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RESEARCH ARTICLE

Optimizing opportunities for oak woodland expansion into upland pastures

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Abstract

1. Woodland expansion is widely advocated for the mitigation of climate change and its impacts. This is supported by ambitious targets for increasing tree cover in the United Kingdom and elsewhere to aid carbon storage, flood mitigation and biodiversity provision. However, it remains unclear whether natural tree establishment can supply demand for expanded treescapes in remote, anthropogenically modified upland landscapes.
2. We assessed natural establishment of NW-European native oak (*Quercus robur*, *Q. petraea*) saplings (< 12 years) in UK upland pasture systems adjacent to established 'Atlantic' oak woodlands on Dartmoor, SW England. We compared the extent of natural sapling colonization (abundance) into pasture sites on the moorland fringe and assessed their survival and growth throughout early life history using long- and short-term grazing exclusion experiments.
3. Natural oak establishment typically occurred on naturally freely draining pasture slopes and at high densities (up to 1900 saplings per ha^{-1}) within 20 m of the nearest adult congeneric. Beyond 20 m from a likely seed source, establishment was limited with no recorded establishment between 75–100 m.
4. The natural establishment of oak saplings in grazed pastures was specific to ontogeny with livestock exclusion only favouring the density of older recruits (8–12 years). Results suggest an age-dependent relationship between ground cover and sapling performance; that is positive association between bare-ground and height for 4–7 year old trees, but little effect for seedlings and younger (0–3 years) saplings.
5. Our scoping study highlights that with informed livestock management, there is significant opportunity for natural expansion of oak woodland into upland pastures where existing propagule sources are present (woodland edge, isolated trees). We signpost, however, that rapid expansion of oak woodland into UK uplands for climate mitigation is likely to require targeted planting and temporary grazing cessation, and there is need for improved evaluation of the effects of grazer exclosure and ontogeny specific ecology to better facilitate native woodland expansion efforts.

KEYWORDS
early tree establishment, grazing management, livestock exclosure, natural woodland regeneration, oak woodland expansion, tree ontogeny, tree planting, UK upland pastures

1 | INTRODUCTION

Afforestation is widely advocated as a key element in attempts to mitigate anthropogenic climate change (Bastin et al., 2019; Griscom et al., 2017). Recent reviews of this potential 'nature-based solution', however, have highlighted the dangers of afforestation for food security, ecosystem service (ESS) provision (Friggens et al, 2020; Mathews et al, 2020) and the logistic and economic costs associated with the large-scale tree planting needed to make a meaningful contribution to carbon budgets (Manning et al., 2015; NCC, 2020; Seddon et al., 2019). Facilitation of natural colonization may be a cheaper, environmentally sensitive and potentially more effective alternative, yet we have limited understanding of where and when we can rely on natural tree recruitment for woodland expansion (Cook-Patton et al., 2020; Crouzeilles et al., 2020; O'Neill et al., 2020).

Economically 'marginal' agricultural systems like upland pasture constitute prime areas for native woodland expansion (O'Neill et al., 2020). Uplands have enormous ESS potential, including carbon storage, natural flood management and nature conservation value, yet historic degradation has severely diminished tree cover and ESS provision (Bonn et al., 2014, 2009). Already typified by very low (< 15%) afforested area, ascribed to progressive but step-phased clearances since the Neolithic (6000 year BP) (Fyfe et al., 2014; Roberts et al., 2018), natural tree recruitment in the UK uplands (>250 – 300 m a.s.l) has been severely limited by overgrazing from historically high livestock densities (Bunce et al., 2018a; Palmer et al., 2004; Sansom, 1999). As areas where agricultural economic returns are sustained only through agricultural subsidy (EU), UK upland pasture slopes represent ideal areas for woodland expansion to meet climate change commitments and UK environmental policy (Bunce et al., 2018b; Committee on Climate Change, 2019; Defra, 2018a). Moreover, when coupled with recent anthropogenic climate change-driven precipitation increases (Burt & Holden, 2010; Murphy et al., 2019), afforestation of over-compacted soils in upland river catchments has the potential to improve hydrological functioning and alleviate downstream flood risk (Murphy et al., 2020; Stratford et al., 2017).

Globally, increased temperatures and precipitation associated with climate change are expected to favour tree growth in upland areas (IPCC, 2014), but successful tree recruitment depends on multiple, interacting biotic and abiotic factors (Worrell & Nixon, 1991). Indeed, our understanding of the influence of climate change on plant regeneration, in general, is poor (Parmesan & Hanley, 2015) and for pastoral uplands, limited seed dispersal, competition with herbaceous plants and browsing by livestock present additional constraints on regeneration potential. Natural colonization of oak may be limited by the availability of seed source and animal vectors (i.e. scatter hoarding birds and rodents; Harmer et al., 2005; Pesendorfer et al., 2016; Ramos-Palacios et al., 2014). Whilst post-dispersal, oaks large seeds (acorns) confer significant benefit to seedlings, once stored energy reserves are spent (usually within a year) saplings are vulnerable to browsing, competition and environmental stressors throughout an establishment phase that may last over a decade (Brookes et al., 1980; Worrell & Nixon, 1991).

