow corridors were contingent on the habitat creation scenario: while hedgerow corridors are important in improving population outcomes when woodlands are created isolated from existing habitat, they have little impact where woodlands are created adjacent. These results highlight the limitations of extrapolating conclusions from studies of past landscape fragmentation, and instead suggest the importance of prioritising evidence from restoration actions, field experiments and modelling scenarios to inform decision-making. These results also illustrate the non-uniform effects of ecological corridors among different spatial targeting strategies, suggesting the importance of considering context-specific impacts in planning and implementing restoration approaches. While creating adjacent habitat is the best option, in reality this is not always possible; if isolated habitat must be created then corridors should be considered as a means to improve local and landscape-scale biodiversity

## **4.2 Introduction**

In recent years there have been efforts to restore historically fragmented landscapes across the globe, with goals of enhancing biodiversity. For example, the United Nations have labelled 2021-2030 the “Decade on Ecosystem Restoration” and the Bonn challenge aims to restore 350 million ha of woodland (Bonn Challenge 2019). These efforts have come alongside calls to improve

connectivity between fragmented patches and across inhospitable landscapes (Lawton 2010; Hilty et al. 2020). Fragmentation here is referring to the splitting apart of habitat, in theory this is a separate process to habitat loss per se, however in practice the two are often interlinked (Fahrig 2003). Connectivity is referring to how the surrounding landscape can facilitate species dispersal or movement between habitat patches (Taylor et al. 1993). Ecological networks are made up of core habitat patches, ecological connecting features such as corridors, and the surrounding matrix, and have the potential to address this. However, evidence is needed to inform strategies that will accrue the most biodiversity benefits over time (Humphrey et al. 2015; Isaac et al. 2018). Historically, restoration ecology - the study of ecosystem restoration - has focused on site-scale factors (Brudvig 2011), but it is now moving to address these challenges by considering landscape-scale connectivity (Damschen et al. 2019).

Evidence on how restored landscapes should be configured is often provided by looking backwards. This is done by observing how the abundance and configuration of habitat in fragmented landscapes affects species distributions (Fourcade et al. 2021). However, observing outcomes of habitat fragmentation will not necessarily inform best practices of habitat creation. This is because when viewing historically fragmented habitats we are seeing a quasi-equilibrium; conversely when performing restoration actions we are interested in the more transient process of colonisation. Thus, it is important to gain insight from studies which consider the creation of habitat and not just its fragmentation. This is currently done in two ways: (1) using historical records to gain insight into

the age of recently created habitat (Watts et al. 2016; Hughes et al. 2023), and (2) creating large-scale ecological experiments to assess in the future (Damschen et al. 2019; Griffin and Haddad 2021). Both of these strategies are important but ultimately hard to do as colonisation lags can last decades, which hampers our ability to assess success under reasonable time frames (Watts et al. 2020). Thus the simulation modelling of landscapes and their ecological processes has become key to guiding restoration planning (Synes et al. 2016).

A range of models have been developed to tackle this problem. These include: Population viability analyses which use population scale parameters to predict future population size and extinction probability (Boyce 1992); circuit theory models where habitat patches and linkages represent nodes and resistors in an electrical circuit (McRae et al. 2008); and species distribution models which correlate environmental variables with current species distributions to then predict future distributions after some environmental change (Araújo and Guisan 2006). However, with advances in computing power, individual based models (IBMs) have recently been favoured as they allow individuals to vary in behaviour, and incorporate demographic stochasticity (Synes et al. 2016). IBMs are process based models which simulate the behaviours of individual members of a population with varying functional and life history traits. The results of these individual behaviours can then be aggregated to draw population level conclusions. Non-spatially explicit IBMs, where an individual's position in space is not accounted for, can be used to model emergent population dynamics as a result of varying life history traits. For example, the rate of cannibalism in

largemouth bass fish is a result of size distributions within populations (Deangelis et al. 1980). Spatially explicit IBMs can model population distributions across landscapes of varying habitat types (Fahrig 1998a; Synes et al. 2020). For example, early spatially explicit IBMs were used to test the effects of habitat fragmentation at different levels of habitat cover. These showed that fragmentation per se is important in landscapes with under 20% habitat cover but has little effect when habitat cover exceeds this threshold (Fahrig 1998a). More recently Synes et al. (2020) used a spatially explicit IBM framework to assess the efficacy of different restoration actions at the landscape scale. This work found that spatially targeting new habitat adjacent to existing habitat patches is the most effective way to increase species populations and improve their mobility across the landscape. There are some drawbacks of IBMs that must be considered. For example, it is difficult to simulate home ranges which leads to an over-emphasis on dispersal movements. This can lead to an overestimation of functional connectivity across landscapes as all individuals will try and disperse to new habitat patches, where in reality some will maintain a home range (Synes et al. 2016).

Ecological corridors are thought to assist many species moving through inhospitable landscapes (Gilbert-Norton et al. 2010). The theory behind their effects on populations at the landscape-scale is also sound: meta-community theory suggests that connecting small habitats increases the potential for small populations to be rescued from extinction (Leibold and Chase 2017) and island biogeography predicts that the more connected a habitat patch is the higher its

colonisation rate will be (MacArthur and Wilson 1967). Thus, there are 2 ways in which the presence of corridors could influence a landscape-scale habitat network: (1) corridors will increase the colonisation rate from existing habitat patches into created habitat patches (Araujo Calçada et al. 2013), and (2) corridors will also prevent the populations of small patches from going extinct by increasing the likelihood that they are rescued by immigration (Staddon et al. 2010). There is also empirical evidence supporting both of these processes from the Corridor Project at the Savanna River Site (Damschen et al. 2006). When assessing recently created habitat fragments the authors found that fragments connected to other fragments were colonised faster and harboured higher biodiversity rates over time; the authors also found that these fragments had lower extinction rates than isolated fragments. It is of course important to consider corridor area and habitat quality when assessing their efficacy, for example a corridor's width mediates the strength of its edge effects (Van Schalkwyk et al. 2020), and a corridor's habitat quality is likely to be important to specialist species more so than generalists (Habel et al. 2020).

A case study of broad scale habitat creation in a system with existing ecological corridors is that of woodland creation in temperate Europe. There are schemes across this region to create new woodland to restore biodiversity (see Forestry England 2022), and there are also ready made ecological corridors in the form of hedgerows. These are cultural landscape features where a line of trees or shrubs is used to delineate field margins. Hedgerows were originally used to produce timber (Baudry et al. 2000), but are now considered important ecosystems in



their own right (Montgomery et al. 2020) and act as corridors for a range of woodland species (Pelletier-Guittier et al. 2020; Vanneste et al. 2020). Currently it is rare for woodland creation strategies to consider the creation or existing placement of hedgerows when creating new woodland patches. For example England's "Woodland Creation Offer" (Forestry England 2022) offers payment for biodiversity outcomes, but does not offer explicit incentive to complement woodland creation with hedgerows. It is important for us to understand how hedgerows and corridors more generally interact with different habitat creation strategies, so that we can implement them effectively in ecosystem restoration initiatives.

#### **4.2.1 Aims and objectives**

The present study aims to address this using the IBM platform "RangeShifter" (Bocedi et al. 2020). RangeShifter is ideal for this study as it is spatially explicit, models dispersal and life history traits stochastically, and allows for dynamic landscapes which change over time. First I tested how the presence of hedgerows may affect population sizes and patch occupancy of null landscapes with no habitat creation implemented. These null landscapes all had varying amounts of woodland cover and woodland fragmentation so I could assess how hedgerows affect different existing landscape configurations. I then tested how the presence of hedgerows may modulate the efficacy of different habitat creation strategies. The same selection of UK landscapes were used, however after a certain period of time new habitat patches (woodlands) were created within them. These

patches were created using one of two algorithms, one which creates habitat adjacent to existing patches and another that creates habitat a minimum distance away from existing patches. In the null landscapes I predicted that hedgerows would help species persist in small patches of habitat that were isolated from larger source populations. This may benefit less patchy landscapes where most of the habitat is in large clumps and smaller patches are very isolated. In habitat creation landscapes I predicted that hedgerows will improve the efficacy of creating isolated habitat patches, but will make little difference to patches created adjacent to existing patches.

## **4.3 Methods**

### **4.3.1 Landscape selection**

Landscapes were selected from a 2125km<sup>2</sup> area covering the East Midlands region of the UK (Figure 13). This area is representative of lowland intensive agriculture in the country where field boundaries are marked with hedgerows rather than stone walls, making it ideal for the study of woodland fragmentation and hedgerow corridors. This is emphasised by the National Forest project occurring in part of the region, where attempts are being made to increase woodland cover (National Forest Company 2022). The region was gridded into 25km<sup>2</sup> cells from which our sample landscapes could be selected. The *LandscapeMetrics* R package (Hesselbarth et al. 2019) was used to calculate the woodland cover percentage and the woodland edge density for each landscape, using the National woodland Inventory (NFI) polygons (Forestry Commission

2020).

I needed an aggregation metric which varied independently from habitat amount. The “Clumpiness” index from “LandscapeMetrics” is generally considered to be unrelated to habitat amount (Wang et al. 2014), however, for the low percentages of woodland cover in the present study this was not the case. I found that edge density (ED) was a reliable metric of habitat fragmentation which did not depend on habitat amount for our range of woodland cover. ED is also known to be an important determinant of habitat fragmentation (Fahrig 2017b).

The percentage cover and ED of woodland was summarised for each 25km<sup>2</sup> cell, and cells with extreme values in either direction were removed. Then the 30th and 70th percentiles were found for each variable’s range across all cells; for example, the range of woodland cover was 5% - 15% and the 30th percentile of this range was 8.3%. Thus, each cell could be categorised as having low (<30th percentile of the range), medium (30th-70th percentile of the range), or high (>70th percentile of the range) woodland cover, and the same for ED. The area of corridors was also extracted to each cell. This was determined using the Vegetation Object Model (Environment Agency 2021) after removing NFI polygons. Although the vegetation object model contains all trees and shrubs outside of woodland, in this region of the UK these are largely made up of hedgerows, and thus referred to here as corridors. For each combination of high, medium, and low woodland cover and ED, the landscapes with the highest and lowest corridor area were found. This resulted in 18 unique landscapes, varying independently in ED, woodland percentage cover, and corridor area (Figure 14). All variables were assessed for

pairwise correlations to ensure they were independently distributed.



Figure 13: A map showing the 2125km<sup>2</sup> area covering part of the midlands in the UK. Red squares indicate the final 18 landscapes selected as model inputs.

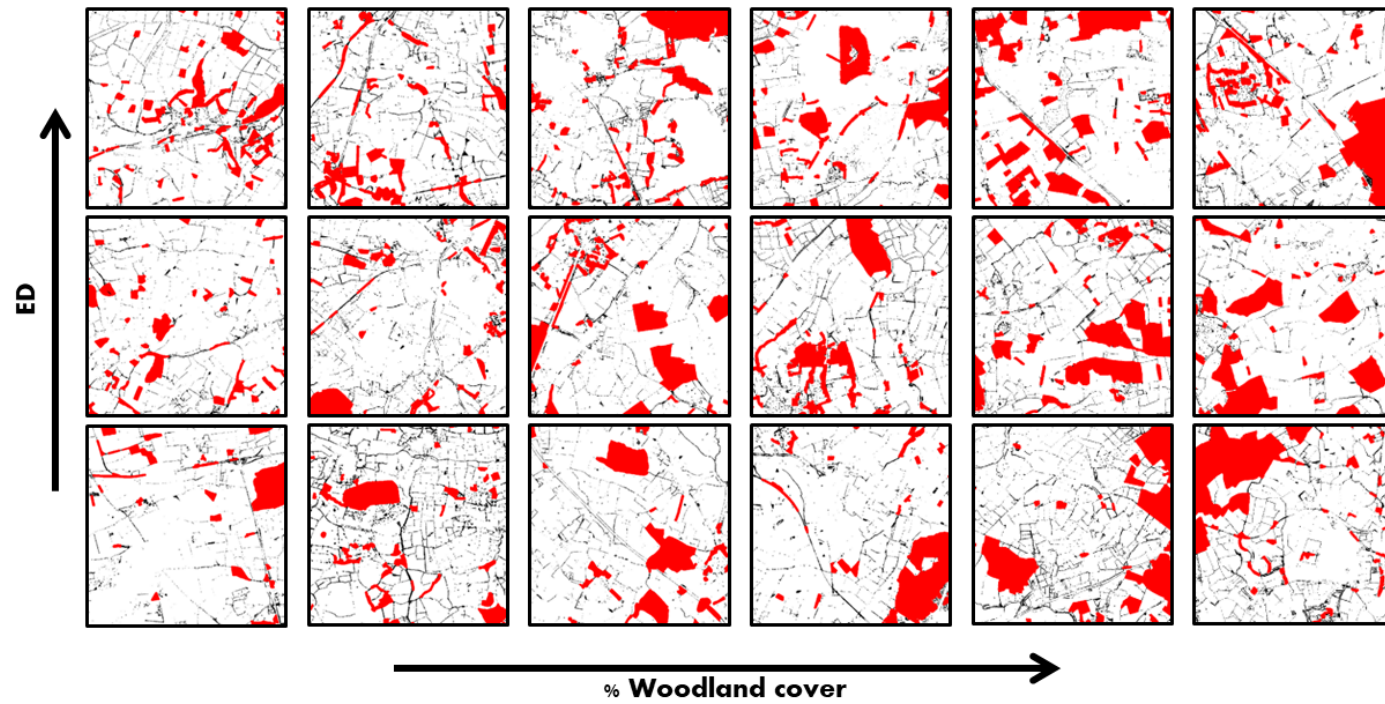


Figure 14: The 18 landscapes chosen to independently vary in woodland percentage cover, woodland edge density and hedgerow area. The percentage woodland cover increases along the x axis where edge density increases along the y axis.

### 4.3.2 Conceptual Species

I have chosen here to use conceptual species. The focus of this work is to assess how ecological corridors affect different habitat creation strategies and it is my aim that conservation practitioners globally can draw from the results. By using conceptual species which cover the parameter space of key traits, such as dispersal ability and carrying capacity, results can be generalised to a range of systems where the target habitat may not be woodland and the target corridor may not be hedgerows. Further, to find a set of real species for which enough data exists within the study region and which also vary sufficiently in key functional traits would be a great challenge. Thus, I follow the approach that a range of modelling studies have used by modelling ecologically relevant conceptual species (Fahrig 1998b; Watts et al. 2010; Synes et al. 2020). Four conceptual species were created with an aim to cover the dispersal and habitat suitability parameter space (Figure 15). Species 1 had long range dispersal capability using a Stochastic Movement Simulator (SMS), and a low carrying capacity. This species could not maintain breeding populations in corridors but could move through them more easily than through the matrix. Species 2 had a medium range dispersal capability using an SMS, and a low carrying capacity. This species could not breed in corridors but again found them easier to move through. Species 1 and 2 represent species that use corridors to move through a landscape but require core habitat to sustain breeding populations. Examples of these in the UK woodland landscape might be red foxes (*Vulpes vulpes*) or roe deer (*Capreolus capreolus*). Species 3 had a medium carrying capacity but was a short range disperser. This

species was able to maintain breeding populations in corridors and dispersed using an SMS. Species 4 had a high carrying capacity, could maintain populations in corridors, and dispersed using a negative binomial dispersal kernel with a mean of 5m. Species 3 and 4 represent smaller taxa which can move through the hedgerow corridors but can also maintain breeding populations within them. Examples of these might be woodland plants such as lords and ladies (*Arum maculatum*), or carabid beetles. All species could persist in woodlands but could not in the matrix Table A3. Sensitivity analyses for each species are shown in Figure A2, here key parameters are tweaked to see how much they affect model outcomes.

### **4.3.3 Simulations**

Simulations were run using the RangeShiftR R package (Malchow et al. 2021) in R version 4.1.2 (R core team 2022). RangeshiftR is a spatially explicit individual based modelling package, which takes rasters as input landscapes and allows individuals to disperse through them and reproduce. The advantage of RangeshiftR for the present study is that it allows dynamic landscapes, where multiple rasters can be loaded into a simulation representing landscape change over time.

Each simulation was run using patch based landscapes, where density dependent parameters are calculated at the patch level rather than the cell level. Here, a patch is defined as a contiguous selection of cells with the same habitat code. First, “null models” were run for each species (Figure 15). These were used to test the interactions between corridors, ED, and woodland percentage cover. This



was done using only the original landscapes with no habitat creation scenarios. For each species in each landscape, simulations were run with corridors present and corridors absent, and replicated 5 times for each. Each species was initiated at half carrying capacity ( $k$ ) in all woodland patches, and simulations were allowed to run for 300 years.

To test for how corridors may interact with different habitat creation strategies, two scenarios were used: create adjacent and create isolated. To do this each of the 18 original landscapes had two algorithms applied, one which added twenty 5ha woodland patches adjacent to existing woodland, and another which added twenty 5ha woodland patches at least 300m away from existing woodland. The amount and size of created woodlands were chosen to represent a 2% increase in woodland cover, which is in line with UK creation targets (DEFRA 2018). Ten landscapes were generated for each original landscape, five using the create adjacent algorithm and five using the create isolated algorithm, to get a more representative result for each habitat creation strategy. A further ten landscapes were generated by removing corridors from these, meaning for every original landscape there were twenty created landscapes, five with habitat created adjacent and corridors present, five with habitat created isolated with corridors present, five with habitat created adjacent and corridors absent and five with habitat created isolated and corridors absent (Figure 15). Simulations were run for 150 years to equilibrate before new habitat patches were added, after which point the simulations were continued for another 150 years. For each species, for each created landscape, there were 5 replicates run. These will be referred to as

“habitat creation models”.

