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RESEARCH ARTICLE

Deer activity limits tree recruitment in woodland creation sites

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Abstract

1. Natural regeneration and tree recruitment are essential for woodland persistence, but deer browsing can disrupt these processes. Browsing impacts are well recognised, yet how local and landscape-scale drivers shape regeneration, recruitment and herbivore pressure over time remains poorly understood.
2. Using a space-for-time approach, we assessed how regeneration, deer activity, browsing damage and tree recruitment vary over time at 82 woodland creation sites across England and Scotland. We used structural equation modelling to test the effects of local and landscape-scale drivers on these processes in England.
3. Regeneration and tree recruitment rates were significantly higher in England than Scotland. Both countries showed similarly low numbers of successive young tree growth stages, with sapling (51–150 cm) and juvenile (151–200 cm) counts being ~5% and 0.7% of seedling (≤50 cm) counts, respectively.
4. Woodland structural attributes influenced deer activity and browsing damage, both being higher in woodlands with lower basal area and greater structural heterogeneity. Browsing damage was also higher in smaller and denser woodlands but was not directly related to deer activity, indicating that woodland structure better predicts deer browsing than deer activity alone.
5. Despite this, deer activity strongly inhibited tree recruitment, with evidence of recruitment failure above an activity threshold of 2 deer plot^{-1} day^{-1}. Unexpectedly, browsing damage facilitated tree recruitment, possibly by reducing competition.
6. Regeneration declined with woodland age, but age had no consistent effect on deer activity, browsing damage or tree recruitment. Low regeneration and recruitment in 81–170-year-old woodlands suggests suppressed understorey regrowth.
7. *Synthesis and applications*. Deer activity and browsing damage in woodland creation sites can be reduced through targeted management of structural attributes. Small, dense, structurally heterogeneous woodlands with low basal area are most vulnerable to deer impacts. To ensure continuous tree recruitment, localised deer activity should be minimised, while avoiding complete exclusion to maintain facilitative

browsing effects. These actions offer practical means to safeguard ecosystem function and woodland longevity.

KEYWORDS
deer damage, ecosystem function, forestry, habitat restoration, herbivory, natural regeneration, ungulate, wildlife management

1 | INTRODUCTION

Over the last three centuries, extensive global deforestation and habitat degradation (Williams, 2003) have contributed to increasing global carbon emissions (IPCC, 2023) and accelerated biodiversity loss (IPBES, 2019). Growing awareness of these threats has prompted large-scale reforestation and habitat restoration efforts aimed at countering forest loss by rapidly increasing tree cover. When properly planned, these initiatives can effectively increase carbon sequestration and provide habitats that support threatened species, ecosystem function and resilience (Holl & Brancalion, 2020).

In the United Kingdom (UK), woodland area has increased from a historic low of 4.7% in the early 20th century to a current figure of 13.5% (Forest Research, 2024), driven largely by targeted efforts to establish new woodland cover (i.e. woodland creation; Harmer et al., 2015). Commitments to further expand woodland cover, including a target of 16.5% total land area in England by 2050 (Environment Act, 2021), seek to continue this positive trend. These commitments reflect ambitions to drive long-term nature recovery, enhance climate resilience and halt biodiversity declines. To achieve these goals, newly created woodlands must be capable of supporting the biodiversity and ecological processes characteristic of natural woodland ecosystems. However, evaluating the long-term effectiveness of woodland creation for ecosystem and biodiversity restoration is challenging due to the difficulties of experimentation over sufficiently large spatial and temporal scales. To overcome this challenge, the Woodland Creation and Ecological Networks (WrEN) project (Watts et al., 2016) uses a large-scale natural experiment and space-for-time approach (Pickett, 1989), where woodlands of different ages are compared to infer biodiversity responses to long-term woodland creation.

As new woodlands age, they progress through a sequence of development stages characterised by distinct structure and growth patterns (Franklin et al., 2002; Oliver & Larson, 1996). New woodlands first enter a stand initiation stage, where high light availability and limited competition allow young trees to establish and grow. As canopies close, woodlands enter a stem exclusion stage, where competition for light and resources suppresses understorey growth and reduces stem density. Over time, tree mortality creates canopy gaps that increase light availability, enabling renewed young tree growth and greater structural complexity; this stage is known as understorey re-initiation (Franklin et al., 2002; Oliver & Larson, 1996). Progression through these stages depends on successful natural regeneration, whereby mature trees produce seed that germinates and establishes new seedlings, ensuring woodland longevity through continual replacement of mature trees.

Regenerating trees provide an attractive food source for ungulates, which browse woody shoots and leaves (Venter et al., 2019). A recent national assessment found that, despite highly patchy distributions, deer have increased in both range and occurrence across Britain, with distribution models suggesting continued expansion (Croft et al., 2019; Mathews et al., 2018). Elevated browsing pressure associated with these increases has contributed to widespread forest degradation, with 40% of Britain's forest stands considered to be in unfavourable condition (Ditchburn et al., 2020). This pressure is likely to persist or intensify without targeted management. Over-browsing by deer in mature woodlands is known to inhibit natural regeneration, reduce biodiversity, and simplify woodland structure (Gill & Fuller, 2007; Gill & Morgan, 2010). Structurally complex woodland creation sites, characterised by a greater diversity of tree sizes, support higher abundance and diversity across multiple taxa (Fuentes-Montemayor et al., 2017; Fuentes-Montemayor et al., 2020; Fuller et al., 2018; Waddell et al., 2024). There is therefore growing concern that deer browsing may drive structural simplification in newly created woodlands, preventing them from developing into biodiverse and self-sustaining ecosystems (Fuentes-Montemayor et al., 2021), and limiting the contribution of woodland creation to biodiversity and nature recovery policy goals (Environment Act, 2021).

Several reviews of wild ungulate impacts have found that high ungulate densities compromise woodland diversity, structure and function, with regeneration inhibited past a tipping point of 4–5 large deer or 10–25 roe deer (*Capreolus capreolus*) per km^2 (Eichhorn et al., 2017; Putman et al., 2011; Ramirez et al., 2018). Browsing can stunt tree growth and cause mortality (Gill & Beardall, 2001), reducing the number of saplings that survive to grow above the browse line (c. 1.5–2 m) and recruit into the mature stand (Ramirez et al., 2018; Rhodes et al., 2018). High deer densities suppress recruitment in ancient European forests, creating demographic bottlenecks (Bond, 2008; Churski et al., 2017; Kuijper et al., 2010). Despite evidence of high, spatially localised deer densities and browsing pressure across the UK (Mathews et al., 2018; Putman et al., 2011), comparable impacts have not yet been assessed in woodland creation sites.

Deer foraging behaviour and damage are influenced by local and landscape-scale woodland attributes, including structure, configuration and surrounding land use (Borowski, Bartoń, et al., 2021; Ohse et al., 2017; Schwegmann, Hendel, et al., 2023). As woodlands age and develop, these attributes change, which can alter the attractiveness of a woodland to deer over time with consequences for browsing pressure, tree recruitment and woodland structural development (Reimoser, 2003). Woodland structure can affect browsing damage as unmanaged broadleaved woodlands with lower tree densities and diverse age classes experience higher levels of damage (Spake et al., 2020), potentially constraining stand development. Landscape context can also influence deer behaviour, with roe deer activity patterns and habitat use varying in response to combinations of surrounding agricultural crop type, phenology and landscape cover (Rigoudy et al., 2024). Similarly, the extent of broadleaved forest cover can increase or decrease deer damage depending on the interacting effects of regional deer densities, climate and perennial cover (Spake et al., 2020), highlighting the context-dependent effects of landscape variables on deer behaviour. Herbivore browsing is also affected by tree species palatability (Borowski, Gil, et al., 2021), which is influenced by digestibility, toxicity, and condition (Armstrong et al., 2023) and has implications for species-specific recruitment success. A combination of local and landscape-scale attributes therefore influences deer impacts through direct effects on deer activity and browsing damage, and indirect effects on tree recruitment and woodland structure. Further investigation is needed to disentangle the interacting drivers and pathways through which deer pressure shapes tree recruitment in woodland creation sites. Answering these questions will clarify long-term deer impacts on ecosystem function and help prioritise management interventions to ensure the value and longevity of newly created woodlands.

