Assessing the role of rewilding in restoring forest structure and composition, to support biodiversity under climate change

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Abstract

High heterogeneity in forest structure and composition can have positive implications for biodiversity, by stabilising local microclimates through natural buffer regions known as microrefugia. Under current and future climate warming, microrefugia are becoming increasingly important. In this study, I identified and measured the height of all trees in ten plots across Carrifran, to quantify how active and passive rewilding at Carrifran, UK, has altered variation in forest structure and composition. I found that the trees growing at Carrifran have developed heterogeneously with clear variation in heights and species diversity across the sample plots, which will facilitate heterogeneity in microclimates and microhabitats that likely supports diversity and climate resilience.

1. Introduction

Rewilding is an increasingly influential approach in ecology that has become more widespread over the past 25 years. Amongst many interpretations of how to describe this deviation from conventional approaches in nature conservation, Pettorelli et al (2018) defined rewilding as "the reorganisation of biota and ecosystem processes to set an identified social–ecological system on a preferred trajectory, leading to the self-sustaining provision of ecosystem services with minimal ongoing management". This acknowledges the initial input required to set the ecosystem on its restoration curve, leading to a self-sustaining environment that effectively becomes 'passive'. Rather than maintaining ecosystems in a fixed state, rewilding generally seeks to restore ecological processes and increase the capacity for ecosystems to develop autonomously. Although the extent and methods of human intervention may vary between projects, it also attempts to holistically incorporate "human-nature reconnection and systemic transformation" (Carver et al, 2025) within this transition.

Yet hesitation and opposition to rewilding exist owing to its perceived unpredictability (Carver et al, 2025), which may be attributed to the lacking evidence base on rewilding outcomes. Fortunately, there is now a growing number of UK-wide projects that are beginning to show the many benefits of rewilding for forest restoration, and this report focuses on one particular example: Carrifran Wildwood.

For centuries, the primary activities at Carrifran Wildwood consisted of sheep grazing and pasturing domestic stock, but in 2000 the Borders Forest Trust acquired Carrifran to "recreate an extensive tract of mainly forested wilderness, with most of the rich diversity of native species present in the area before human activities became dominant", as per their mission statement. Over the next 2 decades, 700,000 native trees and shrubs were specifically planted in chosen areas depending on the local geology, soils, climate and evidence from ancient plant pollen found in deep peat which indicated the vegetation type which previously grew there (Adair & Ashmole, 2022).

Figure 1: Carrifran Wildwood in 2004 and 2021 (Borders Forest Trust, 2026)

To prevent grazing from browsers, which would suppress the establishment and natural growth of vegetation, a perimeter stock fence was installed to exclude sheep and goats. A study by Porton et al (2024) found that the number of naturally colonising trees increased by 16% each year per hectare after sheep were removed, demonstrating that sheep are a key limiting factor as they graze preferentially on seedlings. The earliest plantings have developed into successful woodland ecosystems, with the associated features such as closed canopy, horizontal and vertical structural complexity and leaf litter. Furthermore, as different trees naturally develop different canopy structures and grow to different heights, this can indicate the woodland's successional stage and how effective restoration has been (Nuijten et al, 2021). Therefore, Carrifran represents a mixed restoration approach where active interventions including tree planting and herbivore exclusion were used to initiate woodland recovery, alongside subsequent natural colonisation and ecological development.

This study focuses on the variation in tree species and vertical structural heterogeneity at Carrifran Wildwood following rewilding – both key factors in determining microhabitat availability and microclimate buffering capacity in temperate forests. Different tree species vary in canopy architecture and physiology, which influence the amount of solar radiation that penetrates through the canopy, as well as influencing airflow and the relative humidity. Trees also influence the capture and flow of precipitation, which affects local hydrology. For example, birch trees (*Betula* spp.) are early successional pioneer species that grow tall and fast, and therefore tend to have open and relatively thin canopies. Oak trees (*Quercus* spp.), in contrast, are late successional species that can develop dense, thick and wide canopies that intercept much larger quantities of incoming solar radiation. The way in which different species grow together and reproduce also affects the density of trees, which affects the combined tree canopy architecture both vertically and horizontally (Thomas & Packham, 2007).

The differences in tree species and their physiology strongly links to microclimate, defined as the "local thermal, hydric, and radiative conditions within one metre of the earth's surface, and/or below vegetation, that organisms are exposed to" (Klinges et al, 2025), and can be seen as the resulting outcome when forest structures, local hydrology, topography and landscape features interact. For example, slopes that face north in the northern hemisphere generally receive less solar radiation and therefore experience a more humid microclimate (Sewerniak, 2016). Helbach et al (2022) found that increased forest structural complexity also

increased light heterogeneity which is associated with increasing species richness of understory plants. Stein et al (2014) also found that heterogeneity in vegetation via structural complexity and variation in canopy heights, in addition to topography, displayed strong associations with species richness. These studies suggest that microclimates more accurately represent the living conditions an organism experiences, and subsequently, understanding how microclimatic conditions arise and are maintained is crucial for protection of vulnerable species affected by climate change.