Although the regeneration of upland oak woodland has long been studied (Watt, 1919; Shaw, 1968), we know surprisingly little about what limits and shapes oak establishment in open, high light, non-forest environments characteristic of oak's regeneration niche (Bobiec et al., 2018). Furthermore, the relative influence of browsing and competition from surrounding vegetation are likely to vary through sapling ontogeny, so that the environmental conditions for tree establishment during the seedling development stage may not be the same as those for saplings (Dayrell et al., 2018; Pulido et al., 2010). Only by understanding what determines natural colonization across early ontogeny can ecology inform management policy for the expansion of oak woodland (Rolo et al., 2013) into upland regions and determine to what extent natural woodland regeneration can supplement the UK's forest expansion targets (30,000 ha per year from 2025; Committee on Climate Change, 2019). Using direct field observation and manipulative (livestock exclusion) experiments, the aims of this study were to examine (1) the capacity for natural establishment of native oak on upland moorland fringes and (2) how the potentially interactive effects of browsing and surrounding vegetation affect oak recruitment and performance during the first decade following germination. We synthesis this information to provide management recommendations to land managers for the establishment of native oak into upland pasture systems. We also highlight opportunities to better evaluate the role of grazer exclusion for oak treescape expansion.

2 | MATERIALS AND METHODS

2.1 | Study system

Dartmoor National Park (DNP) (50°34′N 03°59′W) is the largest upland area (954 km^2 and up to 621 m altitude) in the southern British Isles (Mercer, 2009). Like many other UK upland sites, it was once dominated by the 'Atlantic' oak woodlands unique to the NW European coastal fringe and part of the 'temperate rainforest bioclimatic zone' (Ellis, 2016), characterized by a distinct and internationally significant assemblage of epiphytic lichens and understory bryophytes (Ratcliffe, 1968). Upland oak woodland now covers just 3.8% of DNP (8% broadleaf woodland), with three isolated fragments within a region dominated by blanket bog, valley mire, heathland and acid grassland, indicative of the decline of this globally important upland habitat (Dartmoor National Park Authority [DNPA], 2017). While the number of grazing animals on Dartmoor increased dramatically between the 1950s and 2000 (sevenfold increase in sheep), causing extensive and lasting soil compaction (Sansom, 1999), numbers have now stabilized (Silcock et al., 2012). Furthermore, uncertainty over the configuration of post-Brexit farm subsidy such as UK Environmental Land Management Schemes (Defra, 2020) may lead to the abandonment of current land-grazing rights and a subsequent reduction in grazing livestock numbers. This combination of past, present and likely future land use changes, combined with recent climate change makes DNP an ideal location to investigate the potential for natural regeneration of oak woodland in the UK uplands.

2.2 | Natural establishment of native oak

A desktop search using satellite data (Google Maps, 2017) of upland pasture (>250 to 300 m) experiencing woodland/scrub encroachment, combined with preliminary ground truthing site visits in spring 2017 identified six sites with natural oak colonization (Table 1; SI Figure A.1). An additional seventh site (Piles Copse) with oak colonization within fenced exclosures was also selected (Table 1; Figures 1c and 2).

Each site was walked in zigzag lines (to 5 m width) parallel to the woodland edge. Twenty survey lines were walked at incremental distances of 5 m so that each site was walked to a transect distance of 100 m perpendicular from the woodland edge (Figure 1a). A subset (i.e. every other sapling) of all oak seedlings and saplings (trees <12 years old) present were identified, and the estimated sapling age (using bud ring scars; see Clark & Hallgren, 2004), root collar diameter (RCD) and distance to nearest mature congeneric (i.e. most likely seed source; see Harmer & Morgan, 2007) recorded. The surrounding vegetation cover (%) in the immediate area of each tree was quantified (50 × 50 cm quadrats). No distinction was made between *Quercus robur* L. and *Q. petraea* L. individuals due to widespread hybridization (Petit et al., 2003) and the difficulty of distinguishing young trees (Boratynski et al., 2008).

We subsequently focused on three pasture management types with high levels of natural oak colonization (>400 ha^{-1}). These were (1) 'extensive' grazed pasture at Dartmeet with free roaming livestock (at multi-kilometre scale); (2) 'enclosed' grazed pasture at Merrivale where livestock were enclosed within a walled/fenced area and (3) a 'former' un-grazed pasture at Piles Copse where three replicate fenced exclosures were erected in 2006 and one in 2011 (Table 1, Figures 1c and 2 and Supporting Information [SI] Table A.2). Within 20 m of the woodland edge, the density of all saplings (1–12 years old) and their age class (0–3, 4–7, 8–12 years) were recorded (10 × 10 m plots for Dartmeet and Merrivale) using 1 m wide survey lines (Figure 1b). At Piles Copse sapling density within fenced 'former pasture', 'exclosure' plots were compared to 'paired' adjacent unfenced 'open' plots within site (Figures 1c and 2).