The WrEN project site network spans gradients of local and landscape-scale attributes, including woodland size, age and surrounding land-use cover (Watts et al., 2016). This presents an opportunity to investigate how variation in these attributes influences regeneration, deer activity, browsing damage and ultimately tree recruitment in woodland creation sites over time. To address these aims, we used both generalised linear mixed models (GLMMs) and structural equation modelling (SEM). GLMMs tested temporal and regional variation in regeneration, deer activity, browsing damage, and tree recruitment, while SEM assessed the direct and indirect effects between local and landscape-scale woodland attributes. This integrated approach allowed us to explore the ecological processes and causal pathways underlying observed relationships. Findings from this study are intended to inform woodland management practices that support woodland longevity and ecosystem function. Our study addresses the following research questions:

1. How does regeneration, deer activity, browsing damage and tree recruitment in woodland creation sites change over time?
2. How do local and landscape-scale attributes drive regeneration, deer activity, and browsing damage, and how do these factors impact tree recruitment in woodland creation sites?

2 | MATERIALS AND METHODS

2.1 | Study design

Following a systematic site selection process, 82 woodland creation sites were selected for inclusion in this study, located across the midlands of England (35 sites) and central Scotland (47 sites) (Figure 1a). These sites form part of the WrEN project network (Watts et al., 2016) and vary in age (20–170 years at the time of this study), size (0.5–32 ha) and surrounding landscape composition. The resulting chronosequence spans gradients of multiple local and landscape-scale attributes (Table S1; see Watts et al. (2016) for further site selection details). Sites are located in typical lowland agricultural landscapes and are >1 km from each other. Based on prior knowledge, sites with high livestock densities were excluded to minimise interference with camera traps and confusion between deer and livestock browsing impacts; some sites were excluded for other logistical reasons (e.g. human interference). Excluded sites were not spatially clustered and did not represent distinct combinations of site or landscape attributes compared to those included.

2.2 | Woodland and landscape attributes

Woodland age, size and surrounding landscape composition were recorded for each study site. Site age was estimated from the earliest appearance of each woodland patch on digital scans of Ordnance Survey historical land-use maps (1840s–1990s; Ordnance Survey/EDINA: http://digimap.edina.ac.uk). Based on age, woodlands were categorised into development stages of stand initiation (0–30 years; $n=24$), stem exclusion (31–80 years; $n=22$) or understorey re-initiation (81–170 years; $n=36$), as per Oliver and Larson (1996). Woodland size was calculated in hectares (ha) using ArcGIS Desktop 10 (Advanced licence, http://www.esri.com). The proportions of surrounding land with broadleaved woodland cover and agricultural cover (comprising arable and improved grassland) were calculated within buffers from study woodland edges (buffer distances: 100, 250, 500, 1000, 1500, 2000, 2500, 3000 m). Spatial analysis was carried out using the *Simple Features* (Pebesma, 2018) and *Raster* (Hijmans, 2023) packages in R Statistical Software (v4.2.1; R Core Team, 2023). See Appendix S1 for more detail on how these variables were calculated.

2.3 | Vegetation surveys

Local attributes relating to woodland structure, regeneration and deer impacts were recorded at the plot level. Two circular 20 m diameter survey plots were established in representative locations within each woodland, with a minimum distance of 25 m between plot edges and 10 m from woodland edges (Figure 1b). Each plot contained three 3 × 3 m square subplots (six subplots per woodland).

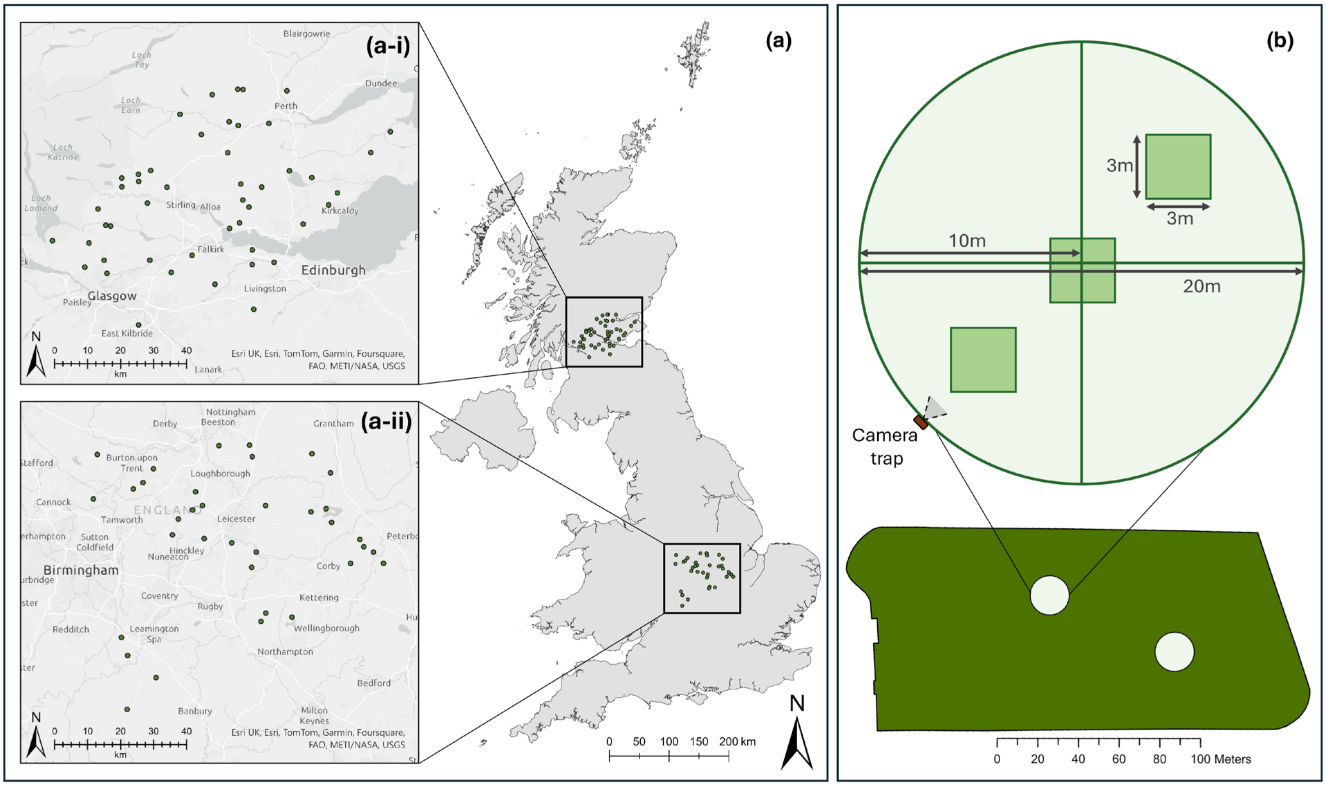

FIGURE 1 (a) Location of woodland creation study sites within the (a-i) Scotland ($n=47$) and (a-ii) England ($n=35$) WrEN study landscapes. (b) Example position of two 20 m diameter survey plots within a woodland. United Kingdom digital boundary source: Office for National Statistics licensed under the Open Government Licence v.3.0. Contains OS data © Crown copyright and database rights 2025 OS AC0000814847.

2.3.1 | Woodland structure

Within each plot, tree diameter at breast height (DBH; 1.3 m above the ground) and species were recorded for each mature tree (≥2 m tall & ≥7 cm DBH), and total tree basal area and standard deviation of DBH (SD DBH) were calculated. Individual stems of multi-stemmed trees were recorded separately if they branched below 1.3 m. Tree SD DBH reflects variability in tree sizes and provides a measure of structural heterogeneity. Canopy cover was measured as a proportion (0–1) using the CanopyCapture mobile app (Patel, 2018), with measurements taken at 1 m above the ground. Plot-level canopy cover was calculated as the mean of subplot measurements.

2.3.2 | Regeneration and recruitment

Within subplots (Figure 1b), all seedlings (≤50 cm tall), saplings (51–150 cm tall), and juvenile trees (151–200 cm tall) were identified to species level and counted. Juvenile trees were assumed to have grown sufficiently tall to escape ungulate browsing to their lead shoot (Ramirez et al., 2018) and were considered to have been successfully recruited. Stem counts were summed across subplots and divided by combined subplot area ($27\,\mathrm{m}^2$) to calculate densities of seedlings, saplings, and juveniles (stems m^{-2}). Stems were counted as individuals if they emerged independently from the ground.