A study by Pierick et al (2026) showed the role of canopy gaps in microclimate heterogeneity, by allowing for high microclimate heterogeneity horizontally, where both warm and cold habitats were found within short distance from each other, in addition to vertical microclimatic heterogeneity. This occurs along a gradient from the canopy to the shaded forest floor in closed canopy forests, as solar radiation can reach further below which results in comparatively warmer air temperature along the vertical tree length. Structurally complex forests have a significant influence on sub-canopy microclimate heterogeneity via buffering effects, which can support increased biodiversity of ground-level plants. This may generate a bottom-up effect, where the diversity and number of arthropods and other small organisms dependent on plants increases in turn.

The difference between the maximum temperature experienced below forest canopies and outside in open areas is expected to increase an average of 0.27 ± 0.16 °C during 2060-2080 (De Lombaerde et al, 2022), giving species that are adapted to lower temperatures the capacity to survive for longer than expected as microclimates under forest have shown slower rates of warming than non-forested regions, creating distinct microrefugia. By providing more time for either adaptation or migration, it plays a crucial role in reducing the risk of extirpation (De Frenne et al, 2021). Furthermore, temperature extremes are also buffered inside forests compared to areas outside of forests, whereby maximum temperatures are lower and minimum temperatures are higher. Zellweger et al (2019) found that in temperate deciduous European forests, the summer maximum temperature was 2.1 °C cooler on average owing to shade being cast by tree species with denser canopies, and the minimum temperature during spring as 0.9°C warmer on average when comparing inside to outside forests as the understorey retains heat. This shows how changes in forest understorey temperatures are typically induced by vegetation height and cover.

The thermophilization rate, which is defined as “the rate of community shift towards more warm-adapted species” (De Frenne et al, 2021) for plant communities habiting forest understoreys are greater affected by the rate of microclimate warming via changes in daily maximum temperatures during the growing season, as opposed to the rate of macroclimate warming. Therefore, increasing microclimatic heterogeneity positively influences biodiversity, through providing cool microrefugia for species whose adaptations to heat lag behind the rate of climate warming (De Frenne et al, 2013). Species adapting their habitats due to changing spatial microclimate gradients have already been recorded, for example frogs in the Philippines occupying niches at higher elevations as conditions become more favourable further towards the canopy (De Frenne et al, 2021).

We predict that rewilding in Carrifran has contributed to increased heterogeneity of forest structure and composition. This in turn may have positive implications for improved biodiversity resilience under climate change by increasing microclimatic heterogeneity, but as microclimate and biodiversity were not measured directly, the potential effects of the observed forest characteristics were evaluated using evidence from existing academic literature.

2. Methodology

2.1 Study areas

The study was conducted at Carrifran Wildwood, a 660 hectare U-shaped valley situated in the Scottish Southern Uplands, forming part of both the Moffat Hills Site of Special Scientific Interest and Moffat Hills Special Area of Conservation (Adair & Ashmole, 2022). Around 44 species of woody vegetation are present (Borders Forest Trust, n.d), with currently three distinct main woodland types, with upland Oak-Birch woodland being the most common due to the wet and cold climate found at Carrifran. Slope Ash-Alder and upland Ash-Elm woodland is also found, but only in areas with moist and richer soils.