Due to site availability only, one site of each pasture management type was sampled. We, therefore, do not provide a formal comparison between the management types due to lack of replication but highlight patterns in oak establishment occurring across the sites.

TABLE 1 Sites of native oak (*Q. robur*, *Q. petraea*) colonization located in the pastoral uplands of Dartmoor, SW England. All sites were located on steep, acid grassland pastures with free draining, podzolic soils. The location (latitude: longitude), altitude, management (pasture system, livestock type [density]), NVC habitat classification (SI Table A.1), and natural features (soil series and pH, slope aspect and angle) are displayed. Management information was obtained from multiple sources (landowners, DNPA, direct observation). Soil type, natural soil hydrology, habitats (Cranfield University, 2019), pH (Centre for Ecology & Hydrology, 2007) were accessed remotely. HSL = higher level stewardship agri-scheme (Natural England, 2013). Information unavailable

	Sites						
	Dartmeet	**Merrivale**	**Ashburn valley**	**Shipley Tor**	**Burford Down**	**Hay Tor Down**	**Piles Copse**
Location (Lat:Long)	50.5481: −3.8750	50.5492: −4.0458	50.5476: −3.7685	50.4537: −3.8550	50.4230: −3.9205	50.5858: −3.7231	50.4384: −3.9111
Altitude (m)	258	305	302	266	248	268	256
Pasture system	Extensive ('commons')	Enclosed	Enclosed (agri-scheme)	Enclosed (agri-scheme)	Enclosed (agri-scheme)	Extensive ('commons')	Former (HLS)
Livestock type (density LSU ha^{-1})	Sheep, cattle, ponies (0.400, Winter = 0.170)	Sheep, cattle	-	Sheep	-	Sheep, cattle, ponies	Cattle, sheep (0.201, Winter = 0.012, Exclosure = 0)
Habitat (UK NVC code)	U4, U20, W23	U4, U20	U20	U4, U20	U4, U20	U20	U4, U20
Soil series (pH)	Moor Gate (4.62)	Moor Gate (4.62)	Moor Gate (6.07)	Moor Gate (6.07)	Moretonhampstead (6.07)	Manod (6.07)	Moor Gate (4.62)
Aspect of dominant slope (angle °)	West (13)	West (11)	West (5)	West (16)	South East (11)	East (14)	West