2.3.3 | Browsing impacts

Regeneration and browsing damage were assessed in August–September 2022 to capture cumulative browsing impacts following the main growing season. Each seedling and sapling recorded was systematically assessed for browsing damage, which was noted as a binary variable (1 = damage present, 0 = absent). Stems were considered browsed if the apical meristem of the leading or sub-leading branches had been removed by herbivory. Plot-level browsing damage was calculated as the proportion of browsed seedlings and saplings across the three subplots. A community-weighted mean palatability score was calculated for each plot based on the abundance and palatability of recorded seedling, sapling, and juvenile tree species (Table S2) using the Woodland Herbivore Impact Assessment (WHIA) palatability index (range 1–6; Armstrong et al., 2023). The WHIA is a method of assessing and monitoring the impact of large herbivores on habitats that are wooded or may develop woodland. Species not listed in the palatability index were assigned indicative scores by an expert (Dr Robin Gill). Plots with no stems present were assigned a palatability score of 0; these zeros represent true absence and were not treated as missing values. Exceptionally rare tree species (≤15 counts across all sites) not listed in the palatability index were excluded from calculations as they account for a negligible proportion of available forage.

TABLE 1 Summary of deer observations recorded by camera traps at survey plots in England ($n = 69$) and Scotland ($n = 90$).

	England			Scotland		
Deer species	Detections	Counts	Activity	Detections	Counts	Activity
Fallow (*Dama dama*)	448	592	0.156	–	–	–
Muntjac (*Muntiacus reevesi*)	1118	1165	0.308	–	–	–
Red (*Cervus elaphus*)	11	15	0.004	123	145	0.031
Roe (*Capreolus capreolus*)	824	910	0.240	2638	2953	0.622
Sika (*Cervus nippon*)	48	60	0.016	–	–	–
Unidentified deer	931	999	0.264	668	720	0.152
Combined species	3380	3741	0.989	3429	3818	0.804
Total trap effort	3784			4751		
Mean trap effort per plot	54.8			52.8		
Trap effort range	21–65			26–126		

Note: Detections = number of 3-image bursts in which deer were present; counts = total number of deer observed across all bursts; trap effort = number of days cameras were operational across sites; activity = total deer counts divided by trap effort (deer plot^{-1} day^{-1}).

2.4 | Deer activity monitoring

Deer activity was recorded at each plot (Figure 1b) using camera trap data collected from an associated mammal monitoring project (unpublished data). Plots in Scotland were monitored between June–October 2020 (24 sites) or 2021 (23 sites), and plots in England between June–October 2022 (35 sites). Camera traps (Browning Spec Ops Advantage (BCT-8A)) were set ~50 cm above the ground and positioned so the field of view covered as much of the plot as possible. Cameras were configured to take three-photo bursts upon triggering, with a 1-min delay between subsequent triggers (see Table S3 for a full list of camera settings used). One camera was rotated between the two survey plots every 4 weeks, with each plot monitored for two 4-week periods. This resulted in 8 weeks of monitoring per plot (16 weeks per woodland). Monitoring periods occasionally deviated from the planned schedule due to logistical constraints, resulting in variation in trap effort among plots (Table 1). Camera placement was consistent to ensure the same field of view was covered on subsequent deployments (Figure 1b). The number of deer detections, obtained from camera trap images, was used to quantify plot-level deer activity. Deer activity was defined as the average number of deer of any species detected by a camera per day (deer plot^{-1} day^{-1}) and indicates the potential browsing pressure exerted by deer on each plot over the survey period. Deer activity was not separated by species to ensure sufficient sample sizes and statistical power. Some livestock and lagomorph (rabbit (*Oryctolagus cuniculus*) and hare (*Lepus europaeus*)) activity were also recorded on camera traps, but preliminary analysis showed no significant effects on browsing damage or tree recruitment, so they were not considered further (Table S4). Due to camera trap disturbance, data from five plots (one in England, four in Scotland) were excluded, with 159 plots from 82 sites retained for analyses.

The work conducted in this study was approved by the University of Stirling's Animal Welfare and Ethical Review Body (Ref: 7949 for camera trapping surveys) and the General University Ethics Panel (Ref: 10624 for herbivory impacts surveys). No additional licences or permits were required for this work.

2.5 | Statistical analysis

2.5.1 | Temporal and regional variation in regeneration, deer impacts and tree recruitment

Regeneration dynamics and woodland structure were expected to vary across woodland development stages (Oliver & Larson, 1996), with potential consequences for deer activity, browsing damage, and tree recruitment. To test the effects of woodland development stage on these variables, we fitted generalised linear mixed models (GLMMs) using the *glmmTMB* package (Brooks et al., 2017) in R Statistical Software (v4.3.2; R Core Team, 2023). The effect of country was also investigated to test for any regional variation in these variables across distinct UK study regions. The interaction between woodland development stage and country was included to test whether stage-related patterns differed between regions. Models included woodland stage, country, and their interaction as fixed effects, with woodland identity as a random effect. If the interaction was non-significant, models were refitted to test the main effects independently. Seedling, sapling, and juvenile tree counts, and deer activity were modelled using a negative binomial distribution, while browsing damage was modelled using a binomial distribution. Post-hoc pairwise comparisons between development stages and country were conducted using estimated marginal means (EMMs) via the *emmeans* package (Lenth, 2025). *P*-values were adjusted for multiple testing using Holm's correction.

2.5.2 | Drivers of regeneration, deer impacts, and tree recruitment

A structural equation modelling (SEM) approach was used to investigate how local and landscape-scale attributes influence regeneration, deer activity, browsing damage, and ultimately tree recruitment (number of juvenile trees 151–200 cm tall) in our study sites. SEM is a multivariate approach that explores causal relationships within a system by testing both direct and indirect effects between variables in complex models. Local and landscape-scale attributes hypothesised to affect the process of woodland tree recruitment, based on ecological knowledge, were used to construct a metamodel (Figure 2). Given the very low tree recruitment, our primary response variable in the SEM, at the Scottish sites (only 14 juvenile trees recorded across 90 survey plots; Figure 3; Table S2) we considered that the Scottish data contributed very limited information on this response, which could limit the reliability and interpretability of model outputs. SEM analysis was therefore restricted to the England dataset, where higher recruitment allowed more robust estimation of relationships. The *piecewiseSEM* package (Lefcheck, 2016) in R was used to test the hypothesised relationships between variables derived from the metamodel (Figure 2). The package identifies missing paths via significant residual correlations between unlinked variables.