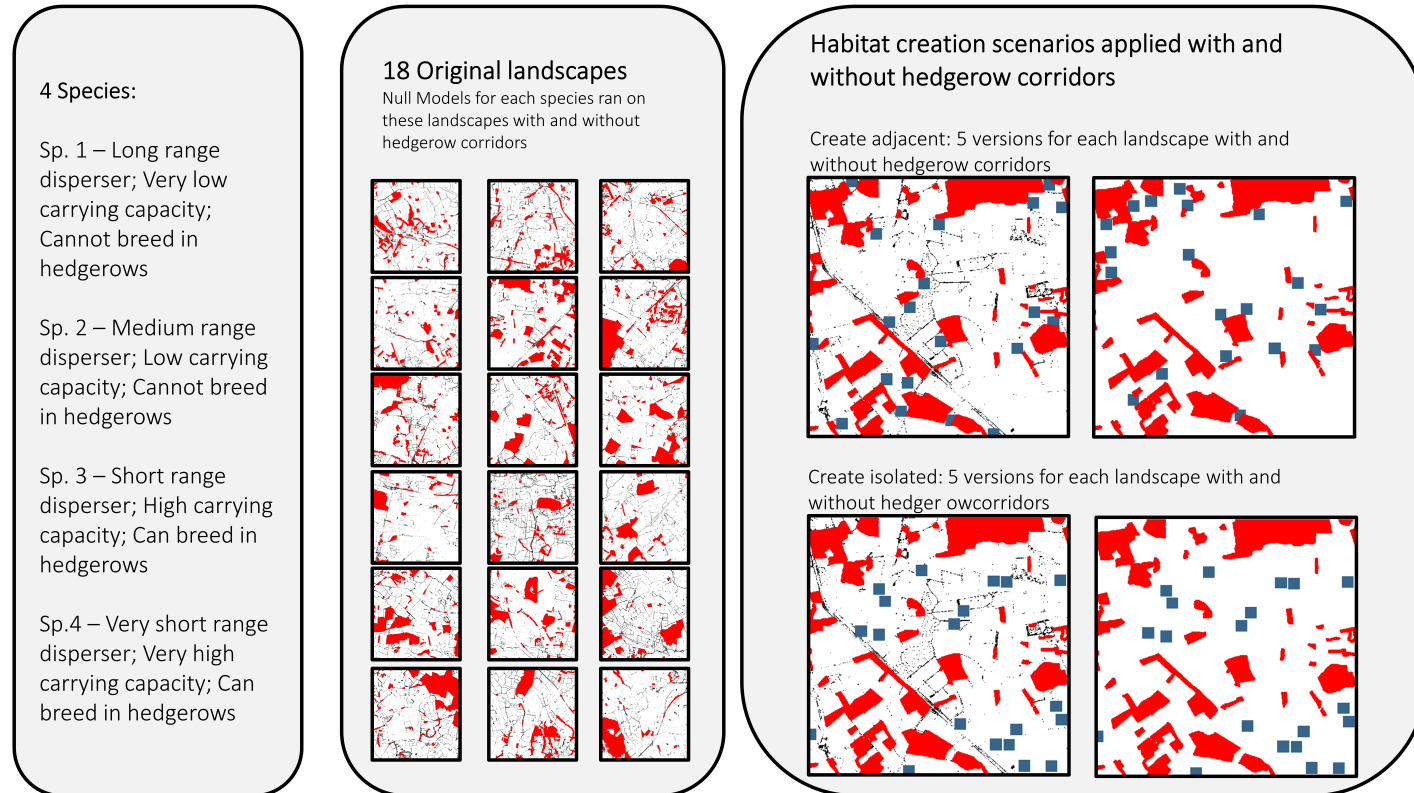


Figure 15: A diagram explaining the four conceptual species, the 18 original landscapes, and the habitat creation scenarios applied for the present study. Null models were run on the 18 original landscapes with hedgerow corridors and without, where habitat creation models were run on landscapes modified using the habitat creation scenarios, again with and without hedgerow corridors.

#### **4.3.4 Extracted metrics**

For the null models using just the original landscapes two metrics were extracted and averaged across replicates. The first was the mean population size of individuals in woodlands for the last 50 years of the simulation. The second was the mean proportion of woodland patches occupied by any individual over the last 50 years of the simulation.

Metrics extracted from habitat creation models were slightly different. The mean population size for individuals in woodlands (original and created) over the last 50 years was taken as the percentage difference in population size between the habitat creation model and the null model of the same landscape without any corridors. So rather than absolute population numbers, this represents how much a habitat creation scenario might increase (or decrease) population sizes. The mean percentage woodland occupancy over the last 50 years in habitat creation models was found as the proportion of mean unoccupied original woodlands in the null landscape which were now occupied after habitat creation. This ignores created woodlands. The mean percentage occupancy and mean population sizes of newly created woodlands over the last 50 years were also found, but this could not be compared to original landscapes as these woodlands did not exist.

#### **4.3.5 Statistical analysis**

To find meaningful interactions between percentage woodland cover, ED and the presence of corridors in null models using just the original landscapes, models were created independently for each species and for each extracted metric. Linear

models assuming Gaussian errors were used to predict the mean population, where Beta regression models were used to predict the proportion of habitat patches occupied. Beta regression was used to deal with the heteroskedasticity inherent in proportional data (Cribari-Neto and Zeileis 2010). All models included landscape level predictors of ED, percentage woodland cover and the binary variable of corridors present or absent. All possible two-way interaction terms were included in global models. The mean proportional occupancy was only tested for Species 1 and Species 2, as Species 3 and Species 4 could persist even in small patches meaning their occupancy did not reduce over time.

To test how habitat creation scenarios are modulated by the presence of corridors, landscape level ED or the percentage woodland cover, linear mixed models and generalized linear mixed models were used with the original landscape as a random effect. Fixed effects included the “within landscape” variables of habitat creation scenario (create adjacent or create isolated) and the binary variable of linear features present or absent. Fixed effects also included the “landscape level” variables of ED and percentage woodland cover of the original landscapes. Two way interaction terms between habitat creation scenario and all other fixed effects were included in global models. To model proportional occupancy outcomes mixed models assuming beta distributed errors were used through the *glmmTMB* R package (Brooks et al. 2017). The proportional occupancy of original woodlands in habitat creation landscapes was again only tested for the bird and mammal.

Linear mixed models and generalized linear mixed models assuming beta

distributed errors were also used to test the population size and proportional occupancy of newly created woodlands respectively. These models included the same predictor variables as those described above testing habitat creation scenarios.

If proportional data included any extremes of 0 or 1, it was transformed using the below equation (where  $n$  = sample size) as beta regression does not accept these values.

$$y * (n - 1) + (0.5/n)$$

These analyses were exploratory by nature, and as such I reduced global models based on AIC scores to find which variables and which interactions explained the population and occupancy outcomes best. To avoid issues of multiple hypothesis testing p values are omitted; the minimum model is reported and the variables included are assumed to meaningfully impact the results.

## **4.4 Results**

### **4.4.1 Null Models**

The best models for predicting the population sizes and proportional occupancies in null landscapes did not include any interaction terms between the presence of corridors and other landscape metrics for any species. The presence of corridors only increased the population size and percentage occupancy of Species 2

(Table A4). There were strong positive effects of percentage woodland cover and ED on all species' populations (Figure 16), which are broken down in Table A4. The best models for predicting the population sizes of Species 2, Species 3 and Species 4 all included an interaction term between the percentage woodland cover and ED. Here, as percentage woodland cover increases, the effect of ED decreases. This same interaction term was included when predicting the proportional occupancy of Species 1 (Table A4) (Figure 17).

The models with the lowest AIC scores predicting species population sizes all had an  $R^2$  of above 0.9, where the best models for predicting the proportional occupancy of Species 1 and Species 2 had an  $R^2$  of 0.23 and 0.4 respectively (Table A4). This is likely explained by the stochastic element of patch occupancy where population levels are more deterministic. If a few patches are reached by single individuals then the proportion of patches occupied can change quite significantly. However, an increase of one or two individuals at the population level has little bearing on results.

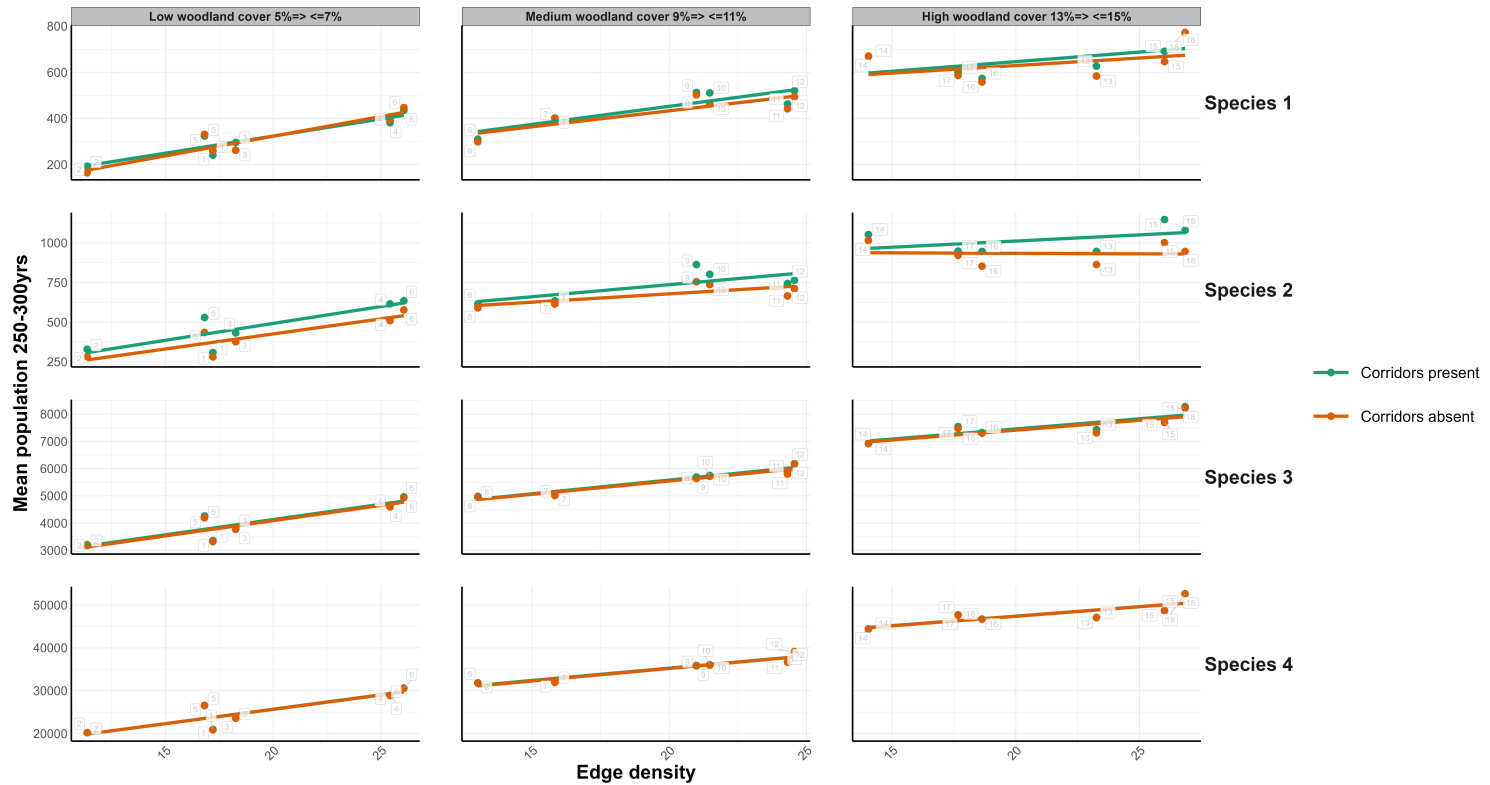


Figure 16: A scatter plot showing the mean population of null landscapes, with no habitat creation, and how this is effected by ED, the percentage woodland cover and the presence of hedgerow corridors. Population sizes were averaged over the last 50 years of simulations, and across 5 replicates for each landscape with and without hedgerow corridors. Rows are separated by species, and columns are separated as a categorical variable for percentage woodland cover so that any interactions between predictive variables can be viewed. The data for corridors present for Species 3 and Species 4 is not visible as these species were able to survive in all small habitat patches, meaning that the presence of corridors had little effect on their populations.



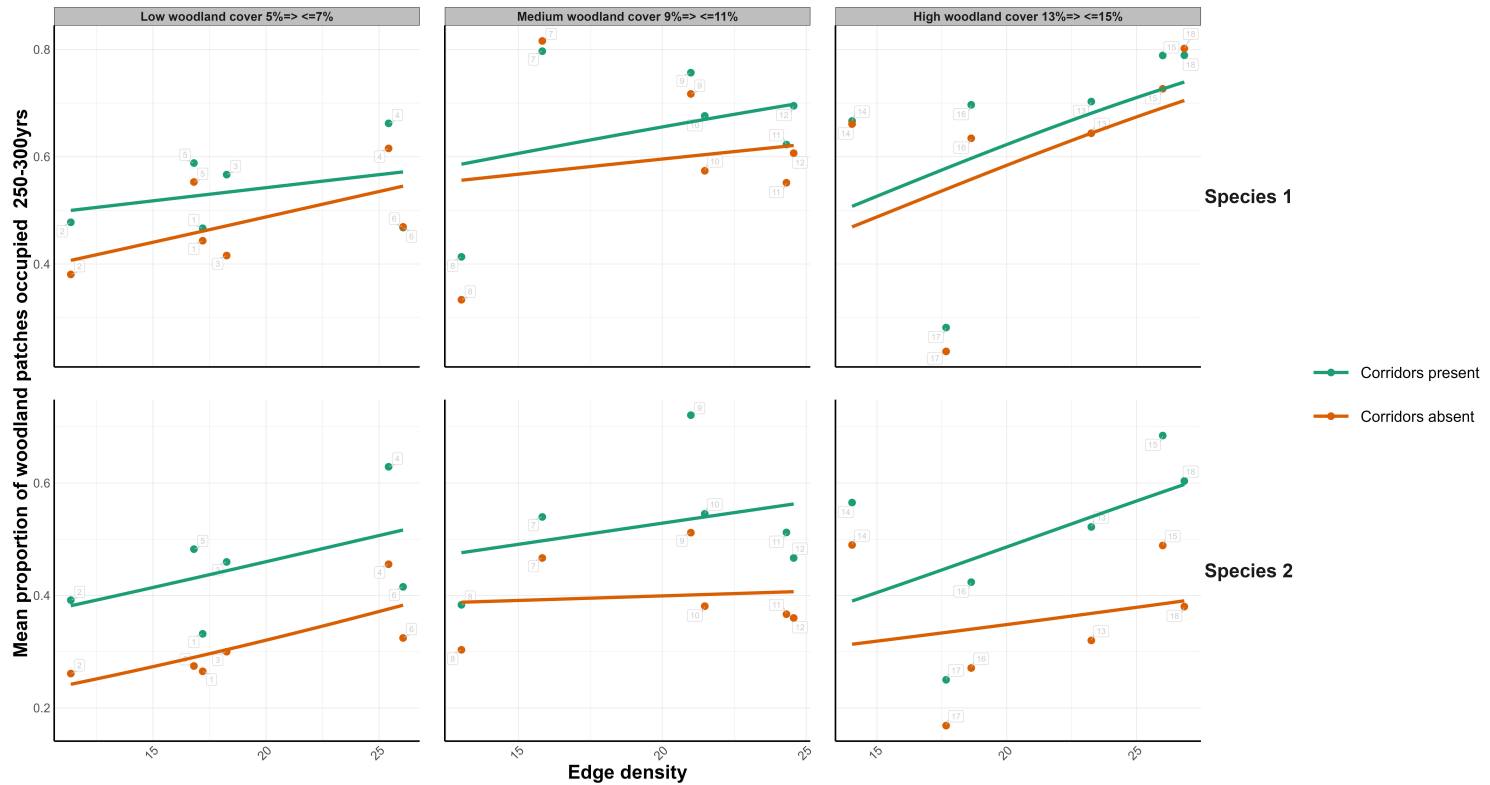


Figure 17: A scatter plot showing the mean percentage of woodland patches occupied in null landscapes, with no habitat creation, and how this is effected by ED, the percentage woodland cover and the presence of hedgerow corridors. Occupancy percentages were averaged over the last 50 years of simulations, and across 5 replicates for each landscape with and without hedgerow corridors. Rows are separated by species, and columns are separated as a categorical variable for percentage woodland cover so that any interactions between predictive variables can be viewed. Species 3 and 4 are able to maintain populations in all small habitat patches, meaning that their occupancy does not change over time. As such they are removed from this plot

#### 4.4.2 Habitat creation models

Creating habitat adjacent to existing patches consistently outperformed creating isolated habitat at increasing population sizes (Figure 18). However, the best models for all species included an interaction term between the presence of hedgerow corridors and the habitat creation strategy. Here, hedgerows increased populations in landscapes with isolated created habitats but had little effect on landscapes with adjacent created habitats (Figure 18). There were also interactions between woodland cover and habitat creation strategy (Figure 18) alongside ED and habitat creation strategy (Figure 19). As both of these metrics increased, the effectiveness of creating adjacent habitat compared to creating isolated habitat reduced. These models all had a marginal  $R^2$  of above 0.8 (Table A4).

Each species had different interaction terms included in their respective best models predicting percentage occupancy of original habitat patches. Species 2's model included an interaction between the presence of hedgerows and the habitat creation strategy, again, where hedgerows increase the effectiveness of creating isolated habitat but less so adjacent habitat. Species 1's model included an interaction between the percentage woodland cover and the habitat creation strategy where creating adjacent habitat is the better option at low woodland covers but creating isolated habitat is preferred when woodland cover is high (Figure 20). ED remained in the models for both species. The Nakagawa  $R^2$  of these models was 0.46 for the bird and 0.91 for the mammal.