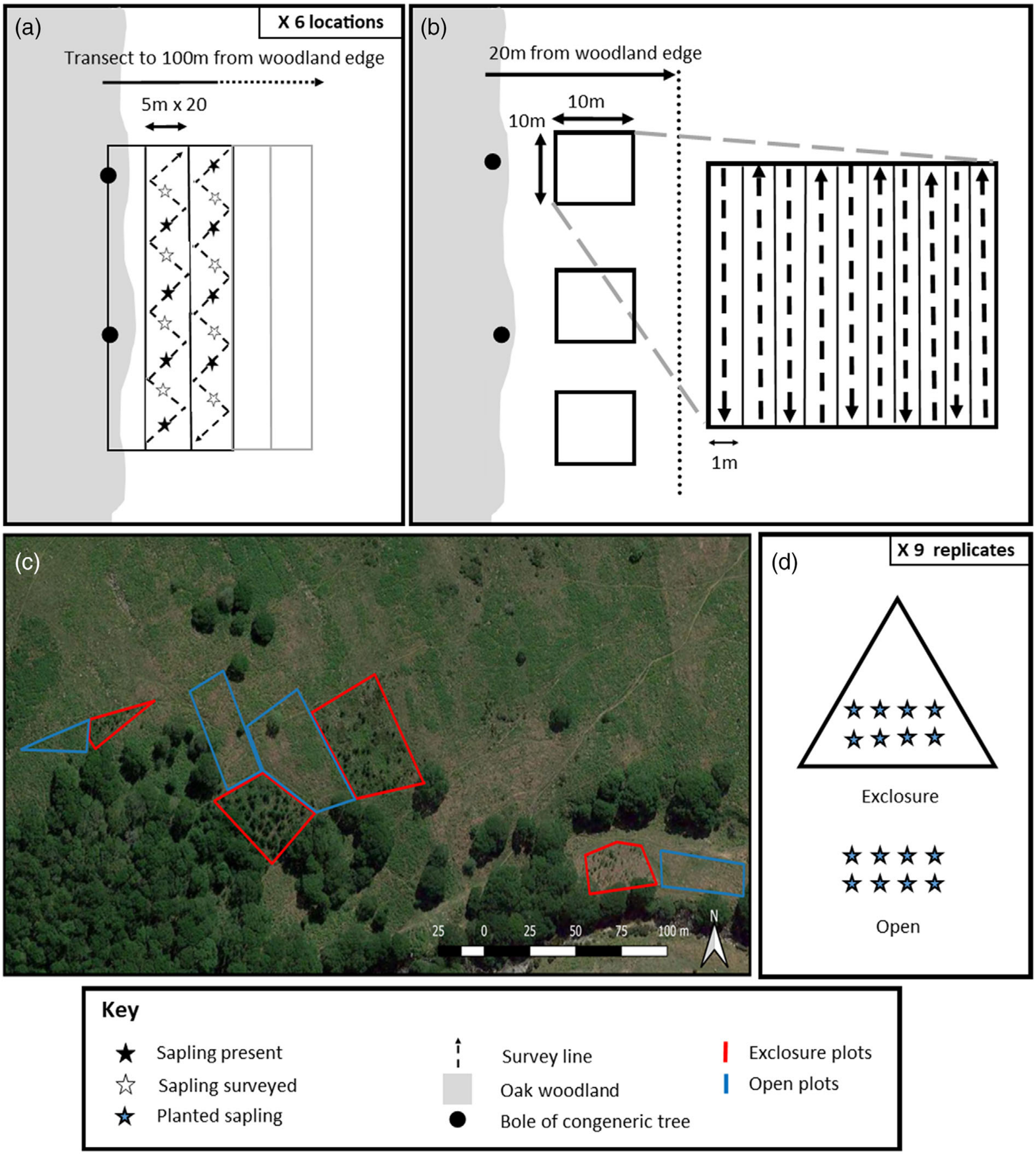

FIGURE 1 Sampling methodology for assessment of natural oak colonization (a), recording density and age class of saplings within 20 m of the woodland edge across pasture management types (b), paired long-term fenced 'exclosure' and unfenced 'open' plots at Piles Copse (c) and short-term grazer exclusion experiment at Dendles Waste (d)

2.3 | Effect of browsing and surrounding vegetation on recruitment and performance

To assess the combined effect of browsing and vegetation on saplings through ontogeny at the three pasture sites, a subset (i.e. every other) of all saplings within 20 m was tagged. Once tagged, the height, condition, early summer and late summer 'lammas' (i.e. July–August) shoot growth and estimated age of each individual was recorded, alongside the cover and height of surrounding ground vegetation (within 50 × 50 cm).

An additional grazer exclusion experiment was established at Dendles Waste (latitude: longitude: 50.4526: −3.9511 [Figure 2; SI Figure A.4, Table A.3]). The site comprised a grazed pasture with a mixture of grassland (NVC U4 *Festuca ovina-Agrostis capillaris-Galium saxatile)* and mire communities (NVC M6 *Carex echinata-Sphagnum fallax*) (Averis et al., 2004). One hundred and forty-four native oak (*Q. robur*

FIGURE 2 Long-term fenced livestock exclosures established in upland pastures at Piles Copse and short-term 'gengard' livestock exclosures at Dendles Waste, both on Dartmoor, SW England. These exclosures were used to assess the performance of naturally establishing and planted native oak saplings

and *Q. petraea*) ($N = 72$ for both) saplings (2-years-old) cultivated from acorns of local provenance, were 'slot planted' in spring 2018. Trees were planted in groups of eight individuals (arranged in four × two arrays), spaced 25 cm apart. Half of the 18 groups were protected with fenced exclosures ('Gengards', New Woods, Forestry, Norwich, UK) with the remainder exposed to browsing by sheep, ponies and deer. Sapling survival, shoot growth, leaf area (length × width of three non-damaged leaves per tree) and browse damage score (Table 2) was monitored throughout summer 2018, alongside the height of surrounding ground flora (15 cm^2 area) (Figure 1d). Subsequently, a random selection of trees from exclosure and open plots were removed in Autumn 2018. After soil was washed from the roots, trees were oven-dried at 80°C for 5 days, and dry weight biomass of shoots, leaves and main root and fine roots determined.

Data handling and analyses were performed using R studio (R Core Team, 2017). Following assessment for normality via the Shapiro–Wilks test, non-parametric statistical tests were utilized. Kendall rank-order correlation (*T*) ('Kendall' package; McLeod, 2011) was used to analyse relationships between tree variables (age, grazing damage, height, RCD, dry mass) and against surrounding vegetation community. Wilcoxon exact rank sum test (*W*) ('exactRankTests' package; Hothorn & Hornik, 2017) was used to compare difference in tree establishment (density, survival, age, grazing damage, shoot growth, leaf size, tree dry mass) and vegetation (cover and sward height) between long- and short-term grazing exclosure and open treatments. Graphs were made on R studio using 'ggplot2' (Wickham, 2009) and 'cowplot' (Wilke, 2017) packages. All data are available via Murphy (2021).

TABLE 2 Tree condition score criteria used to assess 'browse damage' of naturally colonizing young (< 12 years) native oak recruits

Tree condition score	Damage to leaves and leading shoots (% of tree)
1	No damage
2	10% of tree, and/or no other signs of historic damage to stems and shoots
3	25% of tree, and/or signs of minor historic damage to stems and shoots
4	50% of tree, and/or signs of moderate historic damage to stems and shoots
5	>75% of tree, signs of severe damage to stems and shoots