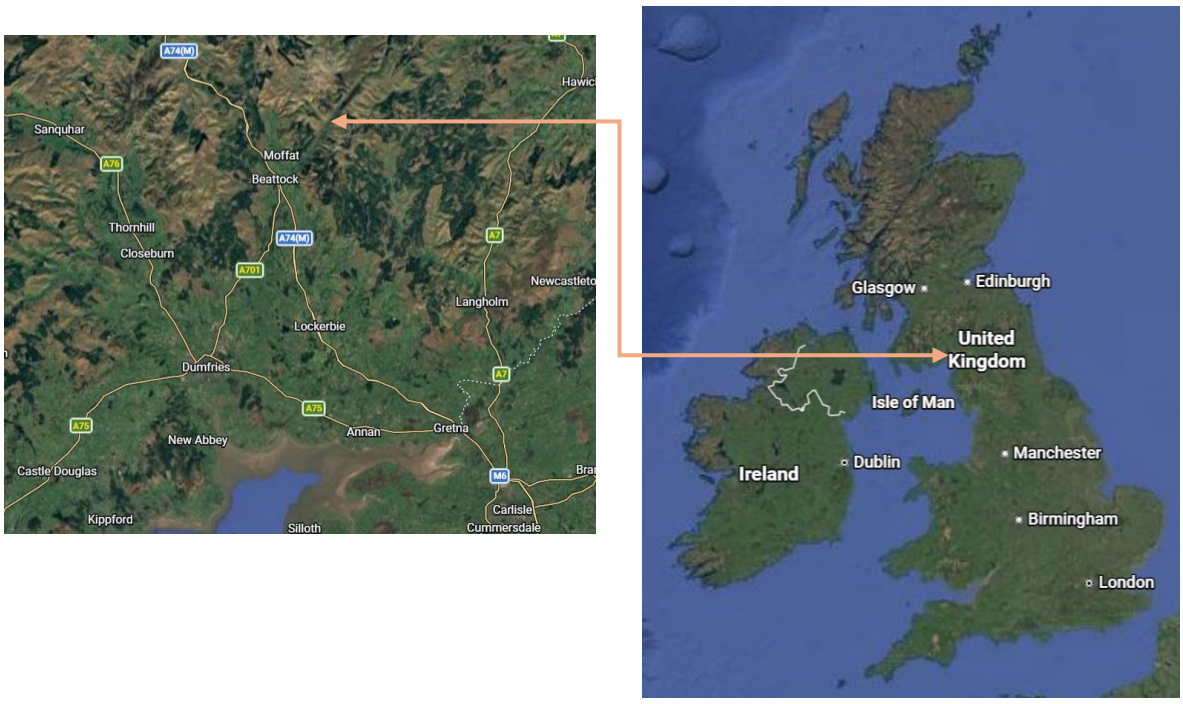

Figure 2: Carrifran Wildwood location in aerial view, via Google Maps

To take into account the environmental heterogeneity of the study site, sampling locations were selected using gradient-based stratified sampling by Principal Component Analysis. Four environmental variables with influence on local microclimates (vegetation cover, slope, aspect and elevation) were used to characterise variation across Carrifran. These variables were then combined using multivariate and ordination analyses, which reduced the

complexity of several environmental measurements into a smaller number of major environmental gradients across the study area (Klinges et al, 2025).

Plot locations were therefore chosen to exhibit Carrifran's variation by strategically distributing them across contrasting environmental conditions, rather than being chosen entirely at random. For example, sampling included the relatively flat valley floor as well as slopes on both sides of the valley to incorporate different elevation, slope and aspect measures. Including north- and south-facing slopes was particularly important because aspect can influence factors such as solar radiation, temperature and moisture, creating different microclimatic conditions. By selecting environmentally distinct but accessible locations, we could measure a representative range of woodland across Carrifran whilst keeping the distance between plots logistically tractable.

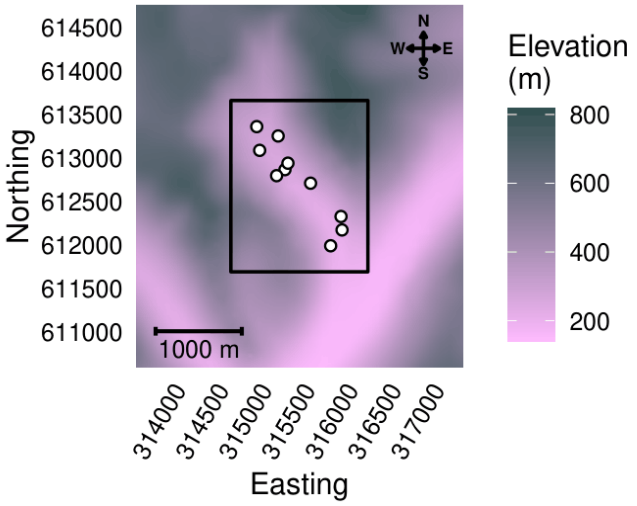

Figure 3: Carrifran Wildwood Elevation Model and Plot Locations

2.2 Measuring Forest Structure

All trees with their stem base included within the 10m circular radius plot (+ 50 cm to account for GPS error) were counted in the survey. The coordinates of each tree stem were recorded to <6 cm accuracy using a differential GPS (Emlid Reach RS3 paired rover and base station setup), which easily allowed individual trees to be distinguished, as well as enabling accurate matching to remote sense layers. For measuring canopy height as a characteristic of vertical structural heterogeneity, a 5m tape measure was used to accurately measure any trees below 3m. For any trees exceeding 3m, height was visually estimated by two independent observers as a multiple of the 1.8m Emlid rover pole. Trees were identified to species level based on distinctive features such as leaf shape, bark colour and texture, and fruit, by observers with prior training in tree identification. Within each plot, the trees were measured in a diagonal pattern and per quarter of the circular area, to reduce the risk of any individuals being overlooked.