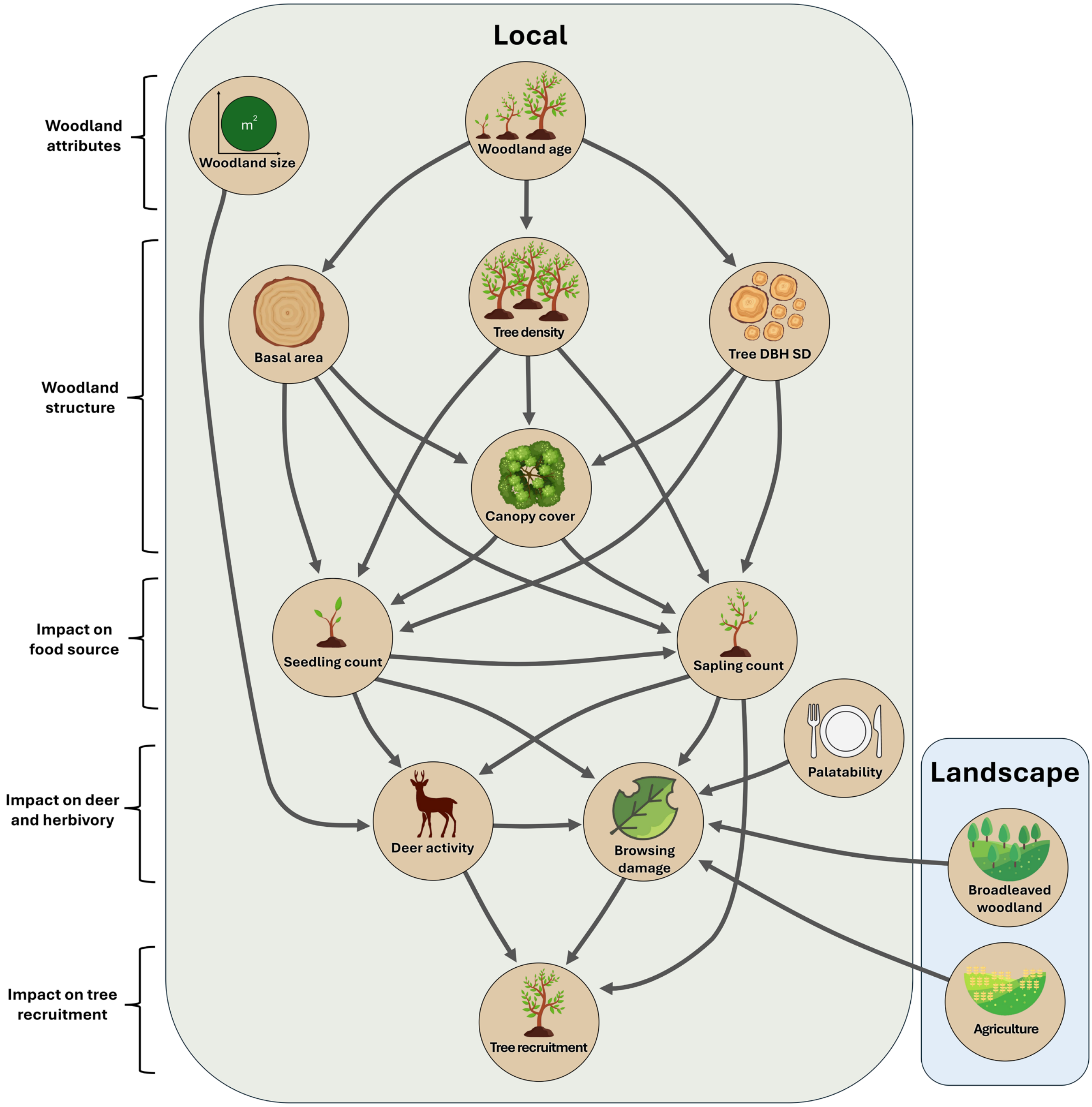

FIGURE 2 Structural equation metamodel showing hypothesised a priori causal pathways by which local and landscape-scale attributes drive tree recruitment in woodland creation sites. Full details on variable selection are provided in Appendix S1.

These were included as directed paths in the SEM where a causal relationship was considered ecologically plausible within the hypothesised causal framework; otherwise, they were modelled as correlated errors (Table S5). A 500 m buffer distance was selected as the most appropriate spatial scale for both landscape variables, following preliminary modelling (see Appendix S1 for further details on SEM variable selection).

The SEM comprised nine component GLMMs, each including site identity as a random effect to account for the non-independence of plots within woodlands. Deer activity was modelled as counts per plot per day (deer plot^{-1} day^{-1}) using a negative binomial distribution, and tree recruitment (juvenile tree counts) was modelled using a Poisson distribution. Seedlings, saplings, and juvenile trees were modelled as counts rather than densities to allow the use of standard count-based distributions such as Poisson and negative binomial (see Appendix S1 for full specifications of all component models). SEM model fit was assessed using Fisher's C and chi-square statistics, with $p > 0.05$ indicating good fit. Significant ($p < 0.05$) and marginally significant ($0.05 \le p < 0.1$) paths between variables were identified from the SEM output, and standardised path coefficients were used to assess the strength of these relationships. Total effects of all variables on each response variable were also calculated from the standardised coefficients (Table S6), representing the sum of direct and indirect effects, with indirect effects calculated as the product of path coefficients along mediating pathways.

3 | RESULTS

3.1 | Regeneration and recruitment in developing woodlands

Across our 82 woodland creation sites, we recorded a total of 36 tree species, with 33 species present as mature trees, 13 as juvenile trees, 21 as saplings, and 25 as seedlings (Table S2). Total numbers of seedlings, saplings, and juvenile trees recorded were approximately four times higher in England than in Scotland (Figure 3; Table S2). The proportional distribution of young tree growth stages was similar between countries, with saplings and juvenile trees representing approximately 5% and 0.7% of seedling counts, respectively (Figure 3).

We found no significant interaction between woodland development stage and country (Table S7) but significant independent effects of development stage on seedling, sapling and juvenile tree counts, and of country on seedling and sapling counts (Table S8). We found significant regional differences in regeneration (seedling and sapling counts) and tree recruitment (juvenile tree counts; Figure 4a–c), with higher mean densities of seedlings, saplings, and juvenile trees recorded across all woodland stages in England than in Scotland (Table S1). Mean seedling density was 4.44 seedlings m^{-2} in England (95% CI: 3.02–5.86) versus 0.78 seedlings m^{-2} in Scotland (0.52–1.05). Saplings averaged 0.2 saplings m^{-2} (95% CI: 0.12–0.29) in England versus 0.04 saplings m^{-2} (0.018–0.07) in Scotland. Mean juvenile tree density was 0.03 trees m^{-2} (95% CI: 0.01–0.04) in England versus 0.01 trees m^{-2} (0.002–0.01) in Scotland.

Post-hoc testing revealed significantly higher seedling (Figure 4a; Table S9) densities in England than in Scotland during stand initiation (0–30 years; Figure 4a). Juvenile tree densities were also higher in England than in Scotland during understorey re-initiation (81–170 years; Figure 4c). In England, seedling densities were significantly higher during stand initiation than during stem exclusion (31–80 years) or understorey re-initiation (Figure 4a). No significant differences were found in seedling densities across stages in Scotland, or in sapling and juvenile tree densities in either country (Figure 4a–c; Table S9).

3.2 | Deer activity and browsing in developing woodlands

Total survey effort across the 82 study sites was 8535 trap days (Table 1). The most frequently detected deer species were muntjac (*Muntiacus reevesi*) in England and roe (*Capreolus capreolus*)

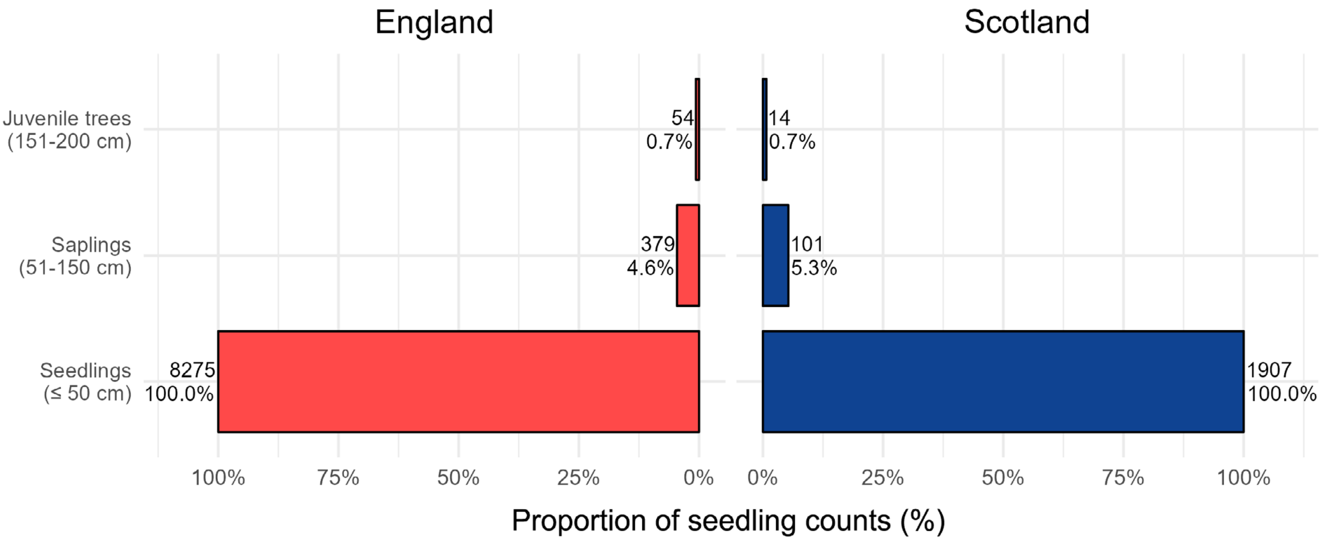

FIGURE 3 Numbers of young trees across seedling, sapling, and juvenile tree growth stages from 35 woodlands (69 plots) in England and 47 woodlands (90 plots) in Scotland. Bar labels show total counts within each stage and proportions relative to seedling counts for each country.