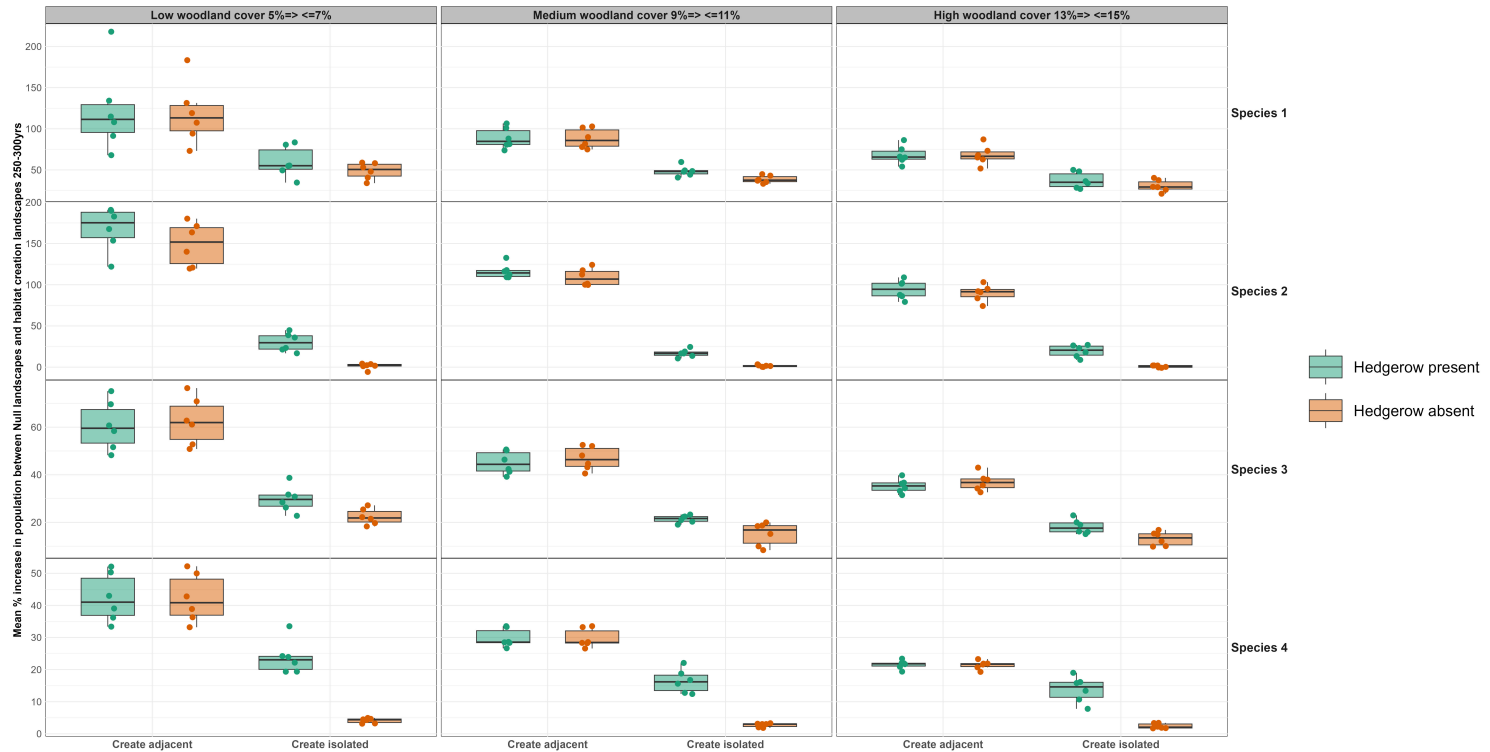


Figure 18: A Boxplot showing how the presence of hedgerow corridors interacts with the different habitat creation scenarios (create adjacent and create isolated) to affect the percentage increase in populations for four different species. The plot is faceted by the percentage woodland cover of original landscapes.

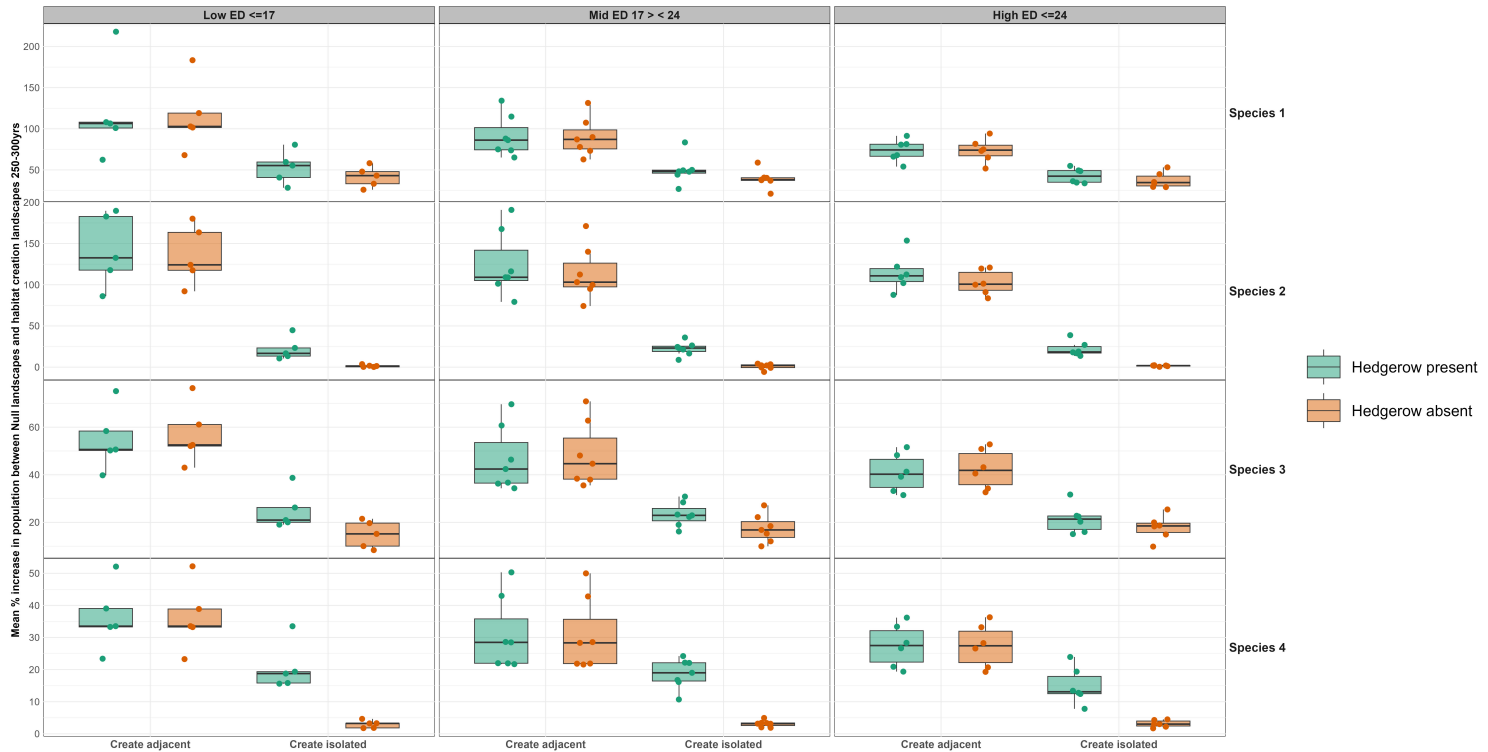


Figure 19: Showing how the presence of hedgerow corridors interacts with the different habitat creation scenarios (create adjacent and create isolated) to affect the percentage increase in populations for four different species. The plot is faceted by ED of original landscapes.

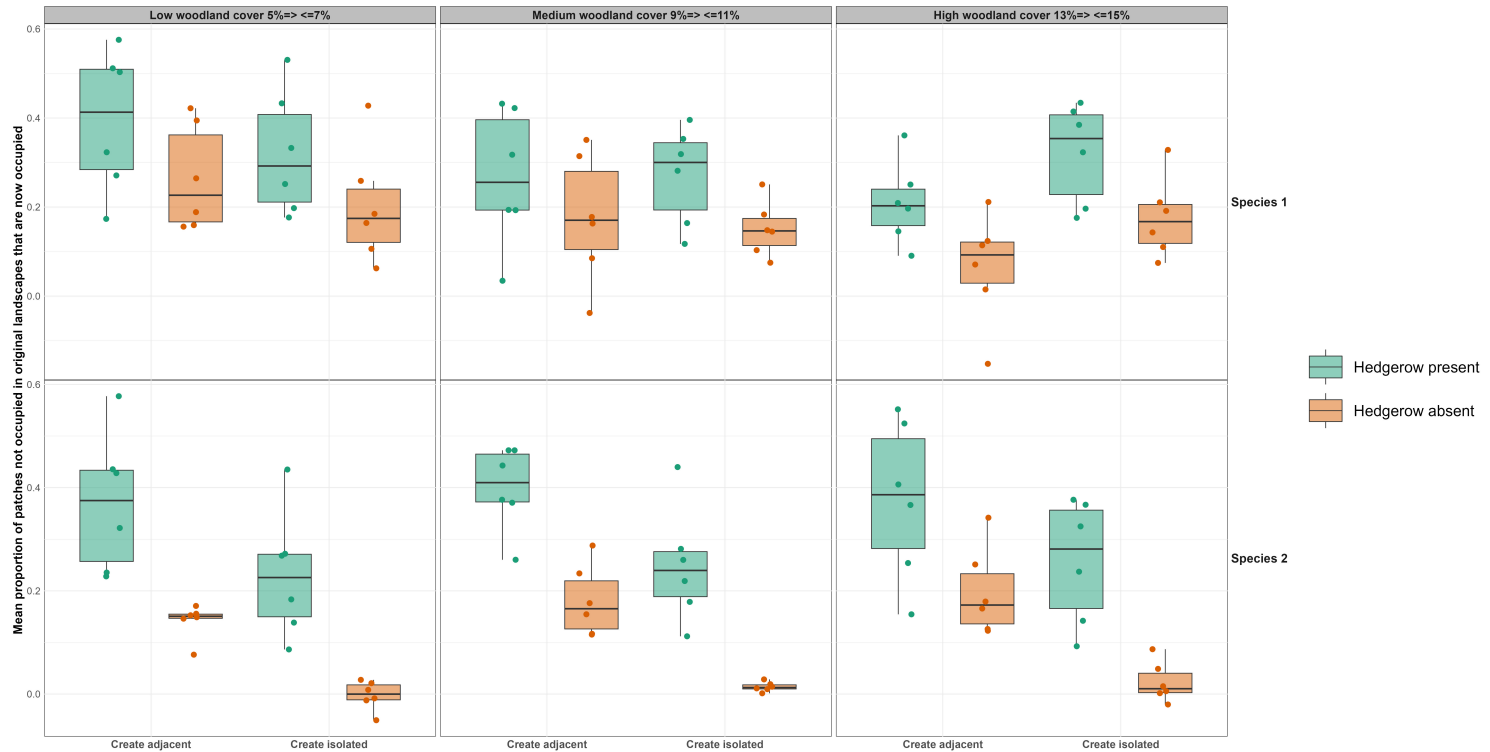


Figure 20: A boxplot showing how the presence of hedgerow corridors interacts with the effectiveness of different habitat creation scenarios (create adjacent and create isolated) in increasing the occupancy of original habitat patches for four different species. The plot is faceted by how much woodland cover there was in the original landscape.

Populations in newly created habitats were always higher in adjacent created habitat than in isolated created habitat (Figure 21). For all species, all two way interactions remained in the models predicting the population sizes of newly created habitats (Table A4). Higher ED in the original landscapes and the presence of hedgerows reduced the effectiveness of creating adjacent habitat compared to creating isolated habitat for all species (Figure 22). Higher percentage woodland cover in the original landscape increased the effectiveness of creating adjacent habitat in all species except Species 4 (Figure 21). All of these models had an  $R^2$  of above 0.9 (Table A4).

Creating habitat adjacent to existing patches incurred a higher proportional occupancy of new habitat patches for all species (Figure 23). However, the best models included an interaction term between the presence of hedgerows and the habitat creation strategy for all species except Species 1 (Table A4) where adjacent created habitat reduced in effectiveness compared to isolated created habitat if hedgerows were present. The best model for the invertebrate also included an interaction term between ED and habitat creation strategy, where higher ED again reduced the effectiveness of adjacent created habitat compared to isolated (Figure 24).



Figure 21: A boxplot showing how the presence of hedgerow corridors interacts with the effectiveness of different habitat creation scenarios (create adjacent and create isolated) to effect the population of newly created patches for four different species. The plot is faceted by how much woodland cover was in the original landscape.

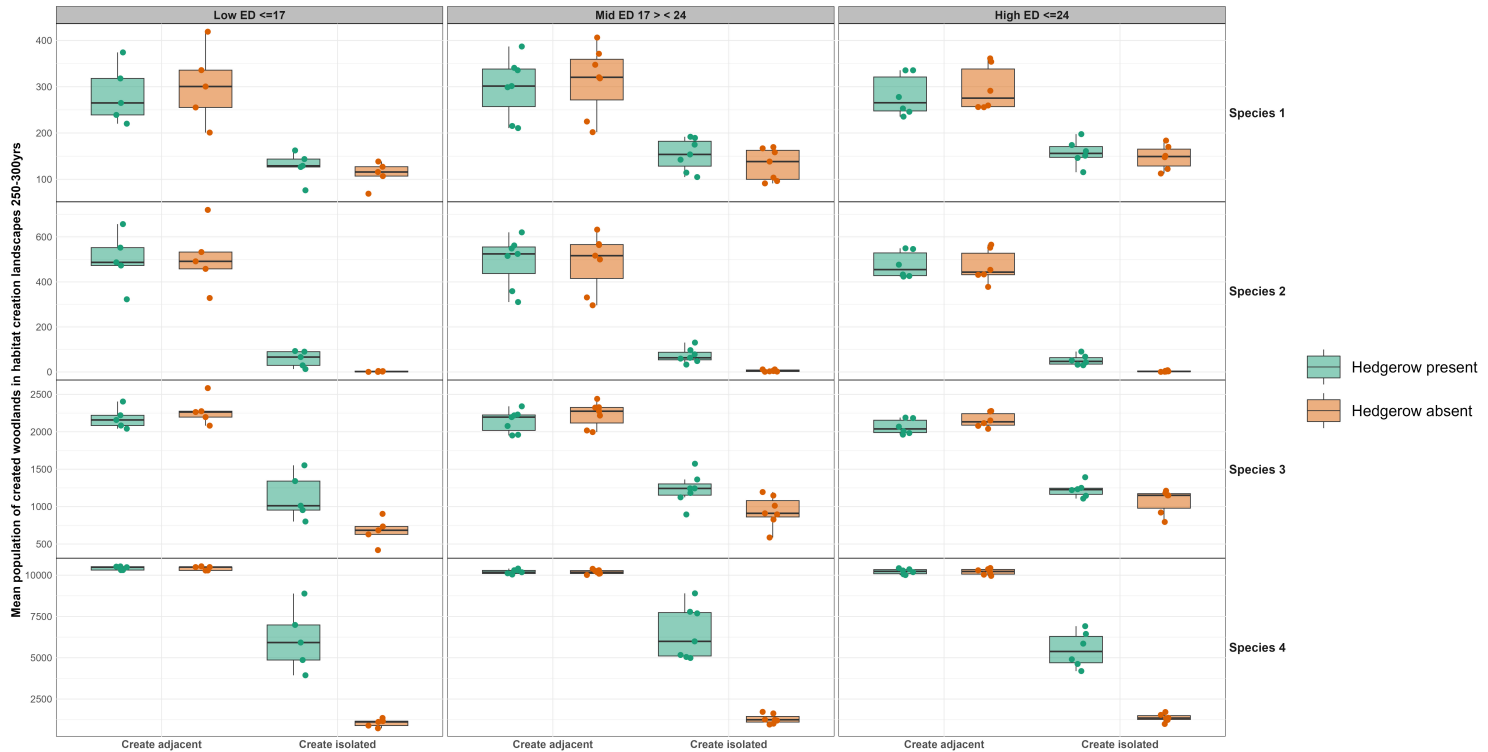


Figure 22: A boxplot showing how the presence of hedgerow corridors interacts with the effectiveness of different habitat creation scenarios (create adjacent and create isolated) to effect the population of newly created patches for four different species. The plot is faceted by the ED of the original landscape.