3. Results

3.1 Tree abundance and density

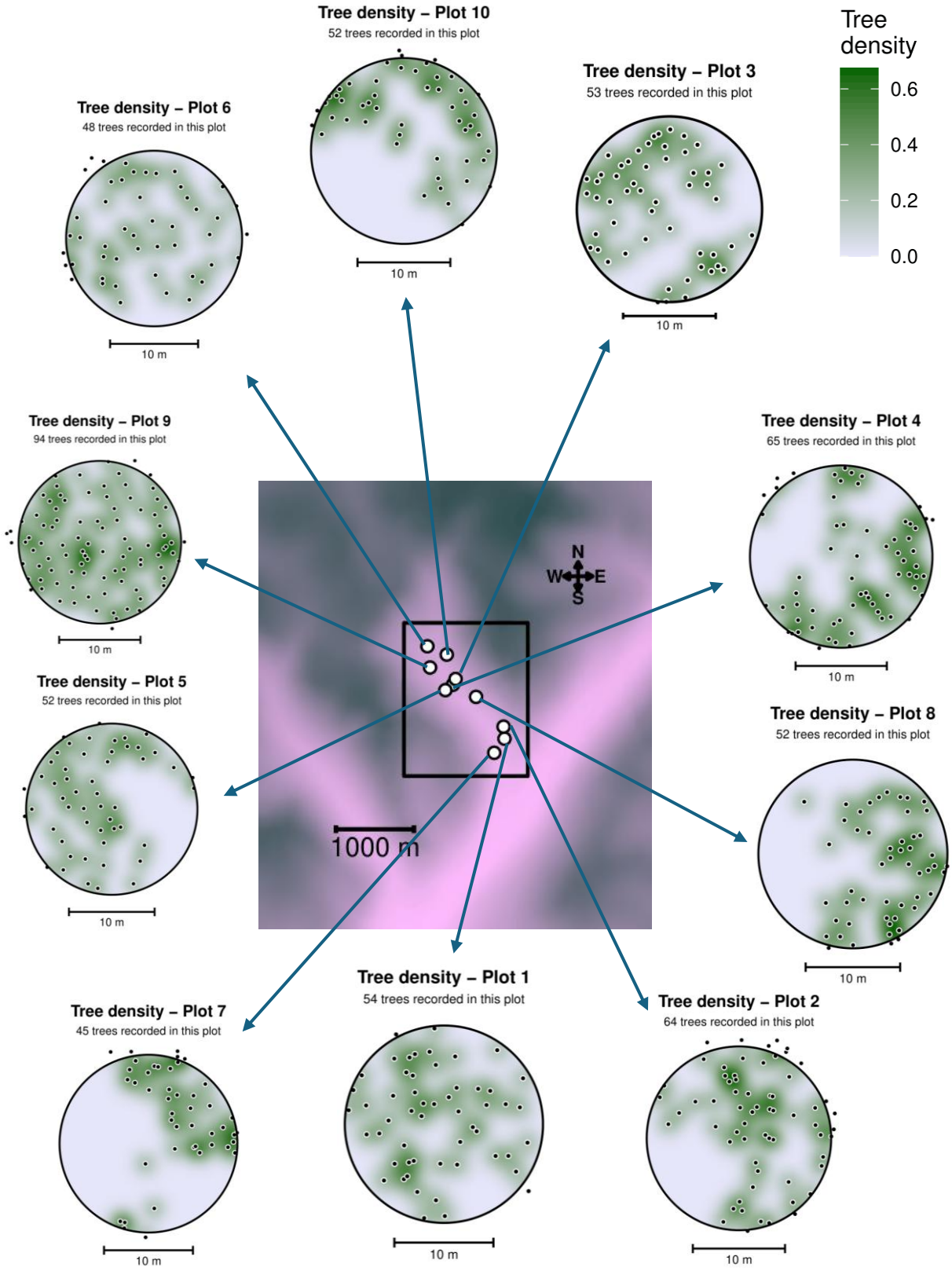

Figure 4: Density heat maps of the 10 tree plots analysed across Carrifran Wildwood

Across the 10 plots, tree density ranged from 45 – 94 trees per 10m radius, with a mean of 57.9 ± 14.1 trees, giving a value per hectare as 1,300 – 2,714 trees. This is similar to the estimated mean average number of trees per hectare in European planted forests, which Lee et al (2023) determined was between 1844 – 2038 trees. Tree abundance was particularly greatest at Plot 9, which is situated on a north-facing slope, and trees were recorded all throughout this plot. However, other north-facing plots such as 5 and 7 did not have as high numbers of trees recorded. Plot 7 had the lowest number of trees present too, followed by plot 6 on the north-western area of the valley. Plots located on south-facing slopes (10, 3, 8, 2, 1) tended to exhibit lower tree abundance in this sample. However, the limited sample size and influence of other environmental variables such as soil moisture and light intensity that were not measured during this study mean that this pattern may not be due to aspect alone. This is similar for plot 4, which although having the second highest number of trees in the plot (65) cannot directly indicate that the valley floor provided more favourable growing conditions for the trees growing there. Regardless of location, slope and topography, tree distribution appeared spatially clustered with only a few outliers, rather than in an even spread within each plot.