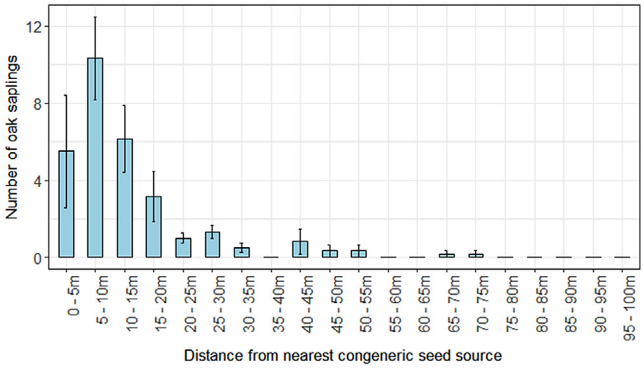

FIGURE 3 Mean (±SE) distance (m) native oak saplings (*Q. robur, Q petraea*) were observed establishing from the nearest congeneric seed source in six upland pastoral locations (Dartmeet, Merrivale, Ashburn valley, Shipton Tor, Burford Down, Hay Tor Common) in Dartmoor, SW England

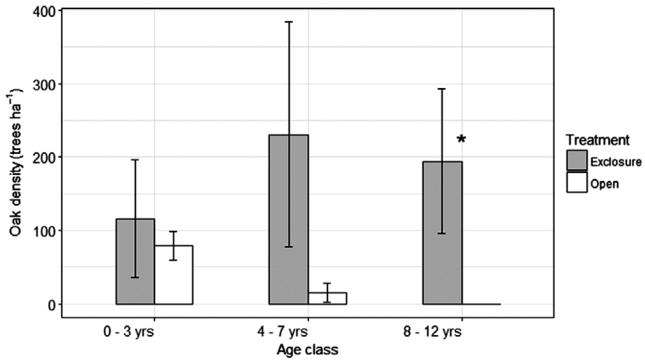

FIGURE 4 Relative effect of browsing on mean (±SE) density of native oak recruits (*Q. robur, Q. petraea*) in exclosure (no livestock) and open (grazed) pasture for three different age classes (0–3, 4–7 and 8–12 years) at Piles Copse, Dartmoor, SW England. Open plots were subjected to winter sheep (0.012 LSU ha^{-1}) and summer cattle (0.201 LSU ha^{-1}) grazing (SI Table 2). Differences between treatments determined using Wilcoxon exact rank sum test are shown as * ≤ 0.05

3 | RESULTS

3.1 | Capacity for natural establishment of native oak

The majority (84%) of saplings in extensive ('commons') and enclosed pasture were observed within 20 m (mean 13 m, max 75 m) of the nearest congeneric seed source (Figure 3). Average sapling age ranged between 2.2 (Hay Tor) and 5.6 years (Ashburn valley) (SI Table A.4), with sites with younger individuals associated with the higher grass cover typical of NVC – U4 (*F. ovina–A. capillaris–G. saxatile* acid grassland) ($T = -1.00$, $p = 0.016$). Sites with larger saplings (i.e. larger RCD) were, by contrast, associated with the higher *Pteridium aquilinum* cover of the NVC U20 (*P. aquilinum–G. saxatile*) and NVC W23 (*Ulex europaeus–Rubus fruticosus* scrub) communities ($T = 1.00$, $p = 0.016$).

Within 20 m of the woodland edge, the average density of naturally colonizing oak saplings (< 12 years old) was 1900, 1300 and 540 saplings per ha^{-1} in enclosed, extensive and former grazed pastures, respectively (SI Figure A.5 for age class). At Piles Copse, sapling density was greater when livestock were excluded ($W = 16$, $df = 3$, $p = 0.028$). Effects, however, varied through early life history (Figure 4). Whilst there was no difference in the density of younger trees in livestock grazed and un-grazed areas (0–3 years $p = 0.685$, 4–7 years $p = 0.060$), a higher density of oak saplings survived to 8–12 years old where livestock were removed (none survived outside exclosures) ($W = 16$, $df = 3$, $p = 0.028$).

3.2 | Influence of grazing and surrounding vegetation on oak establishment and performance

Sapling height gain with age ($T = 0.796$, $p < 0.001$) was greatest where livestock were excluded (former pasture). Here browsing damage remained low (Figure 5), and older saplings were associated with increased bare ground cover and grass height (Table 3). Where livestock were present (in enclosed and extensive pasture), saplings had less height gain (enclosed $T = 0.646$, $p < 0.001$, extensive $T = 0.776$, $p < 0.001$) and sustained greater browsing damage with age than where livestock were excluded (enclosed $T = 0.335$, $p = 0.001$, extensive $T = 0.259$, $p = 0.017$) (Figure 5). Oak saplings in the extensive pasture site were more variable in their browse damage but experienced lower browse damage and had greater height with age. This was concomitant with increases in bare ground and grass cover, and *P. aquilinum* height (Table 3).

The influence of vegetation cover on sapling height altered through early life history, a dynamic which results suggest may vary across pasture management types (Table 4), with no relationship between sapling height and ground cover where livestock were excluded (former pasture site). In both grazed pastures, however, older saplings were taller when growing with lower grass cover, higher bare ground extent, and taller *P. aquilinum* (Table 4). In the grazed sites, younger oak saplings (1–3 years) were taller when growing in higher grass swards. In the extensive pasture system, of the saplings growing amongst taller *P. aquilinum*, only 4–7-year-old saplings experienced lower browse damage and greater shoot growth; here greater shoot growth was also associated with lower grass, and higher bare ground cover (SI Tables A.5 and A.6).