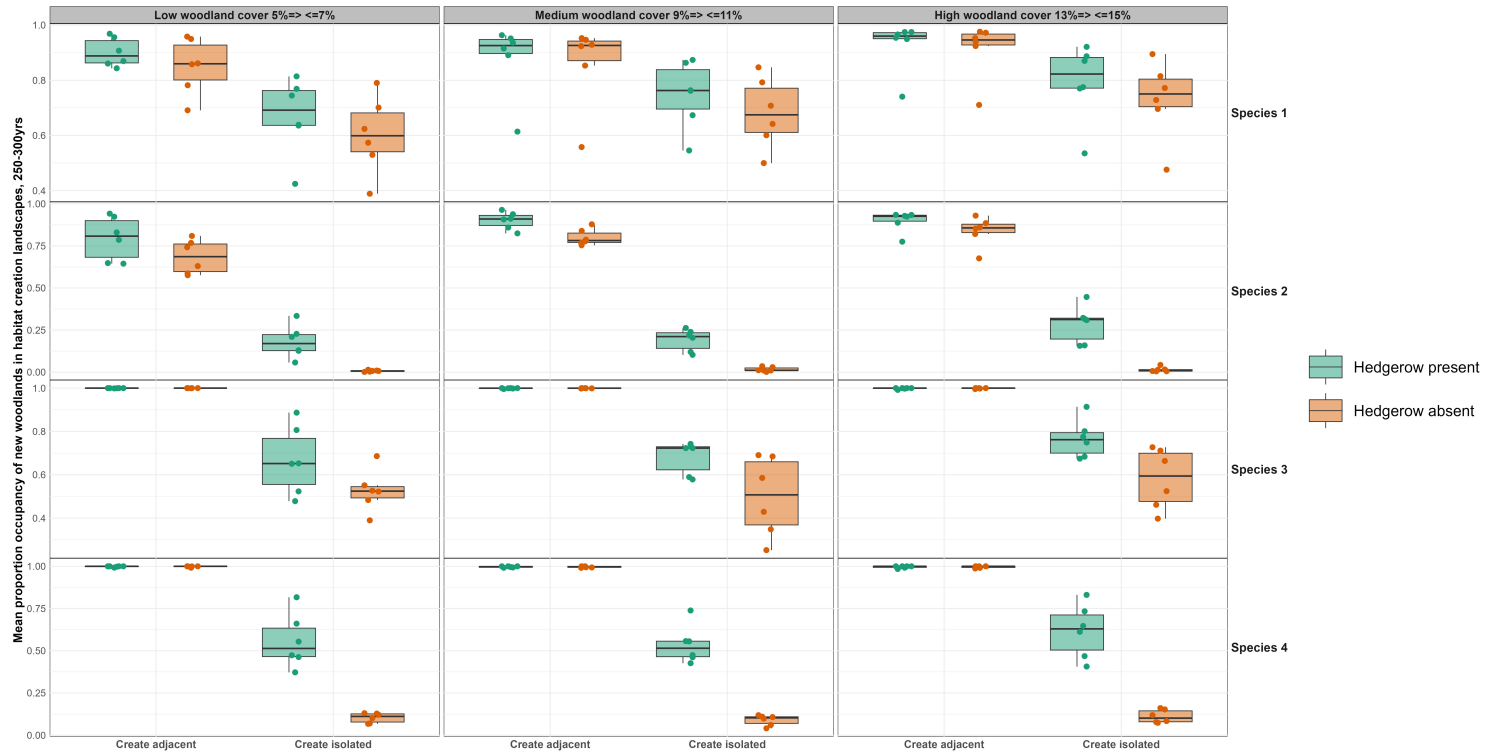


Figure 23: A boxplot showing how the presence of hedgerow corridors interacts with the effectiveness of different habitat creation scenarios (create adjacent and create isolated) to effect the percentage occupancy of newly created patches by four different species. The plot is faceted by how much woodland cover there was in the original landscape.



Figure 24: A boxplot showing how the presence of hedgerow corridors interacts with the effectiveness of different habitat creation scenarios (create adjacent and create isolated) to effect the percentage occupancy of newly created patches by four different species. The plot is faceted by the ED of the original landscape.

## 4.5 Discussion

This research has shown that creating habitat adjacent to existing patches is the most effective method for increasing population sizes and the percentage of patches occupied across a landscape. However, the presence of ecological corridors tempers and sometimes eliminates this advantage by making the creation of isolated habitat a more viable option. This was found to vary between species with differing functional traits. Running simulations on null landscapes and then habitat creation landscapes also demonstrated the importance of using restored habitat to measure outcomes of restoration actions, rather than attempting to extrapolate from the process of fragmentation; the results from these two types of landscape simulations would have led to different restoration recommendations.

Much like Huxel and Hastings (1999) and Synes et al. (2020) I found that creating habitat adjacent to existing patches is generally the preferred method for increasing species population sizes. This was likely due to effects well explored in island biogeography theory, where patches near to source habitat are more speedily colonised than isolated patches which are rarely reached (MacArthur and Wilson 1967). By creating habitat adjacent to existing patches it can be utilized effectively and lead to significant landscape scale population increases. However, there are many restricting factors which may take this decision in other directions when creating native habitats. To take british woodland as an example, a lot of land-owners and farmers will prefer creating woodlands on less productive land (Kassioumis et al. 2004; Staddon et al. 2021) which does not

always reside adjacent to existing woodlands. Further, woodland fragments are not distributed randomly but often remotely in harder to reach places (Rackham 1980), and so creating habitat adjacent to them may be logistically difficult. In these cases creating isolated habitat with long colonisation lags (Brunet et al. 2021) may be the outcome, and ecological corridors in the form of hedgerows will be needed to increase their connectivity. Corridors work by increasing the permeability of the landscape for dispersing species and thus increasing functional connectivity between patches (Taylor et al. 1993). This means that the modelled species could reach further per dispersal event making isolated habitats more viable. Corridors did also improve Species 2's population sizes in landscapes with adjacent created habitat but to a lesser extent. This is likely due to meta-population dynamics (Hanski and Gaggiotti 1999); when small patches lose their populations, corridors allow them to be repopulated. If these small patches have since been extended than they may have become large enough to hold viable populations. These results demonstrate the importance of using restored habitat to provide evidence for restoration actions rather than mirroring evidence from historically fragmented habitats. In the null landscapes higher ED tended to incur higher population levels, this could lead one to believe that creating isolated habitats - which would result in a higher ED - would be the strategy that increases population sizes the most. However, these results show that is not the case.

The proportion of habitat patches occupied was split up between the proportion of unoccupied patches in null landscapes that were subsequently occupied after

habitat creation, and the proportional occupancy of new habitats. This was useful as it allowed us to see how newly created patches increased the occupancy of existing patches either by increasing connectivity or increasing patch sizes. The presence of corridors increased the occupancy of original habitat patches in null landscapes and in those with habitat creation, especially if habitat was created isolated. The effect in landscapes with adjacent created habitat can be explained by the same meta-population theory as described above, where corridors help immigrants replenish empty patches. The effect in landscapes with isolated created habitats is because the presence of corridors makes isolated habitat into more viable ecological stepping stones. Ecological stepping stones are known to increase a range of species' movement across fragmented landscapes (Saura et al. 2014a). Generally creating habitat adjacent to existing patches increased the occupancy of original habitat patches the most, however for Species 1 in landscapes with higher percentages of woodland cover, creating isolated patches outperformed creating adjacent patches. This likely demonstrates long distance dispersing species' ability to make use of fragmented landscapes (Fourcade et al. 2021). In landscapes with low habitat cover this shows that increasing the size of core patches should still be the priority for these species.

The configuration of the original landscapes also affected the efficacy of different habitat creation actions. The population increase in landscapes with adjacent created woodland patches was smaller if the original percentage cover of woodland was already high. This may confirm early work from Fahrig (1998a) whose models showed that habitat configuration does not matter once habitat

cover reaches 20%. This was later formalised as the “habitat amount hypothesis” where species richness or population sizes are a product of habitat amount within a species local area, and how this habitat is configured has little bearing (Fahrig 2013). Hanski (2015) argues that most real landscapes do not have above 20% habitat cover and so habitat configuration should be considered when restoring ecosystems. This is confirmed by the real landscapes used in the present study, and the findings that creating adjacent habitat outcompetes creating isolated patches. The high variation in patch occupancy can also be linked to the Hanski school of thought, where populations in small patches periodically go extinct and are only replenished if nearby populations provide immigrants. This is in contrast to the more deterministic nature of landscape scale population size in null landscapes. This is consistently explained by total habitat amount which links back to the Fahrig school of thought. These findings also link to the conservation triage approach (Rappaport et al. 2015); landscapes with already high habitat cover may not be targeted for restoration actions as they are already providing enough suitable habitat. This precedes an important limitation of this study. The landscapes used were particularly fragmented; none had more than 15% woodland cover. Considering the effect of habitat cover on habitat creation strategies observed even at this level, it should be expected that less fragmented study systems may require different recommendations.

Species’ functional and life-history traits were a key component of this study. In null landscapes the species that could breed in hedgerows (invertebrate and plant) made the least use of them. This is because they could maintain

populations in very small habitat patches and did not need immigration to rescue them from extinction - much like woodland specialists in real fragmented landscapes (Vellend et al. 2006). In landscapes with isolated created habitats these same species benefited the most from hedgerows because of their short dispersal distances. Functional traits limit how a species may move through a landscape or shift its range in response to environmental stress (Stahl et al. 2014; Fourcade et al. 2021), so it was important to consider such a wide range of traits. Unfortunately this modelling framework could not test how species with differing dispersal capabilities interact with each other. This is an important consideration as corridors potentially increase the spread of antagonistic species which may hinder the target species (Haddad et al. 2014).

There are a few limitations of this study that must be recognised. Firstly, hedgerows are very thin examples of ecological corridors, and as corridor width is known to mitigate edge effects - which will be ubiquitous in most hedgerows - using wider corridors may have produced different results (Van Schalkwyk et al. 2020). I also assumed that all hedgerows were of a reasonable habitat quality. Secondly, I did not include created habitat patches of different sizes. Larger sized isolated patches may have made more viable stepping-stones (Saura et al. 2014a), but adding this variation would have been out of the scope of this study. Finally, created habitat patches are known to have long colonisation lags (Watts et al. 2020) and these may not be equal for adjacent and isolated created patches (Hughes et al. 2023). For simplicity our models did not recognise this, and so our colonisation time-frames may be underestimated.

## 4.6 Conclusion

Ecological corridors are rarely considered when modelling and implementing restoration strategies. This study has shown that it is important to do so, not simply because of the empirical evidence for their benefits but also because they have non-uniform effects which vary depending on the spatial targeting of habitat creation. Our findings concur with previous modelling evidence, that creating new habitat adjacent to existing habitat increases populations more so than creating isolated habitat. However, ecological corridors can ameliorate and in some cases reverse this affect by disproportionately speeding up the colonisation of isolated habitat patches, and improving their potential to act as stepping-stones.

This study has also shown the importance of using the creation of habitat to inform restoration actions rather than trying to extrapolate information from studies of previously fragmented landscapes. If results from our null landscapes were taken they may have led to quite different suggestions on how to configure landscape-scale restoration actions.

In the case of native woodlands in temperate Europe many grants for landowners do not stipulate the spatial targeting of woodland creation (outside of occasional trials (Quine and Watts 2009)), and woodland is often created isolated from existing patches. These are not easily reached and are far less beneficial to landscape scale biodiversity, thus ecological corridors in the form of hedgerows are needed in this context. However, these are also rarely considered in grants for woodland creation. This study has shown that stipulating for woodland to be



created adjacent to existing patches or for hedgerow corridors to connect isolated patches will improve biodiversity benefits locally and across landscapes.

## 5 Conclusions

This thesis has used a range of approaches, methods and restoration success metrics to paint a detailed picture of how spatially targeting woodland creation will affect woodland development and biodiversity in a UK context. The main aim of this thesis was to assess the benefits of connecting recent woodland patches to existing mature woodlands, either physically or via a hedgerow corridor. It has done this by addressing important questions identified in Chapter 1: How does spatially targeting woodland creation affect woodland structural development? How long are the ecological time-lags associated with woodland creation and how can we speed these up with ecological connectivity? How can hedgerows acting as ecological corridors improve the usefulness of isolated patches to woodland species.

To answer these questions Chapter 2 used remotely sensed LiDAR data to compare structural development between stands created adjacent to mature woodlands with those created isolated; Chapter 3 quantified how quickly colonisation credit is fulfilled in recent woodland, and tested how spatial targeting can speed this up; and Chapter 4 compared spatial targeting strategies at the landscape scale using simulation models, and then assessed the effects that hedgerow corridors have on these different strategies.

This chapter will consist of three sections. In section one the results of the three empirical chapters will be discussed and then synthesised. Section two will discuss the implications of this thesis for woodland creation schemes across the

UK. Finally, section three will review the limitations of this thesis and identify future research that may lead on from the results.

## **5.1 Discussion and synthesis**

### **5.1.1 Woodland structural development**

Using remotely sensed LiDAR data, Chapter 2 shows that woodlands created adjacent to existing mature woodlands developed faster - in terms of structural diversity and tree height - than those created isolated from other woodlands. Increased structural diversity has been shown to increase bird species richness in English woodlands (Melin et al. 2018) - itself a proxy for overall biodiversity (Gregory and Strien 2010) - and also correlates well with ecosystem functioning and services, such as primary productivity and carbon storage (LaRue et al. 2019; Aponte et al. 2020). As such, the structural development of woodlands should be considered an important metric of restoration success, however it is rarely considered when studying the spatial targeting of woodland creation. The results of this chapter demonstrate the importance of doing so, as different strategies lead to varying results.

### **5.1.2 Benefits to understory plant communities**

Chapter 3 shows that targeting woodland creation adjacent to existing mature woodlands can help to ameliorate the extremely long colonisation lags of specialist understory plants. This finding consolidates previous research showing the importance of connectivity to these communities (Peterken and

Game 1984). These results also confirm the dispersal limitations of woodland plants, as ecological isolation hindered colonisation. However, even well connected woodlands did not fulfill their colonisation credit after 80 years. The colonisation credit remaining in well connected patches could be explained by local conditions hindering establishment. This may have been caused by encroaching *Salix viminalis* causing over-shading in young created woodlands, or by the dominance of native competitors such as *Hedera helix* in more mature created woodlands. These results suggest that local management interventions may still be needed, even when woodland creation is targeted appropriately. This concurs with many studies showing the importance of local habitat conditions to woodland specialist species (Honnay et al. 1999b; Fuentes-Montemayor et al. 2013, 2020).

### **5.1.3 Population persistence across landscapes**

Simulation models in Chapter 4 compared the population dynamics of individual species when employing different spatial targeting strategies for woodland creation at the landscape scale. Lowland agricultural landscapes in the UK are particularly fragmented with rarely any more than 15% woodland cover. The results of Chapter 4 show that extending what habitat is left is a more effective strategy for increasing population size and species movement than creating isolated stepping-stone habitat. This concurs with the results from Synes et al. (2020), who modelled similar scenarios but did not include the presence of corridor features. Many remnant patches are too small to hold viable populations

of woodland species, and thus extending them provides new habitat alongside making the remnant habitat viable. This means that the benefits of this strategy are superadditive in comparison to creating isolated woodland.

#### **5.1.4 Connecting isolated woodlands with hedgerows**

Chapter 4 also demonstrated the importance of ecological corridors in the form of hedgerows to UK woodland landscapes. This provides practical applications to the empirical work on hedgerows showing their use as habitats for a range of species (Pelletier-Guittier et al. 2020; Vanneste et al. 2020). Experimental work from the the Corridor Project at the SRS has shown that ecological corridors increase species richness and reduce local extinctions for a range of species (Haddad 1997; Damschen et al. 2006, 2019). The present thesis shows that this knowledge can be utilised to connect isolated habitat patches and improve population persistence at the landscape scale. Firstly, hedgerows mean that the previously extinct populations within small woodlands can be replenished after the woodland has been extended. Further, it suggests that hedgerows can be used to mitigate restrictions on woodland creation. If non-ecological factors constrain new woodlands to an isolated setting, hedgerows should be used to connect them to source populations. This will improve the population benefits of creating isolated woodlands, however, extending existing woodlands is still the preferred option.

### **5.1.5 Findings across spatial scales**

Taken together, the three research chapters suggest that targeting woodland creation adjacent to existing mature stands will enhance local, and potentially landscape scale, biodiversity most effectively. This targeting strategy is effective for three reasons: (1) created woodlands develop faster structurally; (2) slow colonising species reach the created woodland faster; and (3) extending existing woodlands means that previously small patches can now harbour viable meta-populations, which increases population persistence across the landscape.

These findings consider effects across restoration success metrics (habitat structure, biodiversity, population persistence), but also across spatial scales. Chapters 2 and 3 find benefits at the local scale, where Chapter 4 finds benefits at the landscape scale. It is important to consider the effects of habitat creation at different spatial scales as processes that affect biodiversity and population abundances occur at multiple spatial scales. In turn populations and communities respond to these processes locally, across landscapes, and regionally (Holland et al. 2004). For example, invasive species in temperate forests have been shown to cause increased alpha diversity while decreasing between forest beta diversity (Dyderski and Jagodziński 2021). Thus, different habitat creation strategies may be more effective at different scales (Kunin 1997). However, conclusions drawn from the three research chapters of this thesis mirror each other at the local and landscape scales, meaning the recommendation to create woodland adjacent to existing patches will incur benefits locally and across landscapes.

### **5.1.6 Context dependency**

There will always be trade-offs when making decisions on where to create habitat and many of these are context dependent (Rappaport et al. 2015; Gunton et al. 2017). This was illustrated by Chapter 4, which showed the importance of original landscape configurations to the effectiveness of different habitat creation strategies. Species in landscapes with higher amounts of habitat cover benefited less from extending existing woodland patches compared to species in sparsely covered landscapes. This was because many of the patches in these landscapes were already large enough to harbour viable populations. Creating isolated stepping-stone patches may be the most effective method of maintaining populations in landscapes with higher woodland cover than those used in Chapter 4 (Saura et al. 2014a).

Context dependency was also demonstrated by Species 1 of Chapter 4. As a more mobile species, this species was able to make better use of isolated created habitat, whereas all other species consistently performed better when habitat was created adjacent to existing patches. This was also shown in Chapter 3, as the relatively immobile woodland plant species rarely made it to isolated patches. This confirms work from Fourcade et al. (2021), who showed that more mobile species benefit from more fragmented habitat when shifting their ranges in response to climate change. This highlights a major challenge for restoration ecology; it is hard to draw conclusions from studies of single species or single landscapes as many outcomes are context specific.