3.2 Tree species composition

Figure 5 shows the number of species present and how dominant they are within each plot. The total number of tree species recorded across all 10 plots was 17, with most plots supporting 4-6 species of tree, demonstrating variation in species composition across the 10 plots. The mean species richness per plot was 5.5, with Plot 5 and 7 having 8 species per plot, representing the greatest species richness that was recorded. They both had a north-facing slope location in common, similarly to plots 3, 6 and 10 which had the highest northing values, but also all had only 4 species present.

Plot 1 was dominated in equal amounts by Downy Birch (*Betula pubescens*) and Oak (*Quercus* spp.), previously mentioned as the most distinctly common woodland type at Carrifran Wildwood. This was also seen at Plot 3, 5 and 10, although with plot 3 and 10 there was greater dominance of *Betula pubescens*. This shows that *Betula pubescens* and *Quercus* spp. were common components of the forest composition across most of the plots, although their relative abundance differed.

Alder (*Alnus* spp.) was another common species found at many plots, particularly in Plot 9, 6 and 2. Plot 9, which contained the highest tree abundance recorded, was primarily dominated by *Alnus* spp., contrasting with other plots where *Betula pubescens* and *Quercus* spp. made up a greater proportion of the trees present. Willow (*Salix* spp.) was found in half of the plots sampled (2, 4, 5, 8, 9), with Goat Willow (*Salix caprea*) being the most dominant, followed by Eared Willow (*Salix aurita*) which was particularly abundant in plot 2, and then Grey Willow (*Salix cinerea*). These results suggest that despite some species being widely distributed across the study area, their abundance varied between plots. Ash (*Fraxinus excelsior*) was found in plot 7, making up almost half of the trees found there but nowhere else.

