



Sapling establishment by Scots pine *Pinus sylvestris* following experimental prescribed burning and deer exclusion on heathland beside native forest

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Abstract

Expanding native woodland, including by natural regeneration, helps address the biodiversity and climate crises. For small-seeded trees, like many pine species, disturbances such as fires can enhance seedling recruitment, boosting sapling establishment. We tested this idea on heathland beside semi-natural Scots pine *Pinus sylvestris* forest in Scotland, a heavily deforested country with abundant deer. A replicated experiment was established, comprising 10 blocks within 50 m of seed-trees, each with four 10 × 10 m plots. In each block, two treatment factors, prescribed burning and deer exclusion (by fencing) were applied in all combinations. Seedling establishment to year 5 was reported previously, showing a ~tenfold increase in burnt plots. Here, we report on establishment to year 16, when many young trees were over 25 cm, defined here as saplings. Where deer had access, mean sapling density in burnt plots was 16.9 times higher (95% CLs 5.8–49) than unburnt. This factor was lower where deer were excluded by fencing, though still large (6.6; 2.9–16). Sapling cover and maximum height were also higher in burnt plots than unburnt ones, by factors of 2.3–6.7. There was a tendency for higher stem density in burnt plots where deer were present, but lower height and cover. However, fencing effects were modest, perhaps partly reflecting low deer numbers at our study site. Our results help quantify how disturbances can influence the establishment of trees with small, wind-blown seeds, and support the use of prescribed fire to enhance Scots pine regeneration in similar contexts.

Keywords Browsing · Experiment · Fencing · Fire · Native woodland · Restoration

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Introduction

Restoring and expanding native woodland is an important way to address the nature and climate crises (Hua et al. 2022; Rayden et al. 2023). If native forests were restored across their potential range, this would improve forest connectivity, reducing the risk of extinction debt (Hester et al. 2019) and helping forest fauna re-distribute in response to climate change (Bender et al. 2019). Tree planting can be a predictable approach to woodland creation, but where seed-producing native trees are already present, natural regeneration offers important potential advantages. It might be cheaper than planting, especially at large scale (Nunes et al. 2017), create more natural stand structures (Aubin et al. 2008), and better allow gene pools to track environmental change (Chazdon and Guariguata 2016; Kohler et al. 2020). This could confer greater resilience to future climatic impacts (Sánchez-Salguero et al. 2013; Navarro-Cerrillo et al. 2018) and disease (Napierała-Filipiak and Filipiak 2012). However, for many tree species, factors influencing natural regeneration are poorly understood, reducing our ability to predict outcomes. Hence there have been calls for studies which quantify natural regeneration in different contexts, using approaches such as long-term experiments (Fernandes 2018; Kohler et al. 2020) and measuring factors such as the influence of ungulates (Löf et al. 2019).

For trees with small (e.g. windblown) seeds, disturbance events (i.e. events which destroy biomass, such as fires or trampling by large herbivores) can be particularly important in facilitating seedling establishment (e.g. Lusk 1995; Willis et al. 2015). Such trees include many species of pines *Pinus*, which often grow in regions affected by fire, to which some pines show apparent adaptations such as thick basal bark and self-pruning of lower branches (He et al. 2012; Pausas 2015). After disturbance events like fires, pines can sometimes regenerate prolifically (Prévosto et al. 2012; Tardós et al. 2019); outside their native ranges this can make them troublesome invasives (Davis et al. 2019). New growth in post-fire sites can attract large herbivores, which in turn may strongly influence tree seedling establishment (Tercero-Bucardo et al. 2007).

Fire and other disturbances characterise many woodlands holding pines across Eurasia (Shorohova et al. 2009). In Scotland, a heavily deforested country with high deer numbers (SNH 2016), semi-natural native forests dominated by Scots pine *Pinus sylvestris* have been reduced to scattered fragments, all showing a degree of past human impact (Mason et al. 2004; Summers and Cavers 2021). At many such remnants, conservation work seeks to restore and expand these woodlands, often emphasising the role of natural regeneration (Fletcher et al. 2021; Gullett et al. 2023). Given the urgency of the nature and climate crises, and

government woodland expansion targets (Scottish Government 2019), it is important to consider management techniques that can speed up regeneration, an approach termed “assisted regeneration” (Chazdon et al. 2020; Gullett et al. in press).