After just 7 months of browser exclusion in open pasture without protective vegetation, the survival rate of 2-year-old oaks was 93%, 55% higher than saplings browsed by livestock (Figure 6). Saplings in fenced exclosures also exhibited higher shoot growth ($W = 78$, $df = 8$, $p < 0.001$), were less damaged by grazing ($W = 81$, $df = 8$, $p < 0.001$), had larger leaves ($W = 81$, $df = 8$, $p < 0.001$) and were associated with taller herbaceous vegetation ($W = 73$, $df = 8$, $p = 0.003$). Saplings were larger (mean total dry mass) in exclosure compared to open plots ($W = 81$, $df = 8$, $p < 0.001$), a difference reflected in shoots, leaves, main roots and fine roots (SI Table A.7).

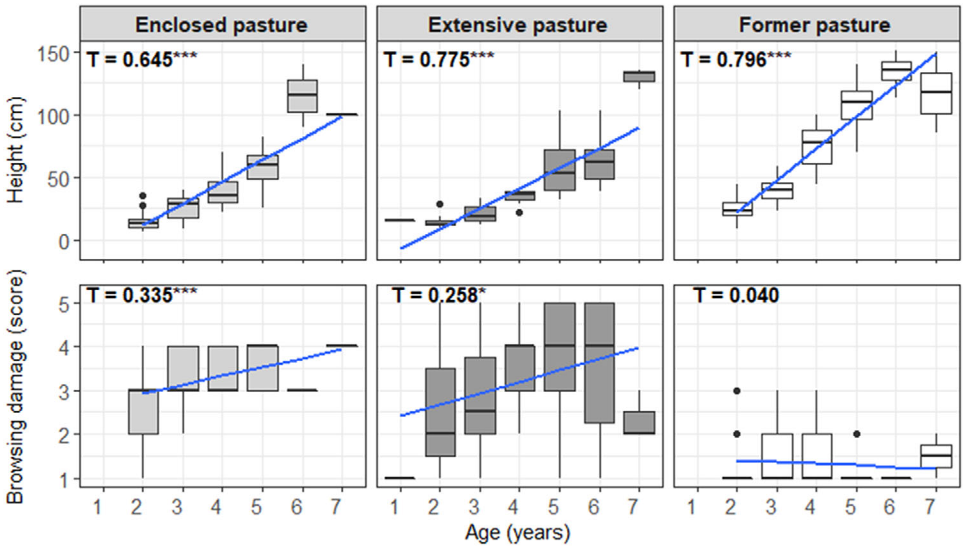

FIGURE 5 Relationship between the age (years) of naturally establishing native oak saplings (*Q. robur*, *Q. petraea*) and their height (cm) and browsing damage (1 = low, 5 = high, see score criteria in Table 2) observed at an enclosed (Merrivale), extensive (Dartmeet) and former (Piles Copse) pasture in Dartmoor, SW England. Changes in tree height and grazing damage with tree age are examined using Kendall rank order correlation (T value and significance denoted * ≤ 0.05, ** $p \leq 0.01$, *** $p \leq 0.001$)

TABLE 3 Relationship between age (years) of naturally establishing native oak (*Q. robur*, *Q. petraea*) and surrounding vegetation (grass, *P. aquilinum* and bare ground cover, grass and *P. aquilinum* height) recorded at three upland pastoral sites, Dartmoor, SW England. Relationships examined using Kendall rank order correlation (T value and significance denoted * ≤ 0.05, ** $p \leq 0.01$, *** $p \leq 0.001$)

	Sapling age versus ground cover		
	Enclosed pasture *(Merrivale)* *df* = 75	Extensive pasture *(Dartmeet)* *df* = 54	Former pasture *(Piles Copse)* *df* = 74
	T	T	T
Grass cover (%)	**−0.365*** **	−0.197	−0.091
P. aquilinum cover (%)	−0.022	0.175	0.076
Bare ground cover (%)	0.177	**0.231***	**0.225***
Grass height (mm)	0.103	**0.255***	**0.247***
P. aquilinum height (mm)	0.148	**0.228***	0.137

TABLE 4 Relationships between height of native oak saplings (*Q. robur*, *Q. petraea*) and the height and cover of surrounding ground flora for younger (1–3 years) and older (4–7 years) saplings growing in extensive, enclosed and former pasture systems of Dartmoor, SW England. Relationships examined using Kendall rank order correlation (T value and significance denoted * ≤ 0.05, ** $p \leq 0.01$, *** $p \leq 0.001$)