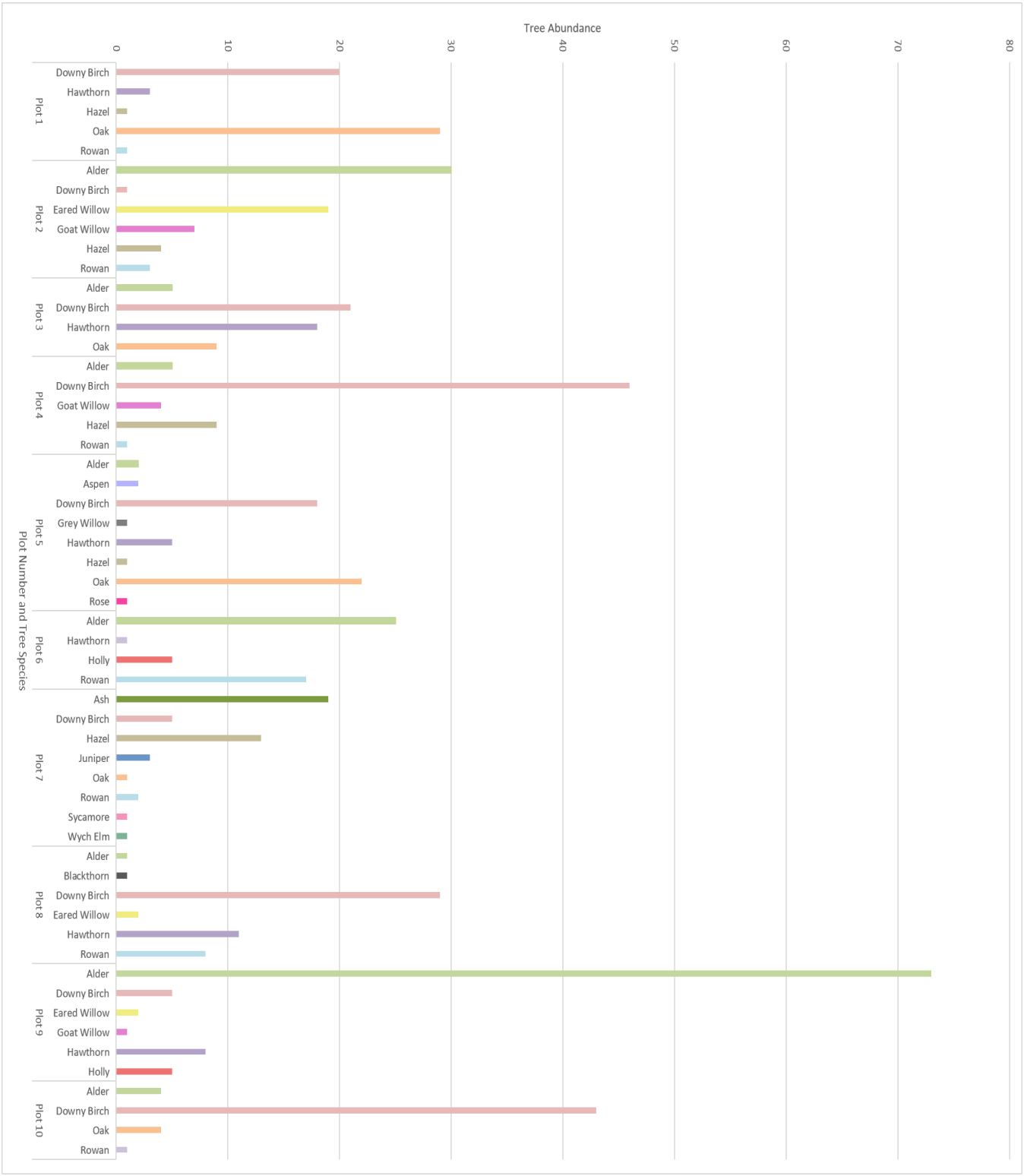

Figure 5: Species richness and composition of tree plots

Therefore plot 7 can be seen as differing considerably in composition from the other plots, despite supporting the greatest number of species in conjunction with Plot 5. Plots 4, 9 and 10 showed stronger species dominance (*Betula pubescens* for 4 and 10, and *Alnus* spp. for 9), whereas the other plots exhibited a more even composition where 2-3 species were found in similar proportions, with a few more sparse vegetation types also found too. The most common species overall was *Betula pubescens*, and the least abundant being Wych Elm (*Ulmus glabra*).

Table 1: Summary Statistics for Tree Plots

Plot	Number of Trees Per Plot	Species Richness	Mean Tree Height	Maximum Tree Height
1	54	5	4.08	8.00
2	64	6	6.12	11.00
3	53	4	3.84	8.00
4	65	5	2.11	4.00
5	52	8	2.67	8.85
6	48	4	2.17	4.00
7	45	8	6.19	11.00
8	52	5	5.21	9.50
9	94	6	2.92	5.00
10	52	4	6.61	9.50

3.3 Woodland structural complexity

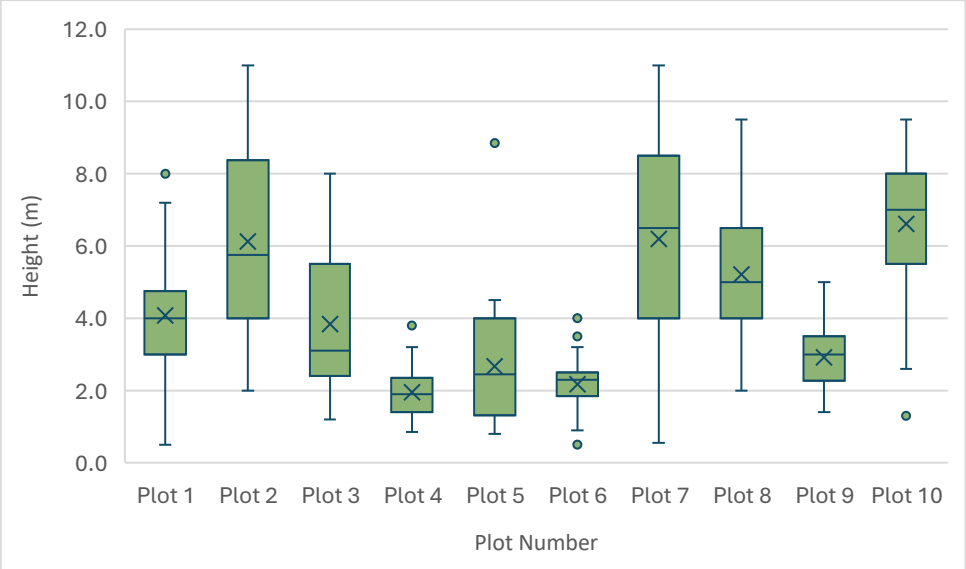

Figure 6: Box plots showing height variation across tree plots, including median, minimum and maximum height and interquartile ranges.

Figure 6 shows how height varied across the 10 tree plots, demonstrating differences in the distribution and variation of tree heights between plots. Plots 2, 7, 8 and 10 had the greatest maximum and median tree heights recorded within, however they also showed some of the greatest variation in height shown through larger interquartile ranges – particularly plot 7. This indicates that these plots had greater vertical height heterogeneity between trees. On the other hand, plot 4, 5 and 6 showed the smallest variation in height, but had the shortest mean and median tree heights per plot. The height distributions for these plots were therefore more uniform in comparison with other plots such as Plot 7. Half of the plots (1, 4, 5, 6, 10) also contained outlying tree heights that were more than 1.5 times the interquartile range either above the third quartile or below the first quartile, indicating that there were individual trees which were substantially taller or shorter than the remaining trees present in their plot. Overall, variation in tree height was observed across all 10 plots, with some having relatively consistent height distributions and others showing much more variation. However, plots with increased species such as plots 5 and 7 with 8 species present were not always more structurally heterogeneous, as despite Figure 6 showing plot 7 had the most variation in tree heights, plot 5 had much less variation and was more similar to the box plots for plot 3 and 10, which each only had 4 species present.