### **5.1.7 Time lags associated with woodland creation**

This thesis shows the importance of considering the long ecological time-lags associated with woodland habitat. These time lags make restoration actions hard to assess, and long-term conservation goals difficult to reach (Watts et al. 2020; Haddou et al. 2022). Chapter 2 demonstrates that woodland develops structurally at different rates depending on its connectivity, and Chapter 3 shows that colonisation lags can be reduced through spatial targeting. However, these chapters also show that woodlands take decades to reach structural maturity *and* to fulfill their colonisation credit, no matter how they are targeted. This means that any biodiversity benefits from increased habitat area or any ecosystem service benefits from mature trees will also take decades to accrue. These time-lags must be considered when measuring restoration successes, as many benefits may not manifest within monitored time-frames. Further, choosing long-term conservation targets with short-term milestones is important.

## **5.2 Implications for woodland creation schemes**

The UK government plans to create 30000ha of woodland a year by 2025. Currently this is facilitated by independent schemes for land owners and farmers, for example the woodland creation scheme in England (Forestry Commission 2021) and the forestry grant scheme in Scotland (Scottish Forestry 2023). There are a number of ways the findings from this thesis could benefit such schemes.



### **5.2.1 Connecting created woodlands**

The influential “Making Space for Nature” report from Lawton (2010) stated that habitat patches in the UK need to be “bigger”, “better”, “more” and “joined”. Largely, woodland creation schemes only address the “more” aspect of this, with little coherent strategy to join or expand remnant patches. In the past there have been trials to offer extra incentive to land owners for extending existing mature woodlands, for example the “Joining and Increasing Grant Scheme for Ancient Woodland” (JIGSAW). This scheme was shown to be effective in reducing landscape fragmentation by minimizing the distance between woodlands on the Isle of Wight (Quine and Watts 2009). Chapter 3 of this thesis also found the woodlands created through this scheme had been colonised by more specialist woodland plant species than woodlands created under non-targeted woodland creation schemes.

However, current woodland creation schemes in the UK offer no incentives or stipulations to consider the spatial configuration of created woodlands. This is despite the fact that ecologists agree habitat configuration is important to species populations and communities when habitat cover is under 20% of a landscapes area (Fahrig 2013; Hanski 2015). This is the case for almost all woodland landscapes in the UK, and thus the placement of newly created woodlands should be considered. The empirical chapters of this thesis have shown how such considerations could speed up the benefits accrued from creating woodland. A strategy of connecting new woodlands to existing patches will increase the speed at which woodlands reach structural maturity as shown in Chapter 2; will reduce

colonisation credit faster as shown in Chapter 3; and will increase the patch occupancy and sizes of populations at the landscape scale, as shown in Chapter 4.

Extra financial incentives may be needed to encourage land owners to create new woodland adjacent to existing woodland. This is because existing woodlands are often surrounded by productive farmland. These incentives could take the form of the previous JIGSAW scheme, where a premium is offered to landowners to create new woodland adjacent to ancient patches. However, connectivity between existing and created woodlands could also be considered over a wider scale. For example, payments could increase as distance between existing woodlands and newly created woodlands decreases, particularly if new woodland is creating corridors between multiple existing woodlands. This strategy would increase the movement and dispersal distances for a range of species between the two existing patches by improving the surrounding matrix quality (Eycott et al. 2012). Connectivity could also be measured by how much existing woodland is in the vicinity of the newly created woodland. It is well explored how more woodland in the surrounding landscape increases the colonisation of new woodlands by specialist woodland species (Peterken and Game 1984; Fuentes-Montemayor et al. 2013; Humphrey et al. 2015). Thus, newly created woodlands surrounded by nearby remnant patches will offer more biodiversity value than woodlands planted completely isolated.

### **5.2.2 Connecting woodlands with hedgerows**

Landscape characteristics such as trees outside of woodlands (Plenderleith et al. 2022) and hedgerows (Pelletier-Guittier et al. 2020) are also known to increase connectivity between new woodlands and remnant patches . Yet these are also under utilised in woodland creation grants. Field boundary grants exist to protect and manage hedgerows (Staley et al. 2023), but there are no incentives to connect woodlands by either using existing hedgerow networks or creating new hedgerows. The lack of consideration for using hedgerows as ecological corridors for woodlands may be due to a lack of clear evidence on what to prioritise when creating new habitat and improving habitat networks (Isaac et al. 2018). The current thesis has tried to address this through the simulations of Chapter 4. The results show that if woodland is to be created in an isolated setting, then existing hedgerows should be utilised to connect it to remnant patches. If hedgerows do not exist to connect created woodland there should be incentives to create one, although this may take longer to accrue benefits (Lenoir et al. 2021). The use of hedgerow grants in unison with woodland creation grants could encourage land managers to connect newly created woodland with hedgerows, which would improve local and landscape scale biodiversity benefits. These specialist grants could take the form of the MOREhedges scheme from the woodland trust (The Woodland Trust 2023). Here, landowners are funded to create hedges that connect existing woodlands. However this scheme does not consider how newly created woodlands can be enhanced by existing hedgerows networks. I would suggest extending this to offer incentives to create woodland

which is connected to existing mature patches by mature hedgerows corridors. These hedgerows would act as sources for the new woodland as they will harbour many woodland species (Litza and Diekmann 2019). They will also act as corridors between the mature woodland and the new woodland, as displayed in chapter 4 of this thesis. Habitat quality is a known determinant of how effective hedgerows are as corridors (Litza and Diekmann 2020), and thus further incentives should encourage the management of existing hedgerows between woodland patches. Examples of this could be to allow hedgerows to grow wider, or to increase their structural complexity. By linking hedgerow creation and management schemes with woodland creation schemes we could effectively join up habitat patches across agricultural landscapes.

### **5.2.3 Carbon sequestration benefits**

This thesis largely addresses biodiversity benefits from woodland creation, however there are many reasons that woodland creation schemes are funded, not least carbon sequestration. Chapter 2 shows that woodlands grow to be more structurally diverse and contain taller trees if created adjacent to an existing mature woodland. Structural diversity has been shown to increase carbon storage in temperate woodlands, which is thought to be due to the maximum utilisation of space (Aponte et al. 2020). Further, larger trees store more carbon than smaller trees (Stephenson et al. 2014). Thus, in UK woodlands extending existing woodland may provide more benefits to carbon storage. This is supported by research that shows a higher proportion of woodland edges leads to a decrease

in large trees, and thus reduces carbon storage potential (Paula et al. 2011). Extending existing woodlands would reduce edge densities and allow more large trees to grow. However, research has also found that small isolated woodlands may store proportionally more top soil carbon due to higher turnover at woodland edges (Valdés et al. 2020). It was outside the scope of this thesis to explore this trade-off and thus it cannot be stated with certainty that extending existing woodlands is best practice for carbon storage.

#### **5.2.4 Management interventions**

Chapter 3 showed the importance of local habitat conditions to the development of biodiversity. The overshadowing caused by *Salix viminalis* created poor habitat conditions for even shade tolerant woodland plants. This means many plants do not establish in created woodlands, even if they are adjacent to existing ancient woodlands. Chapter 3 also shows that poor dispersing woodland plants may never make it to isolated created woodlands. Management interventions may be needed to overcome poor habitat conditions and dispersal limitations. Work in North American subtropical woodlands has shown that manipulating seed arrivals can successfully restore plant diversity (Orrock et al. 2023), and managing structural development through canopy thinning can improve local habitat conditions (Brudvig et al. 2021). However, similar experiments have not been carried out in the temperate woodlands. Such experiments could inform woodland creation policy on how to best manage new woodlands for understory development. Woodland creation schemes in the UK do offer management grants,

but these largely relate to deer exclusion and some structural management.

## **5.3 Future research**

### **5.3.1 Range shifting with climate change**

The findings of this thesis suggest that extending existing woodlands should be a priority in the UK to enhance biodiversity. However, how this may affect species range shifting abilities was not considered. Species are known to be shifting their ranges pole-wards in response to global climate change, and those not able to move quickly enough are under threat (Parmesan 2006). Thus, it is important for habitat creation to be configured in a way that helps expedite species movement. This thesis did not examine the changing climate alongside range shifting, for example: Chapter 4 treated habitat patches as continuously suitable. Further, Chapter 3 examined poor dispersing plant species, and did not consider more mobile species that may have used isolated woodlands as long distance stepping-stones. Hodgson et al. (2012) showed that landscapes that improve range shifting potential do not always match landscapes that improve persistence in non-dynamic climates. The authors found that the clumping of habitat reduced range shifting potential compared to a channeling of stepping-stone habitats. However, Synes et al. (2020) compared the effect of habitat creation and restoration strategies on species range shifting abilities, finding that extending existing patches should still be prioritised in a UK context. Further work could extend on the models of Chapter 4, and examine how hedgerow corridors improve isolated habitat patches in facilitating range shifting.

### **5.3.2 The influence of spatial scale**

Chapter 2 explores the structural diversity of created woodlands but does not test how results might change at different spatial scales. This chapter finds that woodland structural diversity and woodland height are increased locally when woodlands are created adjacent to existing older woodlands. Habitat heterogeneity is thought to increase biodiversity across fragmented landscapes (Fahrig et al. 2011), and structurally distinct patches have been shown to increase arthropod diversity at the landscape-scale (Schalkwyk et al. 2021). This is likely because woodland patches at different stages of development cover a wide niche-space (Menge et al. 2023). Thus, creating woodlands adjacent to existing mature woodlands may increase local structural diversity, but if treated as a landscape-wide strategy may reduce beta and gamma structural diversity. This issue is emphasized by calls to restore areas of open woodland alongside closed canopy habitat (Miklin and Čížek 2014; Hanberry et al. 2020), and for ecological restoration to prioritize complexity rather than targeted reference states (Bullock et al. 2022). Future research could explore the structural development and complexity of recent woodlands at the landscape-scale, and test how different spatial targeting strategies can be employed to enhance this. With widely available LiDAR data covering the UK and the many patches of woodlands planted in recent decades, this scale of research should now be possible.

Chapter 3 also focuses on the local effects of woodland creation. This means the role of isolated woodlands acting as stepping-stones was not assessed. Modelling studies have shown the importance of stepping-stone habitat patches to species

movement abilities, especially for mobile species (Hodgson et al. 2012; Saura et al. 2014b; Rocha et al. 2021). The woodlands in Chapter 3 were so depauperate that they were unlikely to be acting as stepping-stones for woodland plants, however this could be tested for more mobile species. Chapter 3 also only considered alpha diversity and did not assess how adjacent or isolated woodlands contribute to beta or gamma diversity. This is an important subject as woodland understory plant communities are known to be homogenising between woodlands (Vellend et al. 2007). Future studies could test which configuration of woodland creation benefits biodiversity at different spatial scales, by looking at effects on among woodland diversity. Employing the same spatial targeting strategy at the landscape scale may reduce beta diversity as each patch will foster similar communities. Thus, a mixture of strategies should be tested.

### **5.3.3 Mycorrhizae**

Mycorrhizae are known to increase the growth rate of entire woodlands (Anthony et al. 2022), and increased mycorrhizal diversity has been shown to increase herbaceous plant species richness (Guy et al. 2022). This could point to a different mechanism behind the results of Chapters 2 and 3; woodlands created adjacent to mature woodlands are more likely to be colonised by mycorrhizae, which could cause their trees to develop faster, and provide more suitable conditions for understory plants to establish. Mycorrhizal dispersal is not well understood compared to plant dispersal, however there is evidence that isolated sites harbour fewer species (Peay et al. 2010). Future research could extend



on Chapters 2 and 3 of this thesis by exploring the role of Mycorrhizae as a mechanism behind the observed effects.

#### **5.3.4 Negative effects of ecological corridors**

In comparing landscapes with and without hedgerow corridors Chapter 4 identified key interactions between habitat targeting strategies and the presence of ecological corridors. Corridors had a much stronger positive effect on isolated created patches than on patches created adjacent to existing woodland, although this may be because there was little improvement to be made in adjacent patches. Future research could investigate this in terms of biodiversity rather than at the individual species level. By only focusing on individual species, the models of Chapter 4 missed any potential negative effects that ecological corridors may have on communities. An example of these effects is that of invasive or antagonist species (Haddad et al. 2014). Modelling how ecological corridors affect communities rather than individual species could address this. However this would be computationally expensive and thus may be best addressed by natural experiments.

### **5.4 Final remarks**

This thesis has shown that creating woodland patches adjacent to existing mature stands should be prioritised in the UK - and more broadly in temperate settings where woodland cover is low - to accrue the most benefits in the shortest amount of time. Targets for biodiversity recovery are political, and thus do

not represent the length of time required for new woodland habitats to realise their full potential. Spatially targeting woodland creation adjacent to existing patches has been shown to increase structural development and complexity, partly reduce the long colonisation lags inherent in this system, and increase landscape-scale population viability for a range of woodland species. Therefore creating woodlands with this strategy could be the best way to reach short-term biodiversity targets in a reasonable time-frame. Although it is recognised that we cannot always target “reference-states” in ecological restoration, closed canopy native woodland is still of cultural and ecological importance to the UK. This thesis has shown a clear strategy to configure its creation which will add to the patchwork of ecological restoration across the country.

- Aavik T, Thetloff M, Träger S, et al (2019) Delayed and immediate effects of habitat loss on the genetic diversity of the grassland plant *trifolium montanum*. *Biodiversity And Conservation* 28:3299–3319
- Aber JD (1979) Foliage-height profiles and succession in northern hardwood forests. *Journal of Ecology* 60:18–23
- Almeida D, Broadbent E, Zambrano A, et al (2019a) Monitoring the structure of forest restoration plantations with a drone-lidar system. *International Journal of Applied Earth Observation and Geoinformation* 79:192–198
- Almeida D, Stark S, Chazdon R, et al (2019b) The effectiveness of lidar remote sensing for monitoring forest cover attributes and landscape restoration. *Forest Ecology Management* 438:34–43
- Anthony MA, Crowther TW, Van Der Linde S, et al (2022) Forest tree growth is linked to mycorrhizal fungal composition and function across europe. *The ISME journal* 16:1327–1336
- Aponte C, Kasel S, Nitschke CR, et al (2020) Structural diversity underpins carbon storage in australian temperate forests. *Global ecology and biogeography* 29:789–802
- Araujo Calçada E, Closset-Kopp D, Gallet-Moron E, et al (2013) Streams are efficient corridors for plant species in forest metacommunities. *Journal of Applied Ecology* 50:1152–1160
- Araújo MB, Guisan A (2006) Five (or so) challenges for species distribution modelling. *Journal of biogeography* 33:1677–1688
- Arroyo-Rodríguez V, Fahrig L, Tabarelli M, et al (2020) Designing optimal

- human-modified landscapes for forest biodiversity conservation. *Ecology Letters* 23:1404–1420
- Banks-Leite C, Ewers RM, Folkard-Tapp H, Fraser A (2020) Countering the effects of habitat loss, fragmentation, and degradation through habitat restoration. *One Earth* 3:672–676
- Barkham J (1992) The effects of management on the ground flora of ancient woodland, brigsteer park wood, cumbria, england. *Biological conservation* 60:167–187
- Bastin J-F, Finegold Y, Garcia C, et al (2019) The global tree restoration potential. *Science* 365:76–79
- Bates D, Mächler M, Bolker B, Walker S (2014) Fitting linear mixed-effects models using lme4. preprint
- Baudry J, Bunce R, Burel F (2000) Hedgerows: An international perspective on their origin, function and management. *Journal of environmental management* 60:7–22
- Bhagwat S, Kettle C, Koh L (2014) Global forest fragmentation. CAB international
- Bocedi G, Palmer SC, Malchow A-K, et al (2020) RangeShifter 2.0: An extended and enhanced platform for modelling spatial eco-evolutionary dynamics and species' responses to environmental changes. bioRxiv
- Bonn Challenge (2019). <https://www.bonnchallenge.org/>. Accessed 7 Jun 2022
- Boyce MS (1992) Population viability analysis. *Annual review of Ecology and Systematics* 23:481–497

- Brooks ME, Kristensen K, Benthem K van, et al (2017) Modeling count data with ‘glmmTMB’. arXiv preprint arXiv:170901180
- Brouwers NC, Newton AC (2009) Movement rates of woodland invertebrates: A systematic review of empirical evidence. *Insect Conservation and Diversity* 2:10–22
- Brudvig LA (2011) The restoration of biodiversity: Where has research been and where does it need to go? *American journal of botany* 98:549–558
- Brudvig LA, Turley NE, Bartel SL, et al (2021) Large ecosystem-scale effects of restoration fail to mitigate impacts of land-use legacies in longleaf pine savannas. *Proceedings of the National Academy of Sciences* 118:e2020935118
- Brunet J (2007) Plant colonization in heterogeneous landscapes: An 80-year perspective on restoration of broadleaved forest vegetation. *Journal of Applied Ecology* 44:563–572
- Brunet J, Hedwall P, Lindgren J, Cousins SA (2021) Immigration credit of temperate forest herbs in fragmented landscapes—implications for restoration of habitat connectivity. *Journal of Applied Ecology* 58:2195–2206
- Brunet J, Valtinat K, Mayr ML, et al (2011) Understory succession in post-agricultural oak forests: Habitat fragmentation affects forest specialists and generalists differently. *Forest Ecology Management* 262:1863–1871
- Brunet J, Von Oheimb G (1998) Migration of vascular plants to secondary woodlands in southern sweden. *Journal of ecology* 86:429–438
- Bullock JM, Fuentes-Montemayor E, McCarthy B, et al (2022) Future restoration