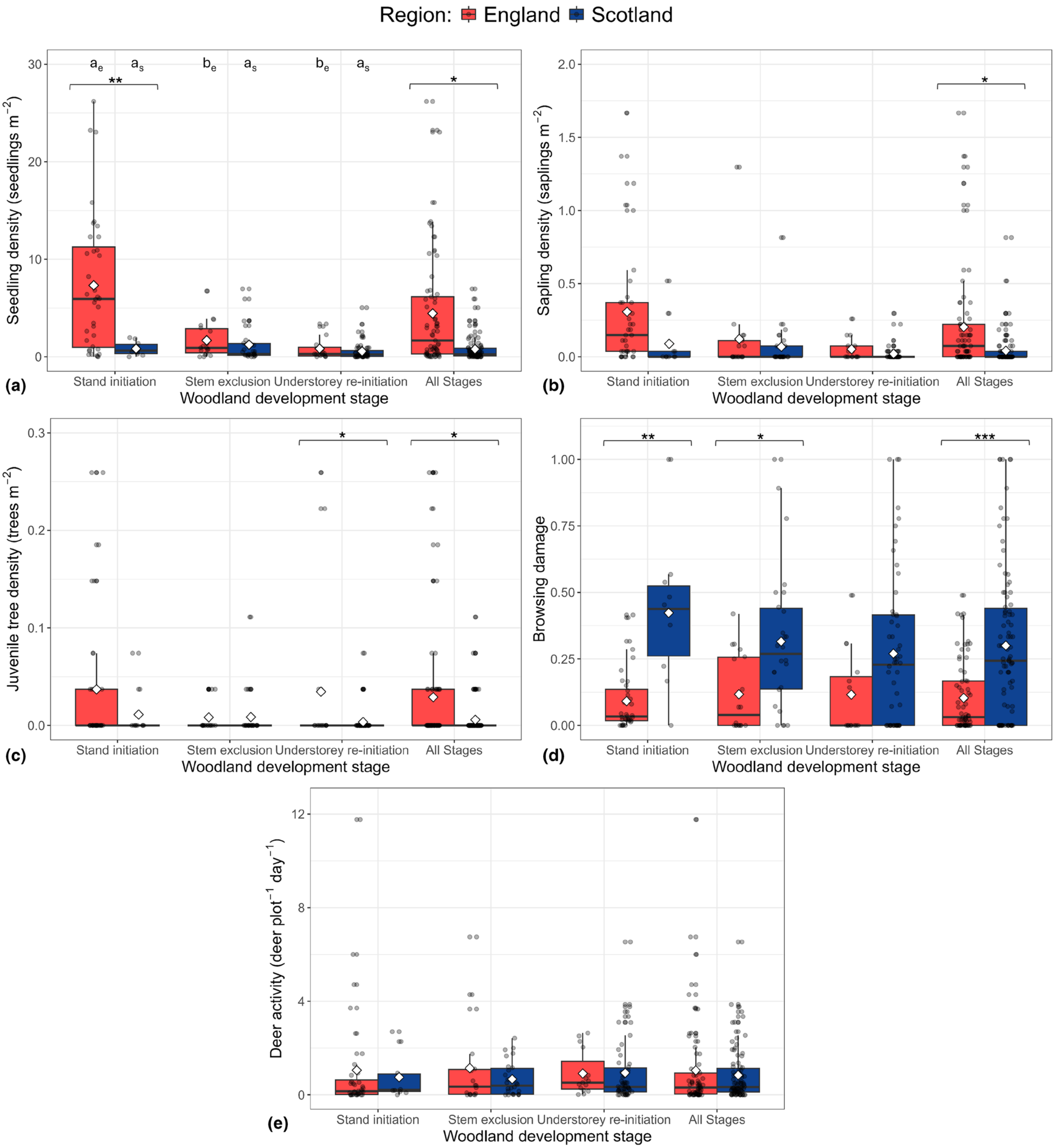

FIGURE 4 Differences in (a) seedling density, (b) sapling density, (c) juvenile tree density, (d) browsing damage (proportion of seedlings and saplings browsed) and (e) deer activity at 35 woodlands (69 plots) in England and 47 woodlands (90 plots) in Scotland, grouped by development stages: Stand initiation (0–30 years), stem exclusion (31–80 years) and understorey re-initiation (81–170 years). Asterisks indicate significant pairwise differences between countries (*$p<0.05$, **$p<0.01$, ***$p<0.001$). Country-level differences across combined stages were tested using likelihood ratio tests. Differences between countries within specific stages were tested using post-hoc comparisons of estimated marginal means. Different letters denote significant differences between stages within each country based on post-hoc testing ($p<0.05$). Subscripts indicate country ($_e$ = England, $_s$ = Scotland); letters should only be compared within the same subscript. The absence of letters indicates no significant differences between stages within a country.

in Scotland (Table 1). Deer activity varied among plots, ranging from 0 to 11.76 deer plot^{-1}day^{-1} in England and 0 to 6.54 deer plot^{-1}day^{-1} in Scotland (Table S1). Deer activity also varied between successive monitoring periods at the same camera locations, with median absolute differences of 0.24 deer plot^{-1}day^{-1} in England (interquartile range = 0.00–0.83) and 0.29 in Scotland (interquartile range = 0.05–0.69). Within each country, deer activity and browsing damage did not differ significantly between woodland development stages (Figure 4d,e; Table S9). Browsing damage was significantly higher in Scottish woodlands than in English woodlands during stand initiation and stem exclusion (Figure 4d), whereas deer activity did not differ between countries across development stages (Figure 4e; Table S9).

3.3 | Drivers of natural regeneration

As expected, woodland structure developed with age, with older sites having higher basal area and structural heterogeneity (SD DBH) but lower tree density (Figure 5; Table S10). Seedling counts were lower (marginally significant) in older woodlands with higher basal areas, and age had an indirect negative effect on sapling counts, mediated through seedling counts and woodland structure. Sapling counts were higher in larger woodlands and where there were more seedlings (marginally significant).

Woodland age had the strongest total negative effect on seedling counts (effect size: −0.674; Table S6), while woodland size had the strongest total positive effect on sapling counts (effect size: 0.181).

3.4 | Drivers of deer activity and browsing damage

Seedling and sapling counts were not associated with variation in deer activity. Browsing damage was also not associated with deer activity but instead was associated with woodland structural attributes (Figure 5; Table S10). Both browsing damage and deer activity were higher in woodlands with lower basal area and greater heterogeneity in tree size (SD DBH; Figure 5). Browsing damage was additionally higher in smaller woodlands, those with higher tree density, and with more saplings. We found no detectable effects of landscape-scale attributes on deer activity, browsing damage, or any other response variable (Figure 5a; Table S10).

Based on total effects (Table S6), structural heterogeneity (SD DBH) had the strongest positive effect on deer activity (effect size: 0.503), while tree density had the strongest total positive effect on browsing damage (effect size: 0.522). While woodland age did not have a direct effect on deer activity or browsing damage (Figure 5), it had indirect effects mediated through woodland structure and regeneration, resulting in a positive total effect on deer activity (effect size: 0.212) and a small total negative effect on browsing damage (effect size: −0.042).

3.5 | Drivers of tree recruitment

In both England and Scotland, no juvenile trees were recorded at plots where average deer activity exceeded two deer detections per plot per day (Figure 6). In England, juvenile tree counts declined with increasing deer activity, whereas no relationship was evident in Scotland (Figure 6), likely due to the very low number of recruited trees available to detect an effect. SEM analysis for England showed that deer activity strongly suppressed tree recruitment (Figure 5; Table S10). Surprisingly, tree recruitment in England was higher at sites with higher browsing damage. Woodland structural attributes influenced tree recruitment indirectly, via effects on deer activity and browsing damage (Figure 5; Table S10).