4. Discussion

Through Figures 4-6, the results indicate that there is variation in both forest composition and structure across the plots at Carrifran, as opposed to its neighbouring "control" valley Blackhope, which remains unforested due to extensive herbivore grazing with effectively zero tree species present. This suggests that different areas may provide contrasting habitat conditions, which previous research indicates can contribute to greater microhabitat and microclimatic variation through creating structural and compositional heterogeneity, with possible benefits for biodiversity. However, this is an implication rather than a demonstrated outcome at Carrifran, as microclimate measurements were not directly recorded in this study and our only measurement of biodiversity was of tree diversity.

The results also suggest that woodland restoration should not be solely assessed from tree abundance or density, particularly when considering biodiversity. Despite plots 2, 4 and 9 containing a relatively high numbers of trees (*Figure 4*), they did not necessarily exhibit the greatest variation in tree height. This implies that although dense regeneration can contribute to substantial vegetation recovery, it may not create the vertical heterogeneity associated with more structurally complex woodland. Therefore, this is an important consideration when considering how to gauge restoration success as other features such as vertical distribution of vegetation should also be included, rather than only referring to tree cover or abundance which may overlook important differences in woodland structure.

Differences in species composition may also help explain some of the variation observed between plots. *Betula* spp. and *Alnus* spp. were dominant within several plots with relatively high tree abundance, which may reflect differences in establishment and growth between species. However, these patterns may not be only due to species-specific growth

characteristics, and could also be heavily influenced by planting history, subsequent competition or environmental conditions such as slope aspect. For example, some sample plots situated on north-facing slopes (Figure 4) typically had greater tree abundance compared to south-facing slopes, which may be partly attributed to lower solar radiation received in the northern hemisphere and therefore a more humid microclimate which can increase soil fertility (Sewerniak, 2016).

Through recording tree species, the data also allows us to determine the woodland's current successional stage. The dominance of species such as *Betula pubescens* in several plots may be consistent with early stages of woodland development, while the presence of *Quercus* spp. indicates the potential for further compositional change as established models of temperate woodland succession suggest that early-successional species can be outcompeted by later-successional species over time (Gough et al, 2021). But as this study was conducted at a single point in time, it cannot yet definitively predict how the woodland at Carrifran develops, however this data can be compared to future studies to determine changes in the relative abundance of *Betula* spp, *Quercus* spp and other species, which will depend on a multitude of factors over time such as local regeneration, competition, natural disturbance, herbivory and seed availability. Such changes in forest composition and canopy development may also alter local microclimatic conditions, particularly if denser canopies form by buffering understorey temperatures to a greater degree (Zellweger et al, 2019).

Microclimate is mostly driven by the interactions between vegetation structure, topography and hydrology. However, unlike topography and to an extent, hydrology, vegetation structure can be significantly changed and improved through restoration work, making the development of heterogenous forest structure an important mechanism that may contribute to stabilised microclimates and increased microrefugia diversity under climate change.

Woodland succession may also influence biodiversity by altering habitat conditions over time, as changes in canopy cover and vertical structure create new niches which may benefit later-successional species, but reduce the habitat area suitable for early-successional or open-habitat species. Therefore, it is important that increasing woodland maturity is not always assumed to always improve species diversity. The rate and area of natural woodland expansion through passive rewilding is often dependent on the availability of seed sources and dispersal distance. Murphy et al (2022) found that distance away from seed banks found in existing woodland is a key limiting factor of natural colonisation, with oak trees being unable to colonise further than 75 metres from woodland and most happening within a 20 metre radius, whilst Spracklen et al (2013) found that colonisation of birch trees could occur up to 100 metres away. These differences may influence future spatial distribution of species tree species in an area as large as 660 hectares such as Carrifran, and reinforces the need for active planting prior to, in addition to sometimes alongside, natural colonisation when restoring woodlands.

The development in forest structure and composition at Carrifran demonstrates the potential value of combining active and passive restoration processes, leveraging the benefits

of both. Initial work to plant trees and exclude herbivores allowed trees to establish across the site, and subsequent rewilding has contributed to expansion of woodland and changes in species composition. With planted woodland, Hughes et al (2026) found that canopy height and vertical complexity was higher, whereas natural colonisation was better for biodiversity due to the slow process of succession, resulting in more complex habitat heterogeneity. Furthermore, Broughton et al (2021) found that passive rewilding is effective at expanding native woodland once seed sources have been established at a low cost and relatively short term too, with each stage of succession offering valuable habitats for biodiversity. Therefore by utilising both approaches at Carrifran, this may have led to the current heterogeneous forest conditions observed across the sampled plots, however this study alone cannot determine the individual impact of each method on these patterns.