- should enhance ecological complexity and emergent properties at multiple scales. *Ecography* 2022:
- Cain SA (1938) The species-area curve. *American Midland Naturalist* 573–581
- Camarretta N, Harrison PA, Bailey T, et al (2020) Monitoring forest structure to guide adaptive management of forest restoration: A review of remote sensing approaches. *New Forests* 51:573–596
- Catano CP, Grman E, Behrens E, Brudvig LA (2021) Species pool size alters species–area relationships during experimental community assembly. *Ecological Society of America*
- Chase JM, Jeliaskov A, Ladouceur E, Viana DS (2020) Biodiversity conservation through the lens of metacommunity ecology. *Annals of the New York Academy of Sciences* 1469:86–104
- Cornell HV, Harrison SP (2014) What are species pools and when are they important? *Annual Review of Ecology, Evolution, and Systematics* 45:45–67
- Craine JM, Dybzinski R (2013) Mechanisms of plant competition for nutrients, water and light. *Functional Ecology* 27:833–840
- Cribari-Neto F, Zeileis A (2010) Beta regression in r. *Journal of statistical software* 34:1–24
- Damschen EI, Brudvig LA, Burt MA, et al (2019) Ongoing accumulation of plant diversity through habitat connectivity in an 18-year experiment. *Science* 365:1478–1480
- Damschen EI, Haddad NM, Orrock JL, et al (2006) Corridors increase plant

- species richness at large scales. *Science* 313:1284–1286
- Davies H (2017) Woodland creation in european countries
- Deangelis DL, Cox DK, Coutant CC (1980) Cannibalism and size dispersal in young-of-the-year largemouth bass: Experiment and model. *Ecological Modelling* 8:133–148. [https://doi.org/https://doi.org/10.1016/0304-3800\(80\)90033-2](https://doi.org/10.1016/0304-3800(80)90033-2)
- DEFRA (2018) A green future: Our 25 year plan to improve the environment. London
- DeJong TM (1975) A comparison of three diversity indices based on their components of richness and evenness. *Oikos* 1:222–227
- Di Sacco A, Hardwick KA, Blakesley D, et al (2021) Ten golden rules for reforestation to optimize carbon sequestration, biodiversity recovery and livelihood benefits. *Global change biology* 27:1328–1348
- Dracup EC, Keppie DM, Forbes GJ (2015) Woodland mouse and vole response to increased structural diversity following midrotation commercial thinning in spruce plantations. *Canadian Journal of Forest Research* 45:1121–1131
- Dunning Jr JB, Borgella Jr R, Clements K, Meffe GK (1995) Patch isolation, corridor effects, and colonization by a resident sparrow in a managed pine woodland. *Conservation biology* 9:542–550
- Dyderski MK, Jagodziński AM (2021) Impacts of invasive trees on alpha and beta diversity of temperate forest understories. *Biological Invasions* 23:235–252
- EDINA (2020). <https://digimap.edina.ac.uk>. Accessed 7 Jan 2020
- Environment Agency (2021) National LiDAR programme vegetation object

- model. <https://www.data.gov.uk/dataset/f0db0249-f17b-4036-9e65-309148c97ce4/national-lidar-programme>. Accessed 14 Mar 2022
- European Commission (2021) New EU forest strategy for 2030
- Ewijk KY van, Treitz PM, Scott NA (2011) Characterizing forest succession in central ontario using LiDAR-derived indices. *Photogrammetric Engineering Remote Sensing* 77:261–269
- Eycott AE, Stewart GB, Buyung-Ali LM, et al (2012) A meta-analysis on the impact of different matrix structures on species movement rates. *Landscape ecology* 27:1263–1278
- Fagan ME, Reid JL, Holland MB, et al (2020) How feasible are global forest restoration commitments? *Conservation Letters* 13:e12700
- Fahrig L (1998b) When does fragmentation of breeding habitat affect population survival? *Ecological modelling* 105:273–292
- Fahrig L (2017a) Ecological responses to habitat fragmentation per se. *Annual Review of Ecology, Evolution, Systematics* 48:1–23
- Fahrig L (2003) Effects of habitat fragmentation on biodiversity. *Annual review of ecology, evolution, systematics* 34:487–515
- Fahrig L (2017b) Ecological responses to habitat fragmentation per se. *Annual review of ecology, evolution, and systematics* 48:1–23
- Fahrig L (1998a) When does fragmentation of breeding habitat affect population survival? *Ecological Modelling* 105:273–292. [https://doi.org/https://doi.org/10.1016/S0304-3800\(97\)00163-4](https://doi.org/https://doi.org/10.1016/S0304-3800(97)00163-4)
- Fahrig L (2013) Rethinking patch size and isolation effects: The habitat amount



- hypothesis. *Journal of Biogeography* 40:1649–1663
- Fahrig L, Baudry J, Brotons L, et al (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology letters* 14:101–112
- Felipe-Lucia MR, Soliveres S, Penone C, et al (2018) Multiple forest attributes underpin the supply of multiple ecosystem services. *Nature communications* 9:1–11
- Fitter AH, Peat HJ (1994) The ecological flora database. *Journal of ecology* 415–425
- Forestry Commission (2020) National Forest Inventory. <https://data-forestry.opendata.arcgis.com/>. Accessed 14 Mar 2022
- Forestry Commission (2015) National forest inventory. <https://data-forestry.opendata.arcgis.com/search?q=nfi%202015>
- Forestry Commission (2021) England woodland creation offer. <https://www.gov.uk/guidance/england-woodland-creation-offer>. Accessed 4 Spring 2023
- Forestry England (2022) Woodland Creation Grant. <https://www.gov.uk/guidance/woodland-creation-grant-offer>
- Fourcade Y, WallisDeVries MF, Kuussaari M, et al (2021) Habitat amount and distribution modify community dynamics under climate change. *Ecology Letters* 24:950–957
- Freitas MG, Rodrigues SB, Campos-Filho EM, et al (2019) Evaluating the success of direct seeding for tropical forest restoration over ten years. *Forest ecology & management* 438:224–232

- Fuentes-Montemayor E, Ferryman M, Watts K, et al (2020) Small mammal responses to long-term large-scale woodland creation: The influence of local and landscape-level attributes. *Ecological Applications* 30:e02028
- Fuentes-Montemayor E, Goulson D, Cavin L, et al (2013) Fragmented woodlands in agricultural landscapes: The influence of woodland character and landscape context on bats and their insect prey. *Agriculture, ecosystems & environment* 172:6–15
- Fuentes-Montemayor E, Park KJ, Cordts K, Watts K (2021) The long-term development of temperate woodland creation sites: From tree saplings to mature woodlands. *Forestry* 28–37
- Fuentes-Montemayor E, Watts K, Sansum P, et al (2022) Moth community responses to woodland creation: The influence of woodland age, patch characteristics and landscape attributes. *Diversity and Distributions* 28:1993–2007
- Fuller L, Fuentes-Montemayor E, Watts K, et al (2018) Local-scale attributes determine the suitability of woodland creation sites for diptera. *Journal of Applied Ecology* 55:1173–1184
- Fuller R, Warren MS (1993) Coppiced woodlands: Their management for wildlife. Joint Nature Conservation Committee Peterborough
- Garnier E, Cortez J, Billès G, et al (2004) Plant functional markers capture ecosystem properties during secondary succession. *Journal of Ecology* 85:2630–2637
- Gilbert-Norton L, Wilson R, Stevens JR, Beard KH (2010) A meta-analytic review

- of corridor effectiveness. *Conservation biology* 24:660–668
- Gill R, Beardall V (2001) The impact of deer on woodlands: The effects of browsing and seed dispersal on vegetation structure and composition. *Forestry: An International Journal of Forest Research* 74:209–218
- Google.inc (2020) Google earth pro
- Government of Canada (2020) 2 billion trees. <https://www.canada.ca/en/campaign/2-billion-trees.html>. Accessed 3 Summer 2023
- Gregory RD, Strien A van (2010) Wild bird indicators: Using composite population trends of birds as measures of environmental health. *Ornithological Science* 9:3–22
- Griffin SR, Haddad NM (2021) Connectivity and edge effects increase bee colonization in an experimentally fragmented landscape. *Ecography* 44:919–927
- Gunton RM, Marsh CJ, Moulherat S, et al (2017) Multicriterion trade-offs and synergies for spatial conservation planning. *Journal of Applied Ecology* 54:903–913
- Guy P, Sibly R, Smart SM, et al (2022) Mycorrhizal type of woody plants influences understory species richness in british broadleaved woodlands. *New Phytologist* 235:2046–2053
- Habel JC, Rasche L, Schneider UA, et al (2019) Final countdown for biodiversity hotspots. *Conservation Letters* 12:e12668
- Habel JC, Ulrich W, Schmitt T (2020) Butterflies in corridors: Quality matters for specialists. *Insect conservation and diversity* 13:91–98

- Haddad NM (1997) Do corridors influence butterfly dispersal and density? A landscape experiment. University of Georgia
- Haddad NM, Brudvig LA, Clobert J, et al (2015) Habitat fragmentation and its lasting impact on earth's ecosystems. *Science advances* 1:e1500052
- Haddad NM, Brudvig LA, Damschen EI, et al (2014) Potential negative ecological effects of corridors. *Conservation Biology* 28:1178–1187
- Haddou Y, Maney R, Matthiopoulos J, et al (2022) Widespread extinction debts and colonization credits in united states breeding bird communities. *Nature ecology & evolution* 6:324–331
- Hanberry BB, Bragg DC, Alexander HD (2020) Open forest ecosystems: An excluded state. *Forest Ecology and Management* 472:118256
- Hanski I (2015) Habitat fragmentation and species richness. *Journal of Biogeography* 42:989–993
- Hanski I, Gaggiotti OE (1999) *Metapopulation ecology*. Oxford University Press
- Hansson L (2000) Edge structures and edge effects on plants and birds in ancient oak-hazel woodlands. *Landscape and Urban Planning* 46:203–207
- Harmer R, Peterken G, Kerr G, Poulton P (2001) Vegetation changes during 100 years of development of two secondary woodlands on abandoned arable land. *Biological Conservation* 101:291–304
- Hermly M, Honnay O, Firbank L, et al (1999) An ecological comparison between ancient and other forest plant species of europe, and the implications for forest conservation. *Biological conservation* 91:9–22
- Hesselbarth MH, Sciaini M, With KA, et al (2019) *Landscapemetrics: An*

- open-source r tool to calculate landscape metrics. *Ecography* 42:1648–1657
- Hill MO, Preston CD, Roy D (2004) PLANTATT-attributes of british and irish plants: Status, size, life history, geography and habitats. Centre for Ecology & Hydrology
- Hilty J, Worboys GL, Keeley A, et al (2020) Guidelines for conserving connectivity through ecological networks and corridors. Best practice protected area Guidelines Series 30:p–122
- HM Treasury (2020) Budget speech 2020. <https://www.gov.uk/government/speeches/budget-speech-2020>. Accessed 3 Jan 2023
- Hodgson JA, Thomas CD, Dytham C, et al (2012) The speed of range shifts in fragmented landscapes. *PloS one* 7:e47141
- Holl KD, Brancalion PH (2020) Tree planting is not a simple solution. *Science* 368:580–581
- Holl KD, Reid JL, Cole RJ, et al (2020) Applied nucleation facilitates tropical forest recovery: Lessons learned from a 15-year study. *Journal of Applied Ecology* 57:2316–2328
- Holland JD, Bert DG, Fahrig L (2004) Determining the spatial scale of species' response to habitat. *Bioscience* 54:227–233
- Honnay O, Bossuyt B, Verheyen K, et al (2002a) Ecological perspectives for the restoration of plant communities in european temperate forests. *Journal of Biodiversity and Conservation* 11:213–242
- Honnay O, Hermy M, Coppin P (1999b) Impact of habitat quality on forest plant species colonization. *Forest ecology and management* 115:157–170

- Honnay O, Hermy M, Coppin P (1999a) Nested plant communities in deciduous forest fragments: Species relaxation or nested habitats? *Oikos* 119–129
- Honnay O, Jacquemyn H (2007) Susceptibility of common and rare plant species to the genetic consequences of habitat fragmentation. *Conservation Biology* 21:823–831
- Honnay O, Jacquemyn H, Bossuyt B, Hermy M (2005) Forest fragmentation effects on patch occupancy and population viability of herbaceous plant species. *New Phytologist* 166:723–736
- Honnay O, Verheyen K, Butaye J, et al (2002b) Possible effects of habitat fragmentation and climate change on the range of forest plant species. *Ecology Letters* 5:525–530
- Hooftman DA, Edwards B, Bullock JM (2016) Reductions in connectivity and habitat quality drive local extinctions in a plant diversity hotspot. *Ecography* 39:583–592
- Hua F, Bruijnzeel LA, Meli P, et al (2022) The biodiversity and ecosystem service contributions and trade-offs of forest restoration approaches. *Science* 376:839–844
- Hughes S, Kunin W, Watts K, Ziv G (2023) New woodlands created adjacent to existing woodlands grow faster, taller and have higher structural diversity than isolated counterparts. *Restoration Ecology* e13889
- Humphrey J (2003) *The restoration of wooded landscapes*. Forestry Commission, Edinburgh
- Humphrey J, Watts K, Fuentes-Montemayor E, et al (2015) What can studies of

- woodland fragmentation and creation tell us about ecological networks? A literature review and synthesis. *Landscape Ecology* 30:21–50
- Huxel GR, Hastings A (1999) Habitat loss, fragmentation, and restoration. *Restoration ecology* 7:309–315
- IPBES (2019) Global assessment report on biodiversity and ecosystem services of the intergovernmental science-policy platform on biodiversity and ecosystem services. Wiley Online Library
- Isaac NJ, Brotherton PN, Bullock JM, et al (2018) Defining and delivering resilient ecological networks: Nature conservation in England. *Journal of Applied Ecology* 55:2537–2543
- Iwasa Y, Cohen D, Leon JA (1985) Tree height and crown shape, as results of competitive games. *Journal of theoretical Biology* 112:279–297
- Jackson ST, Sax DF (2010) Balancing biodiversity in a changing environment: Extinction debt, immigration credit and species turnover. *Trends in ecology & evolution* 25:153–160
- Jacob van Etten RJH & (2012) Raster: Geographic analysis and modeling with raster data
- Kallimanis AS, Mazaris AD, Tzanopoulos J, et al (2008) How does habitat diversity affect the species–area relationship? *Global Ecology and Biogeography* 17:532–538
- Kassioumis K, Papageorgiou K, Christodoulou A, et al (2004) Rural development by afforestation in predominantly agricultural areas: Issues and challenges from two areas in Greece. *Forest Policy and Economics* 6:483–496

- Keenan RJ, Reams GA, Achard F, et al (2015) Dynamics of global forest area: Results from the FAO global forest resources assessment 2015. *Forest Ecology Management* 352:9–20
- Kirby K, Buckley G, Mills J (2017) Biodiversity implications of coppice decline, transformations to high forest and coppice restoration in british woodland. *Folia geobotanica* 52:5–13
- Kirby K, Pyatt D, Rodwell J (2012) Characterization of the woodland flora and woodland communities in britain using ellenberg values and functional analysis. *Working Walking in the Footsteps of Ghosts* 1:66–86
- Kirby K, Thomas R (2017) Restoration of broadleaved woodland under the 1985 broadleaves policy stimulates ground flora recovery at shabbington woods, southern england. *New Journal of Botany* 7:125–135
- Kolk J, Naaf T, Wulf M (2017) Paying the colonization credit: Converging plant species richness in ancient and post-agricultural forests in NE germany over five decades. *Biodiversity Conservation* 26:735–755
- Kunin WE (1997) Sample shape, spatial scale and species counts: Implications for reserve design. *Biological Conservation* 82:369–377
- Kuussaari M, Bommarco R, Heikkinen RK, et al (2009) Extinction debt: A challenge for biodiversity conservation. *Trends in ecology & evolution* 24:564–571
- LaRue EA, Hardiman BS, Elliott JM, Fei S (2019) Structural diversity as a predictor of ecosystem function. *Environmental Research Letters* 14:114011
- Laurance WF (2014) Contemporary drivers of habitat fragmentation. In: *Global*



- forest fragmentation. CABI Wallingford UK, pp 20–27
- Lawton J (2010) Making space for nature: A review of england’s wildlife sites and ecological networks. Defra
- Leibold MA, Chase JM (2017) Metacommunity ecology, volume 59. In: Metacommunity ecology, volume 59. Princeton University Press
- Lenoir J, Decocq G, Spicher F, et al (2021) Historical continuity and spatial connectivity ensure hedgerows are effective corridors for forest plants: Evidence from the species–time–area relationship. *Journal of Vegetation Science* 32:e12845
- Lira PK, Souza Leite M de, Metzger JP (2019) Temporal lag in ecological responses to landscape change: Where are we now? *Current Landscape Ecology Reports* 4:70–82
- Litza K, Diekmann M (2020) The effect of hedgerow density on habitat quality distorts species-area relationships and the analysis of extinction debts in hedgerows. *Landscape ecology* 35:1187–1198
- Litza K, Diekmann M (2019) Hedgerow age affects the species richness of herbaceous forest plants. *Journal of Vegetation Science* 30:553–563
- Liu Y, Schieving F, Stuefer JF, Anten NP (2007) The effects of mechanical stress and spectral shading on the growth and allocation of ten genotypes of a stoloniferous plant. *Annals of Botany* 99:121–130
- Lutz JA, Furniss TJ, Johnson DJ, et al (2018) Global importance of large-diameter trees. *Global Ecology Biogeography* 27:849–864
- MacArthur RH, MacArthur JW (1961) On bird species diversity. *Ecology*

42:594–598

MacArthur RH, Wilson EO (1967) *The theory of island biogeography*. Princeton University Press, Princeton, NJ, USA