Deer activity had the strongest total negative effect on tree recruitment (effect size: −0.874; Table S6). Woodland age did not directly affect recruitment but had a small positive total effect (effect size: 0.047).

4 | DISCUSSION

In this study, we used a large-scale natural experiment design and a space-for-time approach to show that tree recruitment success in woodland creation sites is shaped by deer activity and browsing damage but ultimately driven by interacting effects of local-scale woodland attributes. These findings provide insights for targeting management interventions that influence woodland successional trajectories and support the longevity and ecological function of woodland creation sites. While our structural equation model identified multiple interacting pathways, non-significant relationships should be interpreted as a lack of evidence rather than evidence of no effect, given the complexity of the system and modest sample size.

4.1 | Poor woodland regeneration and tree recruitment over time

Across our study sites, we found proportionally low numbers of young trees within successive growth stages, with only ~5% of seedling counts present at sapling stage and just 0.7% present as juvenile trees. These low proportions suggest low survival rates of young trees, an issue identified as a research priority under projected climate change (König et al., 2022). This pattern is especially concerning in Scotland, where regeneration and recruitment were significantly lower than in England, raising concerns over the long-term persistence of these woodlands.

While the causes of this regional variation remain unclear, potential explanations include differences in climate, growing season length, soil nutrient availability (Churski et al., 2017) and regional variation in deer species distributions and population densities (Mathews et al., 2018). Given the consistently low recruitment observed in Scotland, targeted deer exclusion or protection trials could

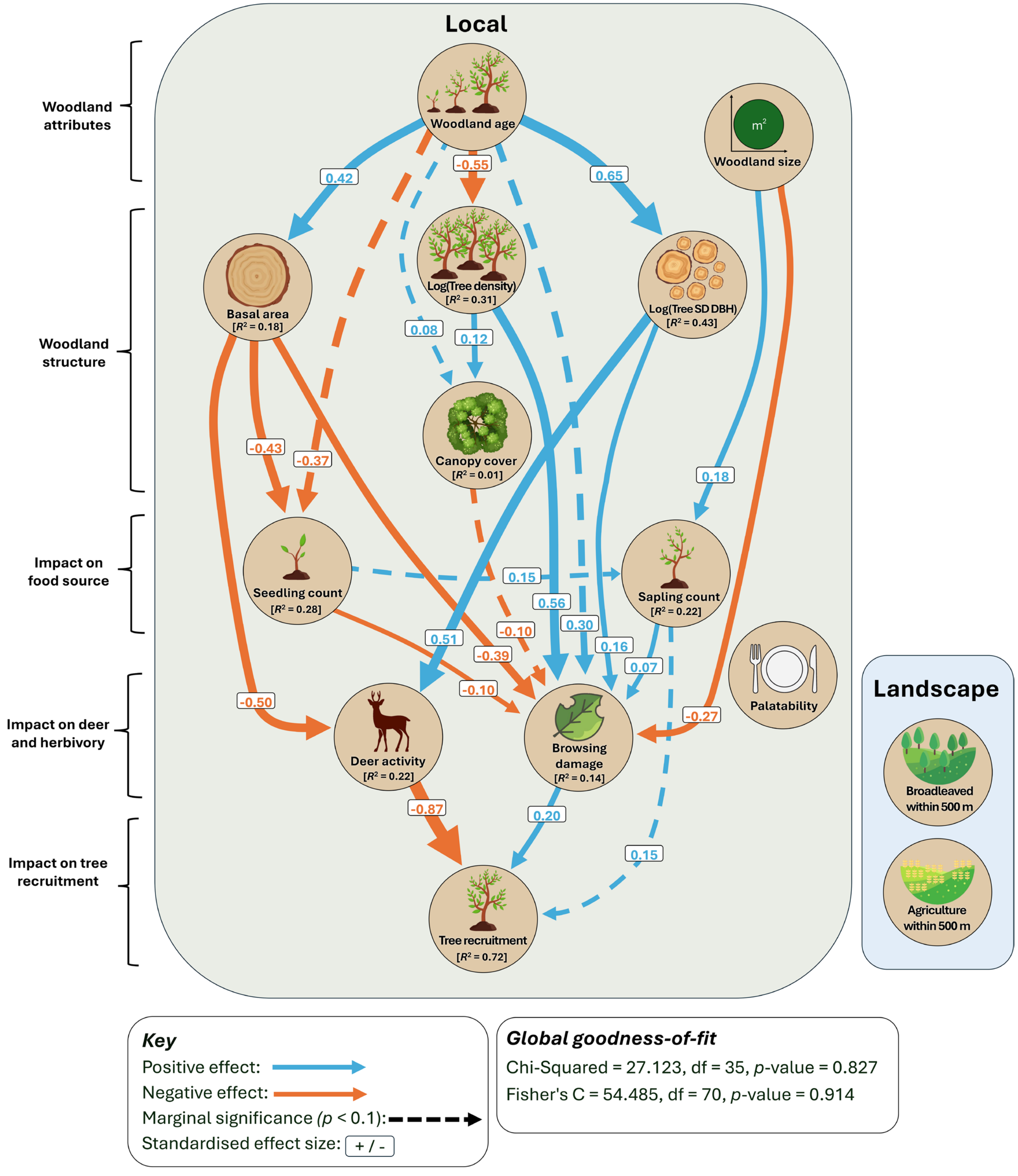

FIGURE 5 Structural Equation Model showing the effects of local and landscape-scale drivers on regeneration, deer activity, browsing damage and tree recruitment in 35 woodlands (69 plots) in England.

help determine the relative influence of browsing pressure versus other environmental constraints on tree recruitment.

Regeneration (seedling and sapling densities) declined with woodland age, and we found no evidence of renewed young tree growth expected in older woodlands (81–170 years) during the understorey re-initiation stage (Oliver & Larson, 1996). Our findings support previous observations from the WrEN site network that many older woodland creation sites lack a distinct understorey layer of regenerating trees (Fuentes-Montemayor et al., 2021). Together, these patterns suggest that successional development

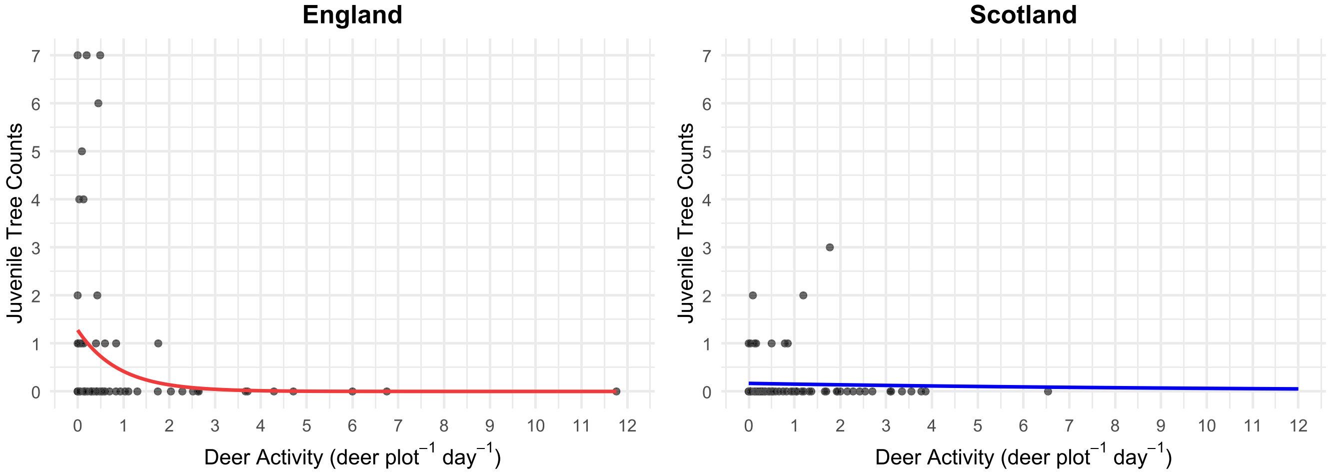

FIGURE 6 Relationship between deer activity and juvenile tree (151–200 cm) counts recorded in 35 woodlands (69 plots) in England and 47 woodlands (90 plots) in Scotland. Fitted curves represent negative binomial regression lines. Axes are held constant across panels to aid comparison, and fitted lines are shown across the full axis range (0–12); in Scotland, maximum observed deer activity was 6.54 deer plot^{-1} day^{-1}, compared to 11.76 deer plot^{-1} day^{-1} in England.

may be suppressed in woodland creation sites, potentially limiting their long-term biodiversity and ecosystem benefits. Sustained ungulate pressure in temperate woodlands is widely documented to result in reduced regeneration and understorey growth (Eichhorn et al., 2017; Ramirez et al., 2018), suggesting that the risk of interrupted successional development is not unique to woodland creation sites.