4.1 Methodological Limitations

Some limitations were present within this study, such as the small number of plots to represent Carrifran Wildwood as a whole. Although this was done due to time constraints, it increases the risk of overgeneralisations when drawing conclusions, or incorrect extrapolations due to the reduced ability to accurately determine the strength of the relationships between forest structure and composition with microclimatic factors. Subsequently, the patterns observed from the selected plots may require further data to be definitive. By only using Carrifran as the area of study, the observations about forest composition and structure cannot be assumed to represent other rewilded sites, as management history, ecological restoration work and approaches to herbivores and public access may significantly affect results. As the study was only conducted at a single time-point during early August, the results do not show the breadth of woodland conditions across the year and any temporal changes in structure and composition. For example, seasonal changes in canopy cover due to foliage differences may slightly change which plots looked to have the tallest trees or greatest variation over the course of the year, which were not accounted for. Visual estimations of height for trees beyond 3m introduced human error. However, each estimation was agreed upon by 2-3 observers and by using a known pole length for comparison, this attempted to reduce the error when recording tree heights. Whilst the lack of primary microclimate data collected at each sample site presents a limitation, these can be modelled from vegetation structure or input later.

Consequently, our results should be interpreted as evidence of variation in forest composition and structure at Carrifran, with the potential implications for microclimate and biodiversity supported by existing literature conducted in temperate forests rather than directly demonstrated by the data gathered from this fieldwork.

4.2 Broader Limitations and Challenges for Rewilding Approaches

Despite the success of rewilding observed at Carrifran Wildwood, there are still some limitations that should not be ignored. As initial actions to rewild an area are still mostly

driven by humans, it risks being subject to pre-existing assumptions about how an area can be transformed, such as which historical ecological baseline to restore it to. Furthermore, the lack of short-term goals due to the natural unpredictability of how an ecosystem responds and the rate at which it is restored means that it can be difficult to gauge success with our current idea of what success looks like. This may mean it is more difficult to attract funding which often hinges on proof of short-term changes that rewilding projects may not always adhere to, as they are more flexible than traditional conservation projects (Blythe & Jepson, 2020).

4.3 Future Research

Firstly, this study would benefit from pairing vegetation structure data with microclimate measurements by using temperature or humidity dataloggers to test the buffering hypothesis directly, and biodiversity indicators to gain direct insight into the strength of the relationship between compositional and structural heterogeneity, microclimate and biodiversity, rather than inferring from academic literature. With more time, it would be beneficial to incorporate pre-restoration data at Carrifran and compare with the data collated during this study, in addition to conducting repeat samplings across multiple rewilding sites of different ages to study in broader detail how forest composition and structure changes after rewilding strategies are implemented. Comparing these changes with comparison sites would also help determine to what extent is rewilding responsible for observed changes. Whilst some drone data was collected to gain aerial imagery of the tree plots, ultimately due to adverse weather conditions the images gathered were not sufficient in volume to incorporate into structural complexity analyses, as this data would be able to provide more information about features such as crown area, gap sizes, and more accurate tree heights.

These approaches would improve understanding of whether heterogeneous forest development can offer essential microclimatic buffering and biodiversity resilience under continued climate change, which is only expected to worsen in severity (Kintisch, 2009).

5. Conclusion

This study reveals widespread variation in tree abundance, species composition and vertical height structure across the sampled plots at Carrifran Wildwood. In particular, tree abundance did not consistently result in increased vertical height heterogeneity, suggesting that simple measures of vegetation recovery may not be sufficient when evaluating the structural development of restored woodland. The observed differences in forest composition and vertical structure through tree heights indicates that Carrifran's woodland has developed heterogeneously, which existing literature suggests would have an impact on local light, temperature and moisture conditions. Most of the current literature analysing how vegetation structure changes with rewilding often uses satellite data that is too coarse to detect finer differences and changes in structure and composition, which this study was able to do with more detail as measurements were taken from the ground. Although these were not measured directly in this study, previous research in temperate forests shows this may have possible

positive influence on microclimatic variation and the diversity of microrefugia, which is increasingly crucial for species not yet adapted to climate change. Further long-term data collection for forest structure, microclimate and biodiversity measurements would be necessary to determine how these relationships develop over time and whether the heterogeneity observed is sufficient at contributing to ecological resilience.

Therefore, the methods of active restoration to establish woodland via intentional tree planting and fences to prevent herbivory, in conjunction with passive rewilding, has created heterogeneous conditions by influencing light availability, temperature and moisture.

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