	Sapling height versus ground cover					
	Enclosed pasture		Extensive pasture		Former pasture	
	Young saplings (1–3 years) *df* = 57	Older saplings (4–7 years) *df* = 16	Young saplings (1–3 years) *df* = 24	Older saplings (4–7 years) *df* = 29	Young saplings (1–3 years) *df* = 41	Older saplings (4–7 years) *df* = 32
	T	*T*	*T*	*T*	*T*	*T*
Grass cover (%)	−0.107	**−0.497****	**−0.447****	**−0.454*** **	−0.007	0.024
P. aquilinum cover (%)	0.142	**0.388***	0.004	0.137	−0.195	0
Bare ground cover (%)	0.092	**0.398***	0.222	**0.399****	−0.093	0.137
Grass height (mm)	**0.394*** **	0.295	**0.337***	0.224	0.209	**0.344***
P. aquilinum height (mm)	0.171	**0.512****	**0.398***	**0.294***	0.123	0.056

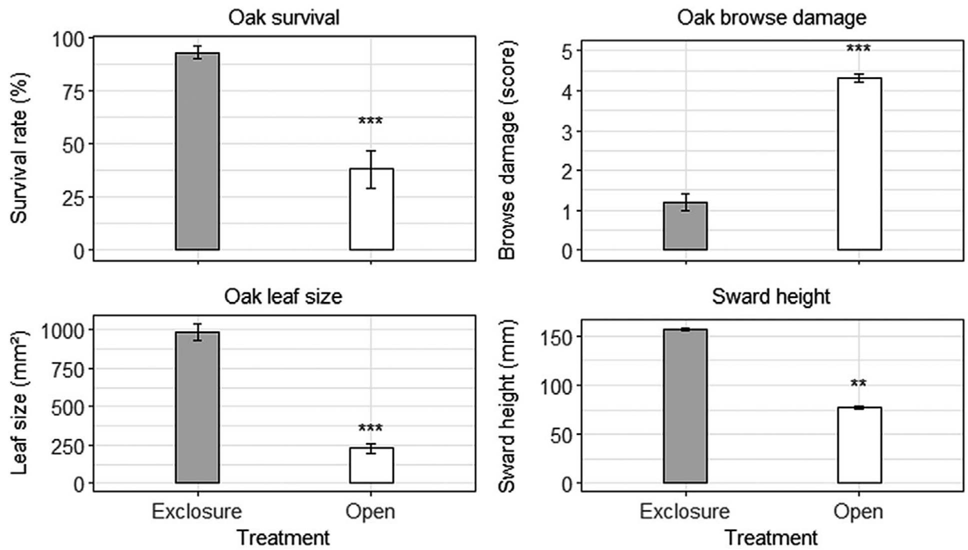

FIGURE 6 The effect of livestock exclusion on the mean (± SE) survival, browsing damage, leaf size, and surrounding vegetation sward height of planted 2-year old native oak trees (*Q. robur*, *Q. petraea*) at Dendles Waste, Dartmoor, SW England. Open plots were subjected to sheep grazing, and pony and deer browsing (0.080 LSU ha^{-1}) (SI Table A.3). Table 2 for browse damage score criteria. Statistical difference ($p < 0.05$) was determined using Wilcoxon exact rank sum test ($n = 9$) and denoted ** $p \leq 0.01$, *** $p \leq 0.001$

4 | DISCUSSION

Understanding the practical constraints on upland woodland establishment is extremely pressing given growing calls for the increased tree cover to facilitate carbon sequestration and additional ESS benefits (Bastin et al., 2019; Cook-Patton et al., 2020; Griscom et al., 2017). Our study finds that natural colonized oak sapling densities on selected UK upland pasture slopes were sufficient (mean of 1246 saplings per ha^{-1}) to satisfy UK woodland creation grant requirements (1100 stems per ha^{-1}) within 20 m of the woodland edge (Defra, 2018b). Vectors like jays and squirrels can transport acorns at high densities (400 ha^{-1}) and over long distances (1.5 km) (Bossema, 1979; Worrell et al., 2014), notably so in lowland settings (Broughton et al., 2021). However, in this UK upland setting, native oak establishment was largely confined to within 20 m of the nearest adult congeneric, and principally located on west-facing pasture slopes with well-drained soils (Table 1). Although sparse recruitment at distance from adult trees could make significant impact at landscape scale over time; even without accounting for mast variability (Hanley et al., 2019; Shaw, 1974; also see SI Figure A.2) our study suggests it is unlikely natural recruitment alone could extend oak woodland cover into upland pastures at the rate required to match UK afforestation targets and climate change mitigation requirements.

Although logistical constraints limited study site availability, our results nonetheless underscore how browsing behaviour by livestock is a major determinant of long-term oak establishment in the UK uplands. Where livestock were present, many fewer saplings survived and were smaller and in poorer condition and did not survive beyond 8 years old without protection. More interestingly, however, our study suggests a complex interaction between sapling establishment, grazers and their impact on the surrounding 'matrix' vegetation.

The association of older saplings (4–7 years) with tall grasses and dense *P. aquilinum* stands suggests this vegetation may have a protective role against browsing, perhaps associated with *P. aquilinum's* toxic metabolites (Barkham, 1978), and/or potential vegetative moderation of climate (Mainali et al., 2020). Sites with youngest saplings (1–3 years) were dominated by open, grazed acid grassland swards (SI Table A.4), indicating that the total absence of grazing may be unhelpful for tree recruitment (see also Morrison et al., 2019), by constraining oaks regeneration niche (Bobiec et al., 2018). Disturbance and opening up of vegetation by grazing animals may allow early seedling establishment and reduce competition from dense *P. aquilinum* growth (Humphrey & Swaine, 1997; Janzen, 1971).