Malchow A, Bocedi G, Palmer SC, et al (2021) RangeShiftR: An r package for individual-based simulation of spatial eco-evolutionary dynamics and species' responses to environmental changes. *Ecography* 44:1443–1452

Marrs R, Kirby K, Le Duc M, et al (2013) Native dominants in british woodland—a potential cause of reduced species-richness? *New Journal of Botany* 3:156–168

McRae BH, Dickson BG, Keitt TH, Shah VB (2008) Using circuit theory to model connectivity in ecology, evolution, and conservation. *Ecology* 89:2712–2724

Melin M, Hinsley S, Broughton R, et al (2018) Living on the edge: Utilising lidar data to assess the importance of vegetation structure for avian diversity in fragmented woodlands and their edges. *Landscape Ecology* 33:895–910

Melles S, Fortin M, Lindsay K, Badzinski D (2011) Expanding northward: Influence of climate change, forest connectivity, and population processes on a threatened species' range shift. *Global Change Biology* 17:17–31

Meng SX, Lieffers VJ, Reid DE, et al (2006) Reducing stem bending increases the height growth of tall pines. *Journal of Experimental Botany* 57:3175–3182

Menge JH, Magdon P, Wöllauer S, Ehbrecht M (2023) Impacts of forest management on stand and landscape-level microclimate heterogeneity of european beech forests. *Landscape Ecology* 1–15

Messaoud Y, Chen HY (2011) The influence of recent climate change on tree

- height growth differs with species and spatial environment. *PLoS one* 6:e14691
- Met Office (2020) UK climate averages. <https://www.metoffice.gov.uk/research/climate/maps-and-data/uk-climate-averages/gcp0j39m4>
- Miklin J, Čížek L (2014) Erasing a european biodiversity hot-spot: Open woodlands, veteran trees and mature forests succumb to forestry intensification, succession, and logging in a UNESCO biosphere reserve. *Journal for Nature Conservation* 22:35–41
- Montgomery I, Caruso T, Reid N (2020) Hedgerows as ecosystems: Service delivery, management, and restoration. *Annual Review of Ecology, Evolution, and Systematics* 51:81–102
- Müller J, Brandl R, Brändle M, et al (2018) LiDAR-derived canopy structure supports the more-individuals hypothesis for arthropod diversity in temperate forests. *Oikos* 127:814–824
- Naaf T, Kolk J (2015) Colonization credit of post-agricultural forest patches in NE germany remains 130–230 years after reforestation. *Biological Conservation* 182:155–163
- National Forest Company (2022) What is the national forest? <https://www.nationalforest.org/about/what-is-the-national-forest>. Accessed 9 Oct 2022
- Olszewski JH, Bailey JD (2022) LiDAR as a tool for assessing change in vertical fuel continuity following restoration. 13:503
- Opdam P, Dorp D ter van, Ter Braak D (1984) The effect of isolation on the

- number of woodland birds in small woods in the netherlands. *Journal of Biogeography* 1:473–478
- Orrock JL, Brudvig LA, Damschen EI, et al (2023) Long-term, large-scale experiment reveals the effects of seed limitation, climate, and anthropogenic disturbance on restoration of plant communities in a biodiversity hotspot. *Proceedings of the National Academy of Sciences* 120:e2201943119
- Paraskevopoulos AW, Catano CP, Brudvig LA (2023) Ant and plant diversity respond differently to seed-based prairie restoration. *Restoration Ecology* e13853
- Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annu Rev Ecol Evol Syst* 37:637–669
- Paula MD de, Costa CPA, Tabarelli M (2011) Carbon storage in a fragmented landscape of atlantic forest: The role played by edge-affected habitats and emergent trees. *Tropical Conservation Science* 4:349–358
- Peay KG, Garbelotto M, Bruns TD (2010) Evidence of dispersal limitation in soil microorganisms: Isolation reduces species richness on mycorrhizal tree islands. *Ecology* 91:3631–3640
- Pelletier-Guittier C, Théau J, Dupras J (2020) Use of hedgerows by mammals in an intensive agricultural landscape. *Agriculture, Ecosystems & Environment* 302:107079
- Pereira L, Oliveira C, Torezan JMD (2013) Woody species regeneration in atlantic forest restoration sites depends on surrounding landscape. *Natureza Conservação* 11:138–144

- Peterken G (2000) Rebuilding networks of forest habitats in lowland england. *Landscape Research* 25:291–303
- Peterken G, Game M (1984) Historical factors affecting the number and distribution of vascular plant species in the woodlands of central lincolnshire. *The Journal of Ecology* 155–182
- Petit S, Griffiths L, Smart SS, et al (2004) Effects of area and isolation of woodland patches on herbaceous plant species richness across great britain. *Landscape ecology* 19:463–471
- Plenderleith FA, Palmer SC, Travis JM, et al (2022) The consequences of tree disease and pre-emptive felling on functional and genetic connectivity for woodland invertebrates. *Ecological Informatics* 72:101820
- Pollard CJ (1971) *Hedges*. Collins, London
- Quine C, Watts K (2009) Successful de-fragmentation of woodland by planting in an agricultural landscape? An assessment based on landscape indicators. *Journal of Environmental Management* 90:251–259
- R core team (2022) R version 4.1.2. <https://www.R-project.org/>
- Rackham O (1980) *Ancient woodland, its history, vegetation and uses in england*. London
- Rackham O (2008) Ancient woodlands: Modern threats. *New Phytologist* 571–586
- Rappaport DI, Tambosi LR, Metzger JP (2015) A landscape triage approach: Combining spatial and temporal dynamics to prioritize restoration and conservation. *Journal of Applied Ecology* 52:590–601

- Rocha ÉG da, Brigatti E, Niebuhr BB, et al (2021) Dispersal movement through fragmented landscapes: The role of stepping stones and perceptual range. *Landscape Ecology* 36:3249–3267
- Roussel J-R, Auty D, Coops NC, et al (2020) lidR: An r package for analysis of airborne laser scanning (ALS) data. *Remote Sensing of Environment* 251:112061
- Rural Payments Agency (2021) Countryside stewardship: Woodland creation and maintenance grant manual (from 9 february 2021)
- Saura S, Bodin Ö, Fortin M (2014a) EDITOR's CHOICE: Stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks. *Journal of Applied Ecology* 51:171–182
- Saura S, Bodin Ö, Fortin M-J (2014b) EDITOR's CHOICE: Stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks. *Journal of Applied Ecology* 51:171–182
- Schalkwyk J van, Pryke J, Samways M, Gaigher R (2021) Maintaining high vegetation structural diversity in the landscape promotes arthropod diversity in dynamic production areas. *Landscape Ecology* 36:1773–1785
- Scottish Forestry (2023) Forestry grants
- Shirley HL (1929) The influence of light intensity and light quality upon the growth of plants. *American Journal of Botany* 354–390
- Smith GF, Gittings T, Wilson M, et al (2007) Identifying practical indicators of biodiversity for stand-level management of plantation forests. In: *Plantation forests and biodiversity: Oxymoron or opportunity?* Springer, pp 67–91

- Spake R, Bellamy C, Gill R, et al (2020) Forest damage by deer depends on cross-scale interactions between climate, deer density and landscape structure. *Journal of Applied Ecology* 57:1376–1390
- Spencer J, Kirby K (1992) An inventory of ancient woodland for england and wales. *Biological conservation* 62:77–93
- Staddon P, Lindo Z, Crittenden PD, et al (2010) Connectivity, non-random extinction and ecosystem function in experimental metacommunities. *Ecology letters* 13:543–552
- Staddon PL, Urquhart J, Mills J, et al (2021) Encouraging woodland creation, regeneration and tree planting on agricultural land: A literature review. *Natural England* 1–126
- Stahl U, Reu B, Wirth C (2014) Predicting species' range limits from functional traits for the tree flora of north america. *Proceedings of the National Academy of Sciences* 111:13739–13744
- Staley JT, Wolton R, Norton LR (2023) Improving and expanding hedgerows—recommendations for a semi-natural habitat in agricultural landscapes. *Ecological Solutions and Evidence* 4:e12209
- Stanturf JA, Palik BJ, Dumroese RK (2014) Contemporary forest restoration: A review emphasizing function. *Forest Ecology & Management* 331:292–323
- Stauder IR, Navarro LM, Pereira HM (2020) Range size predicts the risk of local extinction from habitat loss. *Global Ecology and Biogeography* 29:16–25
- Stephenson NL, Das A, Condit R, et al (2014) Rate of tree carbon accumulation increases continuously with tree size. *Nature* 507:90–93

- Synes NW, Brown C, Watts K, et al (2016) Emerging opportunities for landscape ecological modelling. *Current Landscape Ecology Reports* 1:146–167
- Synes NW, Ponchon A, Palmer SC, et al (2020) Prioritising conservation actions for biodiversity: Lessening the impact from habitat fragmentation and climate change. *Biological Conservation* 252:108819
- Taylor PD, Fahrig L, Henein K, Merriam G (1993) Connectivity is a vital element of landscape structure. *Oikos* 571–573
- The Woodland Trust (2023) More hedges - the woodland trust. <https://www.woodlandtrust.org.uk/plant-trees/trees-for-landowners-and-farmers/morehedges/>
- UNEP (2022). <https://wedocs.unep.org/20.500.11822/37848>.
- University of Maryland (2023) GEDI ecosystem LiDAR. <https://gedi.umd.edu/>
- Uzoh FC, Oliver WW (2006) Individual tree height increment model for managed even-aged stands of ponderosa pine throughout the western united states using linear mixed effects models. *Forest Ecology Management* 221:147–154
- Valdés A, Lenoir J, De Frenne P, et al (2020) High ecosystem service delivery potential of small woodlands in agricultural landscapes. *Journal of Applied Ecology* 57:4–16
- Van Schalkwyk J, Pryke J, Samways M, Gaigher R (2020) Corridor width determines strength of edge influence on arthropods in conservation corridors. *Landscape ecology* 35:1175–1185
- Vanneste T, Van Den Berge S, Riské E, et al (2020) Hedging against biodiversity loss: Forest herbs' performance in hedgerows across temperate europe.



- Journal of Vegetation Science 31:817–829
- Vashum KT, Jayakumar S (2012) Methods to estimate above-ground biomass and carbon stock in natural forests-a review. *Journal of Ecosystem Ecography* 2:1–7
- Vellend M, Verheyen K, Flinn KM, et al (2007) Homogenization of forest plant communities and weakening of species–environment relationships via agricultural land use. *Journal of Ecology* 95:565–573
- Vellend M, Verheyen K, Jacquemyn H, et al (2006) Extinction debt of forest plants persists for more than a century following habitat fragmentation. *Ecology* 87:542–548
- Wang X, Blanchet FG, Koper N (2014) Measuring habitat fragmentation: An evaluation of landscape pattern metrics. *Methods in ecology and evolution* 5:634–646
- Watson JE, Whittaker RJ, Dawson TP (2004) Habitat structure and proximity to forest edge affect the abundance and distribution of forest-dependent birds in tropical coastal forests of southeastern madagascar. *Biological Conservation* 120:311–327
- Watts K, Eycott AE, Handley P, et al (2010) Targeting and evaluating biodiversity conservation action within fragmented landscapes: An approach based on generic focal species and least-cost networks. *Landscape Ecology* 25:1305–1318
- Watts K, Fuentes-Montemayor E, Macgregor NA, et al (2016) Using historical woodland creation to construct a long-term, large-scale natural experiment:

- The WrEN project. *Ecology and Evolution* 6:3012–3025
- Watts K, Whytock RC, Park KJ, et al (2020) Ecological time lags and the journey towards conservation success. *Ecology* 4:304–311
- Whigham DF (2004) Ecology of woodland herbs in temperate deciduous forests. *Annual review of ecology, evolution, systematics* 35:583–621
- Whittet R, Cottrell J, Cavers S, et al (2016) Supplying trees in an era of environmental uncertainty: Identifying challenges faced by the forest nursery sector in great britain. *Land Use Policy* 58:415–426
- Wiggins HL, Nelson CR, Larson AJ, Safford HD (2019) Using LiDAR to develop high-resolution reference models of forest structure and spatial pattern. *Forest ecology and management* 434:318–330
- Willi J, Mountford J, Sparks T (2005) The modification of ancient woodland ground flora at arable edges. *Biodiversity & Conservation* 14:3215–3233
- Zhang K, Chen S-C, Whitman D, et al (2003) A progressive morphological filter for removing nonground measurements from airborne LIDAR data. *IEEE transactions on geoscience remote sensing* 41:872–882

## 6 Appendix

Table A1: Displaying how woodland samples are spread across ages, adjacent or isolated and geology.

	Adjacent mature created woodlands	Adjacent young created woodlands	Isolated mature created woodlands	Isolated young created woodlands
Argillaceous rock	2	2	5	0
Argillaceous rock mixed w/ sandstone	6	3	9	2
Chalk	1	3	3	5
Sandstone	3	6	13	0

Table A2: The results of 3 linear models assuming Gaussian error structures: the first predicting canopy height in the form of Relative Height at the 90th percentile, the second predicting the foliage height diversity, and the third predicting change in canopy height between 2011 and 2021. \*= P between 0.01 and 0.05, \*\*= P< 0.01 and - = non-significant. Substrate compared to Argillaceous rock and year planted compared to mature woodlands planted before 1980

Response Variable	R2	Predictors	Description	Estimates	SE	P
Canopy height (RH90) (m)	0.47	Adjacency	Whether an older adjacent neighbour was present at the point of woodland creation. Woodlands planted in isolation are the reference category	1.90	1.470	*
		Woodland age	Whether woodlands are young created woodlands (1995-2005) or mature created woodlands (1970-1990). Young created woodlands are the reference category	5.00	0.900	**
		Underlying geology (Argillaceous rock +Sandstone)	The underlying geology of the target woodland Argillaceous rock taken as reference category	0.85	1.170	-
		Underlying geology (Chalk)		0.50	1.560	-
		Underlying geology (Sandstone)		0.52	1.160	-
		Mean elevation	The mean elevation of the target woodland	-0.02	0.010	*
		Northness	The mean aspect of the target woodland calculated as the cosine of the aspect radians	1.32	1.170	-
Foliage Height Diversity (m)	0.40	Adjacency		0.05	0.016	*
		Woodland age		0.09	0.010	**
		Underlying geology (Argillaceous rock + Sandstone)		0.03	0.020	-
		Underlying geology (Chalk)		-0.04	0.030	-
		Underlying geology (Sandstone)		-0.01	0.020	-
		Mean elevation		0.00	0.000	**
		Northness		0.01	0.020	-
Growth (rh90) (m)	0.31	Adjacency		6.75	4.700	-
		Woodland age		9.73	4.700	-
		Underlying geology (Argillaceous rock + Sandstone)		-11.40	6.660	-
		Underlying geology (Chalk)		-4.39	8.890	-
		Underlying geology (Sandstone)		7.73	6.580	-
		Mean elevation		-0.08	0.070	-
		Northness		-1.70	6.640	-

Table A3: Full parameters used in Rangesifter for all 4 conceptual species

Profile	Short range dispersing plant, sometime carried by birds long distance, emmigration prob only becomes likely once cell is nearly full to mimick slow spread	short range dispersing invert, which is more likely to disperse especially in high densities. Asexual	Large ranging bird which is dependent on finding a mate, disperses when population at much lower densities. High fecundity but high juvenile mortality	medium ranging mammal dependent on finding a mate
<b>Population</b>				
Reproduction	asexual	asexual	Sexual	Sexual
Stages	1	1	juve+1	juve + 1
Max age	na	na	8	4
Min age stage 2				
Fecundity(juve, 1, 2) ?			c( 0, 5)	(0, 4)
Development prob (juve, 1, ) ?			c(1)	(1,)
Survival prob (juve, 1, 2) ?			c(1, 0.5)	(1, 0.6)
Transition matrix			(0, 5, 1, 0.5)	(0, 4, 1, 0.6)
Rmax	10	10		
Fecundity denDep			Y	y
Matrix	0	0	0	0
Broadleaved woodland	250	30	2	5
Hedge	125	15	0	0
<b>Emigration</b>				
K dependent	f	t	t	t
Emigprob	1	c(0.5, 3, 0.5)	c(0.5, 10, 0.5)	c(0.5, 5, 0.5)
<b>Transfer</b>				
Dispersal method	Double kernal	SMS	SMS	SMS
Distance I	5			
Distance II	100			
Prop kernal I	0.999			
Full kernel	t			
Mortality	0.5	0.1		
Perceptual range		2	20	10
PR method		2	2	2
Directional persistance		5	15	10
Memory size		1	1	1
<b>Goal type</b>		<b>2</b>	<b>2</b>	<b>2</b>
Goal bias		5	5	5
Alpha DB		2	2	2
Beta DB		10	10	10
Matrix (step mortality)		0.1	0.01	0.04
Broadleaved		0	0	0
hedge		0	0	0
Matrix (cost)		10000	1000	10000
Broadleaved		1	1	1
hedge		1	1	1
Settlement	Die if unsuitable	Settle if suitable	male Settle if suitable and mate, female settle if suitable non natal	Settle if suitable and mate

Table A4: Results of statistical models predicting the populations and proportional occupation of 4 conceptual species across simulated landscapes

Model	Species/R2	Predictor	Estimate	SE	t / z value	df	p
Null Model predicting the population sizes within woodlands	Bird R2 9.92	Presence	13.5000	15.600	0.800	32.00	0.39
		of corridors					
		ED	9.9000	1.700	5.800	32.00	< 0.001***
		% woodland cover	39.4900	2.400	16.400	32.00	< 0.001***
	Mammal R2 0.94	Presence of corridors	69.7200	21.200	3.200	32.00	0.003**

(continued)