Although canopy cover had no detectable effect on regeneration in this study, a broader absence of canopy gaps, resulting from a lack of management or natural disturbance (Seaton et al., 2025), may nonetheless limit light availability and suppress tree regeneration and recruitment potential. The national decline in woodland management may exacerbate these effects by increasing shading (Seaton et al., 2025) and exposure to deer damage (Spake et al., 2020). In contrast, the use of natural processes to establish new woodlands (Bauld et al., 2023) often results in more canopy gaps (Hughes et al., 2026), potentially facilitating greater light availability, understorey regeneration, and alternative successional trajectories.

4.2 | Woodland structure drives deer activity and browsing damage

We found no detectable direct relationship between deer activity and browsing damage, indicating that deer presence alone is a poor predictor of browsing in woodland creation sites. Browsing appears to be selective, rather than increasing consistently with deer density or activity as reported in previous studies (Borowski, Gil, et al., 2021; Putman et al., 2011; Rhodes & St. Clair, 2018). Instead, our results support evidence that impacts on broadleaved woodlands are context-dependent (Spake et al., 2020), driven by variation in woodland attributes that influence attractiveness to deer (Reimoser, 2003) and result in spatially heterogeneous impacts (Ramirez et al., 2018). Variation in deer activity between camera monitoring periods at the same plots may also have reduced the detectability of a direct relationship between activity and browsing damage by contributing to cumulative impacts that do not align with daily activity estimates.

Local-scale woodland attributes exerted a stronger influence on deer activity and browsing damage than woodland age, as neither response varied significantly across age-related woodland development stages. Deer activity and browsing damage were higher in woodlands with lower basal area and greater structural heterogeneity, consistent with evidence that deer prefer to forage in stands with low tree volumes and greater variation in tree size (Spake et al., 2020). Such conditions may offer greater foraging opportunities due to diverse understorey vegetation (Waddell et al., 2024). Browsing damage was additionally higher in smaller woodlands, with higher tree density and more abundant saplings, highlighting the importance of these attributes in shaping local browsing pressure.

Together, these results indicate that woodland structural characteristics can be used to identify sites where deer activity and browsing are most likely to constrain woodland development, and which can be modified through management interventions to reduce attractiveness to deer. However, such interventions involve trade-offs, as structurally heterogenous woodlands typically have high biodiversity value and structural modification may have unintended negative consequences for other woodland taxa (Fuentes-Montemayor et al., 2017, 2020; Fuller et al., 2018; Waddell et al., 2024). In this study, we found no evidence that landscape-scale attributes influenced deer activity or browsing damage, in contrast to previous findings (Rigoudy et al., 2024; Spake et al., 2020). We also found no evidence that seedling and sapling counts influenced deer activity, which may reflect temporal mismatches between pulses of regeneration and fluctuating deer populations. In contrast, browsing damage increased with sapling abundance, indicating that while small-scale food availability may not influence habitat use in fragmented forest ecosystems (Schwegmann, Hendel, et al., 2023), it can shape localised browsing behaviour. The greater nutritional value of saplings makes them a preferred food source (Ohse et al., 2017), and therefore more susceptible to disproportionate browsing damage (Borowski, Gil, et al., 2021; Kuijper et al., 2010).

Woodland size further influenced browsing damage, with lower damage observed in larger woodlands, despite no detectable difference in deer activity. Browsing damage can increase where deer experience higher competition for resources (Borowski, Gil, et al., 2021), with concentrated browsing pressure in smaller woodlands leading to intensified local damage (Kay, 1993; Moore et al., 1999). The abundant and diverse vegetation supported by larger woodlands (Waddell et al., 2024) may dilute browsing pressure on regenerating trees (Gaudry et al., 2022; Schwegmann, Mörsdorf, et al., 2023) by allowing deer to satisfy nutritional needs faster (Moser et al., 2006; Ohse et al., 2017). In England, larger average woodland size and higher regeneration, driven largely by abundant, highly palatable ash (*Fraxinus excelsior*; Table S2), may have contributed to this dilution effect, helping to explain the substantially lower mean browsing damage observed (10%) compared to Scotland (30%). This interpretation is supported by our SEM results, which showed that larger woodland size and higher seedling counts were associated with reduced browsing damage, independent of landscape-scale forage availability.

Differences in deer species composition may also contribute to regional variation in browsing damage. Roe deer, the most frequently detected species in Scotland, are primarily browsers rather than grazers and can cause high impact on seedlings and saplings (Armstrong et al., 2023). The more diverse deer assemblage in England, including large proportions of muntjac, roe and fallow, may have mitigated damage to regenerating trees through varied diets that include higher proportions of non-woody vegetation. This variation in species composition may also contribute to within-country heterogeneity in browsing damage, although species-specific effects were not explicitly assessed in this study. Muntjac preference for structurally complex environments (Chapman, 2021; Hemami et al., 2005) may also help explain the positive association between structural heterogeneity and deer activity and browsing damage observed here. Although other herbivores can influence browsing dynamics, preliminary analyses indicated no detectable effects of livestock or lagomorph activity in this study. Woodlands with consistently high livestock pressure may experience different browsing dynamics, but such conditions were intentionally under-represented in this study.

4.3 | Tree recruitment is suppressed by deer activity but aided by browsing

Our results show that deer activity (deer plot^{-1}day^{-1}) has a strong negative effect on tree recruitment in English woodland creation sites. Across both England and Scotland, no juvenile trees were recorded at plots where average deer activity exceeded 2 deer plot^{-1}day^{-1}, indicating a critical upper threshold, beyond which recruitment fails. Below this threshold, lower deer activity was associated with increased tree recruitment, with the highest and most consistent recruitment occurring at very low deer activity (~0.5 deer plot^{-1}day^{-1}). The critical upper threshold (2 deer plot^{-1}day^{-1}) identified here is similar to the 2.5 deer (*Odocoileus* spp.) or elk (*Cervus canadensis*) camera^{-1}day^{-1} critical recruitment threshold reported in regenerating aspen forests in North America (Rhodes et al., 2018). Our findings support existing evidence that high ungulate densities can negatively impact forest diversity, function, and structure (Eichhorn et al., 2017; Kuijper et al., 2010; Ramirez et al., 2018) and demonstrate that newly created woodlands are similarly vulnerable to ungulate impacts documented in mature woodlands. By constraining tree recruitment, high deer activity may limit the long-term development of woodland creation sites (Fuentes-Montemayor et al., 2021), with implications for biodiversity value, climate resilience and wider policy objectives.

The inhibition of tree recruitment by deer activity found in this study was not directly explained by browsing damage. Instead, suppressed recruitment may result from the cumulative effects of deer presence, including browsing pressure in combination with trampling and soil compaction, which can limit young tree establishment (Ramirez et al., 2018). Contrary to previous findings that browsing damage negatively impacts tree recruitment (Churski et al., 2017; Rhodes et al., 2018), our results show that low-intensity browsing (mean proportion of seedlings and saplings browsed in England = 10%, range: 0%–49%) is associated with higher recruitment. This relationship may reflect underlying environmental conditions that promote successful recruitment but also attract deer browsing to regenerating trees and may therefore be partly mediated by sapling densities. Higher sapling counts were associated with both increased browsing damage and (marginally significant) increased tree recruitment. While high sapling densities attract higher browsing pressure, which can stunt growth and create demographic bottlenecks (Bond, 2008), some saplings may escape browsing and reach recruitment height (>150 cm), where resource availability allows (Churski et al., 2017). Additionally, selective removal of stems through browsing may reduce competition in dense sapling stands, thereby promoting the growth of surviving individuals.