Our study signposts the potentially shifting negative and beneficial role of grazers on oak establishment, underscoring the critical importance of large herbivores and disturbance in woodland establishment processes (Morrison et al., 2019; Vera, 2000). For example, fast rotational grazing (typified by short intensive grazing events and rest periods) can promote greater tree regeneration (four-fold higher) than conventional grazing (Fischer et al., 2009). This interaction reflects the importance of spatio-temporal variation in disturbance, and how low livestock grazing densities can encourage heterogeneous vegetation (with grazed and un-grazed patches of tall herb and thorny shrub) promoting 'nurse' vegetation which may support tree development through early life stages (Smit et al., 2015). This appears to be a mechanism reflected in our study, and we recommend more emphasis on how the interplay between grazer intensity and plant community impacts regeneration trajectories of focal tree species (throughout upland regions) as a vital prerequisite to inform policy on woodland expansion. In the context of our results, we recommend:

1. Livestock grazing (particularly cattle) close to congeneric seed source may be useful for oak establishment by reducing dense and competitive vegetation (such as *P. aquilinum*) (Pakeman et al., 2019) which evidence suggests providing little additional

benefit for young (1–3 years) saplings (Humphrey & Swaine, 1997; Janzen, 1971)(Table 4; SI Table A.4). Future studies should explore the effectiveness of fast rotational or 'mob grazing' using multiple long-term, manipulative 'pull factor' effects (Lunt et al., 2021) and paired fenced and/or invisible fencing exclosures (Alday et al., 2021; Jachowski et al., 2014). These could be established across a range of settings and topographies to better ascertain how livestock management vegetation structure influence oak recruitment (density and age profile) away from adult congeneric trees.

2. On sites where oak seedlings and saplings (1–3 years) have colonized, livestock should be excluded for a minimum period of 12 years to increase sapling survival, growth and establishment. Subsequently, livestock could be returned where vegetation provides protective refugia from grazing (Smit et al., 2015). Long-term paired grazed and non-grazed exclosure could systematically assess how the method (design and technology), length and character (animal type, density, season) of livestock exclosure alter oak woodland establishment and ESSs provision through time. Baseline and regular monitoring of subsequent tree recruitment characteristics (survival, condition, height, age profile – using tagged trees), graze intensity (animal density, dung counts), vegetation (plant cover and height) and supportive abiotic metrics (e.g. soil compaction, hydrology, carbon) within and across paired sites would help refine management requirements to balance the inevitable trade-offs with forest expansion initiatives (Strassburg et al., 2019).
3. Diminished regeneration processes limit natural oak expansion along many UK upland valley slopes where current ESS provision is low and where woodland establishment is required for rapid soil hydrological recovery (Murphy et al., 2020). In these areas, planting and/or applied nucleation (Holl et al., 2020) together with grazing management in adjacent areas may enhance medium-term regeneration conditions by increasing availability of mast seed and scatter-hoarding birds and rodents. Future research should assess the optimal size, positioning and management of nucleation and/or grazing exclosure needed to facilitate the natural expansion of oak treescapes into highly modified upland landscapes.
4. Older and larger oak saplings (4–7 years) could be planted directly into areas where dense vegetation protects saplings from animal livestock. Experimental planting which helps better define where, how and at what stage trees should be planted into protective vegetation (Rolo et al., 2013) may eliminate the need for tree-guards and/or fencing and could significantly improve the costs, social acceptance, and environmental sensitivity of expanded oak treescapes.

5 | CONCLUSIONS

Whilst natural tree colonization is increasingly highlighted as a low cost environmentally sensitive mechanism to meet international woodland expansion targets (Cook-Patton et al., 2020; Crouzeilles et al., 2020), our findings suggest expansion of oak woodland into UK upland pasture systems for climate change mitigation is likely to require strategic planting and informed livestock management. Although limited to a single region (Dartmoor), our scoping study provides impetus to a wider assessment of the role of livestock management and ontogeny-specific ecology for the creation of resilient future treescapes. Assessment of the impact of livestock exclosure on woodland regeneration potential and ESS provision should be integrated into current and future woodland expansion initiatives. Further understanding may better inform policy mechanisms, facilitate more equitable land management decisions and be particularly beneficial for the establishment of 'long-lived pioneer' species (e.g. oak) associated with high carbon storage and biodiversity provision (Mitchell et al., 2019; Rüger et al., 2020), and species with marked ontogenetic shifts during establishment (Dayrell et al., 2018).

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CONFLICT OF INTEREST

There are no conflicts of interest to declare.

AUTHORS' CONTRIBUTIONS

TM and PL designed the study methodology; TM collected the data; TM analysed the data; TM, PL and MH led the writing of the manuscript. JE contributed to multiple manuscript drafts. All authors contributed critically to the drafts and gave final approval for publication.

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