Model	Species/R2	Predictor	Estimate	SE	t / z value	df	p
		ED	7.9900	2.300	3.500	32.00	0.002**
		% woodland cover	64.5000	32.800	19.600	32.00	< 0.001***
	Invertebrate R2 0.99	Presence of corridors	42.1700	43.760	0.900	32.00	0.34
		ED	65.2000	4.770	13.600	32.00	< 0.001***
		% woodland cover	418.2000	6.770	61.700	32.00	< 0.001***

(continued)

Model	Species/R2	Predictor	Estimate	SE	t / z value	df	p
	Plant R2 0.99	Presence of corridors	43.9000	275.670	0.100	31.00	0.87
		ED	188.4000	87.000	2.200	31.00	0.04*
		% woodland cover	2373.5400	165.700	14.300	31.00	< 0.001***
		% woodland cover x ED	- 1853.0000	825.000	-2.200	31.00	< 0.001***



(continued)

Model	Species/R2	Predictor	Estimate	SE	t / z value	df	p
Null model predicting the proportion of woodland patches occupied	Bird pseudo R2 0.24	Presence	0.2000	0.180	1.150		0.24
		of					
		corridors					
		ED	0.0400	0.010	2.300		0.02*
Mammal R2 pseudo 0.37	Mammal R2 pseudo 0.37	%	0.0380	0.028	1.400		0.16
		woodland					
		cover					
		Presence	0.5800	0.130	4.300		<
		of					0.001***
		corridors					
		ED	0.0300	0.010	2.500		0.01*

(continued)

Model	Species/R2	Predictor	Estimate	SE	t / z value	df	p
		% woodland cover	0.0065	0.020	0.310		0.7
Model predicting percentage increase in population sizes between null landscapes and habitat creation landscapes	Bird R2 marginal 0.82 / conditional 0.94	Presence of corridors	5.3900	2.140	2.500	50.00	0.015*
		ED	-3.2300	0.700	-4.520	18.70	< 0.001***

150

(continued)

Model	Species/R2	Predictor	Estimate	SE	t / z value	df	p
		% woodland cover	- 598.0000	101.600	-5.880	18.70	< 0.001***
		Create adjacent	141.6000	10.200	13.840	50.00	< 0.001***
		ED x Create adjacent	2.8900	0.460	6.190	50.00	< 0.001***
		% woodland cover x Create adjacent	- 348.0000	66.000	5.300	50.00	< 0.001***

(continued)

Model	Species/R2	Predictor	Estimate	SE	t / z value	df	p
	Mammal R2	Presence	9.9000	2.800	3.500	49.00	<
	marginal 0.96 /	of					0.001***
	conditional 0.98	corridors					
		ED	-1.4000	0.480	-2.900	23.00	0.008**
		%	-	68.860	-11.600	23.00	<
		woodland	800.0000				0.001***
		cover					
		Create	222.6000	9.700	22.800	23.00	<
		adjacent					0.001***
		Corridors	-10.9000	3.900	-2.750	49.00	<
		present x					0.008**
		Create					
		adjacent					

(continued)

Model	Species/R2	Predictor	Estimate	SE	t / z value	df	p
		ED x	-1.6000	0.400	-3.800	49.00	<
		Create					0.001***
		adjacent					
		%	-	61.700	-11.800	49.00	<
		woodland	733.5000				0.001***
		cover x					
		Create					
		adjacent					
	Invertebrate R2	Presence	-1.7700	2.650	-0.940	66.00	0.34
	marginal 0.893 /	of					
	conditional NA	corridors					
		ED	-0.3000	1.140	-2.550	66.00	0.013*

(continued)

Model	Species/R2	Predictor	Estimate	SE	t / z value	df	p
		% woodland cover	-2.1300	0.210	-10.000	66.00	< 0.001***
		Create adjacent	31.8900	1.870	17.000	66.00	< 0.001***
		Corridors present x Create adjacent	-8.0300	2.650	3.020	66.00	0.003**
	Plant R2	Presence of corridors	0.0090	1.020	0.097	49.00	0.92
	marginal 0.95 / conditional 0.951						

(continued)

Model	Species/R2	Predictor	Estimate	SE	t / z value	df	p
		ED	-0.5100	0.110	-4.500	45.00	< 0.001***
		% woodland cover	-249.9000	16.000	-15.600	45.00	< 0.001***
		Create adjacent	55.5000	3.500	15.600	49.00	< 0.001***
		Corridors present x Create adjacent	-14.8000	1.400	-8.100	49.00	< 0.001***

(continued)

Model	Species/R2	Predictor	Estimate	SE	t / z value	df	p
		ED x	-0.4500	0.150	-2.800	49.00	0.006**
		Create					
		adjacent					
		%	-	22.400	-8.100	49.00	<
		woodland	182.6000				0.001***
		cover x					
		Create					
		adjacent					



(continued)

Model	Species/R2	Predictor	Estimate	SE	t / z value	df	p
Model predicting proportion of remaining patches occupied after habitat creation	Bird: Nakagawa R2 marginal 0.463 / conditional 0.88	Presence of corridors	0.6800	0.090	7.030		< 0.001***
		ED	0.0460	0.026	1.750		0.079
		% woodland cover	-0.1200	0.040	-3.200		0.001**
		Create adjacent	1.0200	0.290	3.460		< 0.001***

(continued)

Model	Species/R2	Predictor	Estimate	SE	t / z value	df	p
		% woodland cover x Create adjacent	0.1000	0.030	3.730		< 0.001***
	Mammal: Nakagawa R2 marginal 0.85 / conditional 0.91	Presence of corridors	1.5500	0.130	11.500		< 0.001***
		ED % woodland cover	0.0500 0.0000	0.020 0.030	2.780 -0.030		0.005** 0.97

(continued)

Model	Species/R2	Predictor	Estimate	SE	t / z value	df	p
		Create adjacent	1.1000	0.120	2.780		< 0.001***
Model predicting the population sizes of created habitats	Bird: R2 marginal 0.92 / conditional 0.97	Presence of corridors	-16.2000	5.390	-3.000	49.00	0.004**
		ED	-1.4000	1.240	-1.090	18.89	0.29
		% woodland cover	16.0000	1.770	9.040	18.89	< 0.001***
		Create adjacent	143.4400	18.620	7.700	49.00	< 0.001***

(continued)

Model	Species/R2	Predictor	Estimate	SE	t / z value	df	p
		Corridors present x Create adjacent	-32.0400	7.630	4.200	49.00	< 0.001***
		% woodland cover x Create adjacent	11.6400	1.190	9.850	49.00	< 0.001***
		ED x Create adjacent	4.3900	0.830	5.270	49.00	< 0.001***

(continued)

Model	Species/R2	Predictor	Estimate	SE	t / z value	df	p
	Mammal: R2	Presence	1.9100	10.790	0.170	49.00	0.85
	marginal 0.97 /	of					
	conditional 0.98	corridors					
		ED	-3.4800	1.830	-1.890	23.20	0.07
		%	26.3900	2.600	10.120	23.27	<
		woodland					0.001***
		cover					
		Create	309.1400	37.270	8.290	49.00	<
		adjacent					0.001***
		Corridors	-56.2000	15.270	-3.680	49.00	<
		present x					0.001***
		Create					
		adjacent					

*(continued)*

Model	Species/R2	Predictor	Estimate	SE	t / z value	df	p
		% woodland cover x Create adjacent ED x Create adjacent	24.1000	2.360	10.200	49.00	< 0.001***
		ED x Create adjacent	3.5000	1.660	2.100	49.00	0.04*
	Invertebrate: R2 marginal 0.9 / conditional NA	Presence of corridors	-91.9300	46.000	-1.990	50.00	< 0.001***
		ED	-10.8700	5.580	-1.950	34.70	0.059

(continued)

Model	Species/R2	Predictor	Estimate	SE	t / z value	df	p
		% woodland cover	25.7700	6.260	4.120	15.00	< 0.001***
		Create adjacent	1903.0000	145.000	13.120	50.00	< 0.001***
		ED x Create adjacent	-29.5500	6.850	-4.320	50.00	< 0.001***
		Corridors present x Create adjacent	-	65.060	-5.920	50.00	< 0.001***
			385.1600				

(continued)

Model	Species/R2	Predictor	Estimate	SE	t / z value	df	p
	Plant: R2	Presence	10.3000	258.340	0.040	51.00	0.9
	marginal 0.95	of					
	/conditional 0.96	corridors					
		ED	-2.9300	21.600	-0.140	15.00	0.89
		%	20.2200	30.750	0.650	15.00	0.52
		woodland					
		cover					
		Create	9015.0000	258.000	34.800	51.00	<
		adjacent					0.001***
		Corridors	-	365.000	-13.150	51.00	<
		present x	4805.0000				0.001***
		Create					
		adjacent					



(continued)

Model	Species/R2	Predictor	Estimate	SE	t / z value	df	p
Model predicting the percentage occupancy of created habitats	Bird: Nakagawa R2 marginal 0.75 / conditional 1	Presence of corridors	0.3300	0.070	4.280		< 0.001***
		ED	0.0800	0.020	3.110		0.002**
		% woodland cover	0.0400	0.040	1.490		0.13
		Create adjacent	1.3200	0.080	16.120		< 0.001***

(continued)

Model	Species/R2	Predictor	Estimate	SE	t / z value	df	p
	Mammal: Nakagawa R2 marginal 0.98 / conditional 0.99	Presence of corridors	0.6500	0.120	5.610		< 0.001***
		ED	0.0200	0.020	1.140		0.25
		% woodland cover	0.0900	0.030	2.970		0.003**
		Create adjacent	5.4800	0.220	24.350		< 0.001***

(continued)

Model	Species/R2	Predictor	Estimate	SE	t / z value	df	p
		Corridors present x Create adjacent	-2.1700	0.240	8.830		< 0.001***
	Invertebrate: Nakagawa R2 marginal 0.98 / conditional 1	Presence of corridors	-0.2000	0.280	-0.090		0.92
		ED	0.0490	0.169	2.900		0.003**
		% woodland cover	0.0300	0.020	1.300		0.2

*(continued)*

Model	Species/R2	Predictor	Estimate	SE	t / z value	df	p
		Create adjacent	4.2000	0.220	18.580		< 0.001***
		Corridors present x Create adjacent	-0.7800	0.280	2.750		0.006**
	Plant: Nakagawa R2 marginal 0.98 / conditional 1	Presence of corridors	-0.0100	0.380	-0.030		0.96
		ED	0.0100	0.020	0.560		0.57
		% woodland cover	0.0200	0.030	0.890		0.37

(continued)

Model	Species/R2	Predictor	Estimate	SE	t / z value	df	p
		Create adjacent	5.8300	0.310	18.290		< 0.001***
		Corridors present x Create adjacent	-2.4400	0.400	6.100		< 0.001***

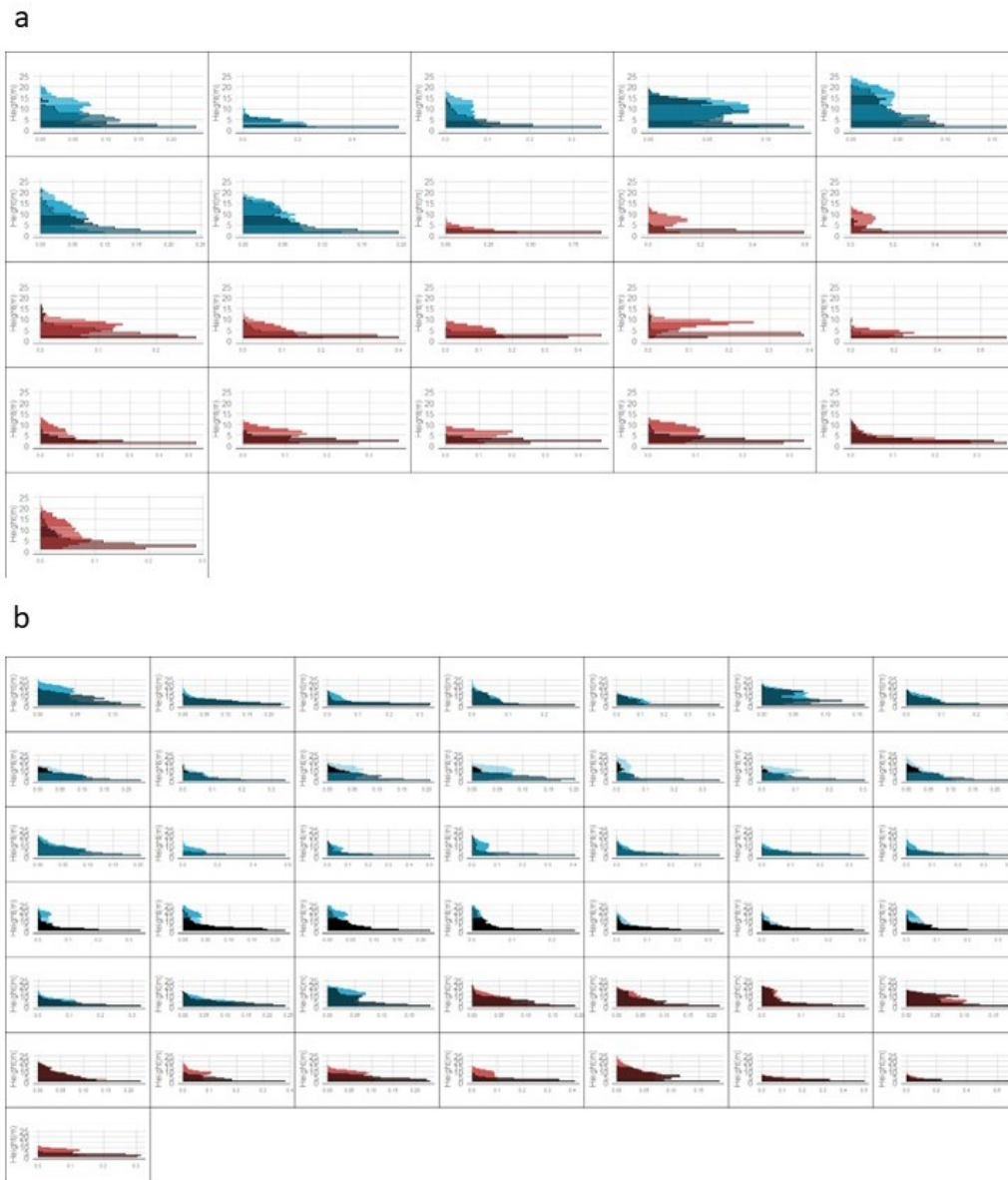


Figure A1: Height profiles of each individual created woodland calculated as the proportion of LiDAR returns in each 1m height bin. The top set (a) of figures are young created woodlands, where the bottom (b) set of figures are mature created woodlands. Bars filled with colours were created using LiDAR data from 2021, where transparent were created using LiDAR data from 2011. Red = those with adjacent neighbours, Blue = those planted in isolation

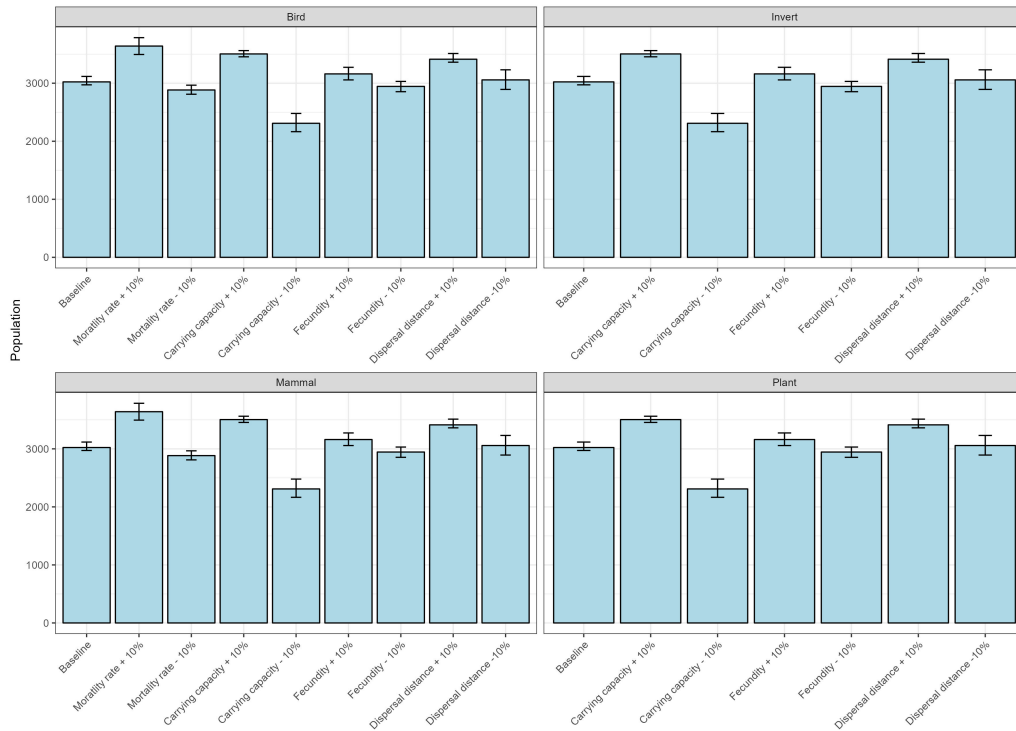


Figure A2: Bar graphs showing results of the sensitivity analysis. This explored how key parameters affect model outcomes by increasing or decreasing their values by 10%. Bars display the mean population outcomes after 5 model iterations, and error bars show the full range of population outcomes after 5 model iterations. Dispersal distance in SMS species ( , ) is controlled by the step mortality parameter. Mortality rate is not included for x or x as it is built into the fecundity parameter