Browsing may also indirectly promote tree recruitment by suppressing competitive non-woody vegetation, such as bramble (*Rubus fruticosus agg*.), which can outcompete regenerating trees under low browsing pressure (Harmer et al., 2005; Laurent et al., 2017; Seaton et al., 2025). However, dense bramble can also facilitate the growth of fast-growing tree species by protecting them from browsing (Harmer et al., 2010), indicating that the interaction between browsing and bramble cover may depend on the tree species present. Understorey dynamics are further shaped by canopy composition and disturbance. The prevalence of ash trees in the canopy, and the impacts of ash dieback (caused by the fungus *Hymenoscyphus fraxineus*), are also key drivers of understorey vegetation dynamics in British woodlands (Combes et al., 2024; Seaton et al., 2025). Ash dieback kills many infected young trees before they reach maturity (Combes et al., 2024), potentially explaining the low number of juvenile ash trees recorded relative to ash seedlings and saplings in this study. At the same time, canopy gaps created by ash mortality increase light availability, creating opportunities for tree regeneration and promoting greater ground-flora richness (Seaton et al., 2025). Deer interact with these disturbance-driven changes by suppressing bramble and other generalist shrubs but also by directly inhibiting young tree growth. Together, these interacting pressures shape woodland successional trajectories: while ash dieback may increase opportunities for regeneration, whether these translate into successful recruitment will depend primarily on deer activity and browsing intensity (Lettenmaier et al., 2025).

4.4 | Management implications and recommendations

We identified several interacting local-scale drivers that influence deer activity and browsing damage through different pathways, with both processes having distinct effects on tree recruitment success. Managing these drivers can help to shape woodland development and support long-term restoration goals in woodland creation sites. The recommendations outlined below are primarily informed by relationships identified in English woodland creation sites. Given the regional differences in regeneration and recruitment dynamics and deer impacts identified here, management priorities may differ in Scotland. Based on our findings, we recommend the following:

- To prevent tree recruitment failure and disrupted ecosystem function, minimise localised deer activity through targeted control measures, aiming to keep levels below 2 deer $\text{plot}^{-1}\,\text{day}^{-1}$. Substantially lower activity levels (<0.5 deer $\text{plot}^{-1}\,\text{day}^{-1}$) are likely required to maximise tree recruitment potential.
- Use deer activity as a simple, coarse indicator of likely tree recruitment success in newly established woodlands.
- Consider that complete deer exclusion (e.g. fencing) may remove low-intensity browsing, which was associated with higher tree recruitment in this study, and that alternative measures to reduce deer activity may be favourable.
- Prioritise protection or targeted management of woodlands that are dense, structurally heterogeneous, and have low basal area, as these conditions attract higher deer activity.
- If reducing browsing damage is a priority, focus interventions on smaller woodlands with low basal area, high sapling and tree densities, and greater structural heterogeneity, where browsing damage is most concentrated.
- In older woodlands, management should focus on supporting natural regeneration and recruitment, including reducing deer activity where required, to facilitate effective understorey re-initiation and long-term woodland persistence.

AUTHOR CONTRIBUTIONS

Elisa Fuentes-Montemayor, Kirsty J. Park and Kevin Watts conceived the ideas; Elisa Fuentes-Montemayor, Kirsty J. Park, Kevin Watts and Robin Gill designed the methodology; Matt Guy calculated landscape metrics; Josh Weaver and Matt Guy collected camera trap data; Josh Weaver and Erika Tonhauser collected vegetation data; Eleri Kent collated camera trap data; Emily H. Waddell advised on statistical analysis; Josh Weaver carried out statistical analysis; Josh Weaver led the writing of the manuscript; all authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

Authors report no conflict of interest in this study. Elisa Fuentes-Montemayor is an Associate Editor of *Journal of Applied Ecology* but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

Data available from DataSTORRE: Stirling Online Repository for Research Data: http://hdl.handle.net/11667/274 (Weaver et al., 2026).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Variable selection and model specification for Structural Equation Model (SEM).

Table S1. Summary statistics for each of the 14 variables included in the Structural Equation Model, and number of woodlands and survey plots, split by country and woodland development stages of stand initiation (0–30 years), stem exclusion (31–80 years) and understorey re-initiation (81–170 years).

Table S2. Tree species identified in survey plots in 35 English woodlands (69 plots) and 47 Scottish woodlands (90 plots), split into development categories of mature tree (≥2 m tall & ≥7 cm DBH), juvenile tree (151–200 cm tall), sapling (51–150 cm tall) and seedling (≤50 cm tall). For mature multi-stemmed trees, individual stems were counted separately if branching occurred below 1.3 m. Palatability scores taken from Woodland Herbivore Impact Assessment Method User Guide (Armstrong et al., 2023). Original palatability score scale has been reversed so that more palatable species have higher scores; 6 = most palatable, 1 = least palatable. Asterisks indicate palatability scores assigned by an expert (Dr Robin Gill) for species that were not included in the original table. Tree species with no palatability score were not found in the original WHIA table and either were not recorded at seedling, sapling or juvenile growth stages, or records were too rare (≤15 total counts) to warrant assigning a score.

Table S3. Settings used for camera traps (Browning Spec Ops Advantage, model BCT-8A).

Table S4. Results from generalised linear mixed models (GLMMs) testing the effect of different herbivores on browsing damage (proportion of seedlings and saplings browsed) and tree recruitment (count of juvenile trees 151–200 cm tall). Each model included woodland identity as a random effect, with fixed effects for deer, lagomorph, and livestock activity (detections $\text{plot}^{-1}\,\text{day}^{-1}$). Lagomorphs include European rabbit (*Oryctolagus cuniculus*) and European hare (*Lepus europaeus*); livestock includes domestic cattle (*Bos taurus*), goats (*Capra hircus*), horses (*Equus caballus*) and sheep (*Ovis aries*). Browsing damage was modelled using a binomial error distribution. Tree recruitment was modelled with a Poisson error distribution.

Table S5. Full list of missing paths suggested by *piecewiseSEM* during model specification that were not included in the original hypothesised SEM metamodel (Figure 2 in main text). Each path was evaluated for ecological plausibility and either incorporated as a directed relationship where a causal direction could be justified or modelled as a correlated error where no defensible causal direction could be specified.

Table S6. Total effects between variables in the structural equation model for England. Total effects represent the sum of direct and indirect effects derived from standardised path coefficients, with indirect effects calculated as the product of coefficients along mediating pathways. For each response variable (columns), the strongest total effect is highlighted in bold.

Table S7. Likelihood ratio tests comparing generalised linear mixed models (GLMMs) with and without the age (woodland development stage) × country interaction term for each response variable. For each variable, models with and without the interaction term were compared using a likelihood ratio test (Chisq). AIC values are shown for both models. Values of $p < 0.05$ indicate that the interaction term significantly improves model fit. Seedling, sapling, juvenile tree count and deer activity models were fit using a negative binomial distribution and browsing damage model using a binomial distribution. All models included woodland identity as a random effect. Model assumptions were checked using simulated residuals in the *DHARMa* package (Hartig, 2024).

Table S8. Likelihood ratio tests for the main effects of age (woodland development stage) and country on each response variable, from generalised linear mixed models (GLMMs) fitted with a random effect of woodland identity. Seedling, sapling, juvenile tree count and deer activity models were fit using a negative binomial distribution and browsing damage model using a binomial distribution. For each variable, the significance of age and country was tested by comparing models with and without each effect. p-values <0.05 indicate a significant effect of age or country on the response variable. Model coefficients are reported for the levels of age (stem exclusion and understorey re-initiation) and country (Scotland), including estimates, standard errors, z-values, and p-values.

Table S9. Post hoc comparisons of estimated marginal means between age (woodland development stage) classes within each country and between countries within each age class, resulting in nine pairwise contrasts per response variable. Significance tests were performed on the log scale, with Holm's adjustment for multiple comparisons applied across a family of nine tests. Estimates are reported as ratios of geometric means.

Table S10. Model output from Structural Equation Model testing local and landscape-level drivers of tree recruitment at 69 plots within 35 woodland creation sites in England. Standardised Estimate = standardised path coefficients in Figure 5 of the main text. DF = degrees of freedom. Marginal R^2 values are given for each component model.

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