In earlier studies beside a Scottish native pinewood, we used experiments on formerly-forested open heathland to test how prescribed burning influenced Scots pine seedling establishment, first at a small scale using sown pine seeds (Hancock et al. 2005), then at a larger scale using natural seed-fall (Hancock et al. 2009). In the second experiment, reflecting concerns that deer might heavily browse post-fire regeneration, we also manipulated deer abundance using fencing. These experiments showed that fire boosted seedling establishment (3.5-fold or 9.8-fold in the first 2 or 5 years: Hancock et al. 2005 and 2009, respectively). The second experiment also found that seedling survival was enhanced on burnt plots, implying that seedling numbers on burnt and unburnt plots might further diverge over time. Contrasting with burn effects, deer effects on seedling counts were relatively modest, perhaps reflecting low deer numbers (by Scottish standards) at our study site. Here, we build on this earlier work, by using data from the second experiment, gathered in years 6, 11 and 16 after burning and deer exclusion. Our aims were to determine the effects of these managements on the establishment of young Scots pine trees, using three measures of recruitment: (i) stem density; (ii) canopy cover; and (iii) height.

Methods

The study area, experimental design, and field methods were set out in detail in our earlier paper (Hancock et al. 2009). Here we present the main details for completeness, then add the details of how we presented and analysed the data resulting from later years of the experiment.

Study area

The study took place at Abernethy National Nature Reserve (Beaumont et al. 2005; Summers 2018), which is largely managed by the nature conservation charity RSPB, and located within the Cairngorms Connect landscape restoration partnership area (www.cairngormsconnect.org.uk) in Scotland's Cairngorms National Park (Fig. S1). Extensive, ancient, semi-natural pinewood is an important feature of the reserve, and expanding this woodland to the natural tree line (~650 m for pine in this region: Nagy et al. 2013) is a priority management objective. The study plots were on previously-wooded, open heathland at the edge of mature semi-natural pinewood i.e. within 50 m of mature

seed trees, and at altitudes of 380–440 m, on shallow peat soils (averaging ~29 cm deep: Hancock et al. 2009). At Braemar weather station (327 m altitude, ~25 km to south-east), mean monthly temperatures during the study period averaged 1.8 °C and 12.5 °C in January and July respectively, and mean annual rainfall was 898 mm; means at Aviemore, which is nearer but lower, were 2.3 °C, 14.2 °C and 985 mm (data from UK Met Office). Deer densities around the experimental areas were estimated at the start (2003) and end (2018) of the study period, respectively, as around 4.7 and 5.9 km⁻² for red deer *Cervus elaphus* and 8.7 and 6.3 km⁻² for roe deer *Capreolus capreolus* (unpublished RSPB estimates from dung counts). Assuming mean body weights around 90 and 25 kg for red and roe deer

respectively (approximate mid-points of values for comparable areas, given by Harris and Yalden 2008), these densities imply around 6–7 kg ha⁻¹ of deer biomass (the estimate remaining within 10% for the two surveys), with ~65–75% of this being red deer. Maximum browse heights for these deer species are approximately 1.1 and 1.8 m for roe and red deer, respectively (Hodge and Pepper 1998).

Experimental design

At the start of the study, we established ten experimental blocks, considered typical of areas that might be suitable for prescribed burning to encourage tree regeneration. Blocks initially held few Scots pine seedlings or saplings. They mainly comprised reasonably uniform, dry-heath vegetation, i.e. they were open, but formerly wooded, heathland or moorland habitats, typified by a substrate of feather mosses *Hypnales* and an abundance of the dwarf ericaceous shrub, heather *Calluna vulgaris*. In suitable conditions, heather burns readily, reflecting characteristics seen in some other flammable plants such as elevated, fine dead shoots, where fires tend to start (Davies and Legg 2011). Blocks were within 50 m of cone-bearing Scots pine trees, to be within range of pine seed-fall, and accessible for machinery, to enable burning and fencing. Using burning to seek to promote sapling establishment, our approach differed in intent and regime from traditional, cultural burning of this heathland (moorland) type in the region i.e. we planned a single burn, followed by a long fire-free period during which any woodland that developed could progress to maturity. Since the area meeting block-selection criteria was not mapped, random selection was not possible. Instead, block locations were chosen, spread around the forest edge (Fig. S1), during a series of visits by reserve and science staff.

Each block comprised four adjoining 10 m × 10 m plots, each holding four 5 m × 5 m quadrats (Fig. 1). In spring 2002, two adjacent plots at each block were burned. Fire characteristics were typified by low intensity (mean flame lengths ~0.7 m) and low severity in terms of substrate impacts (mean ~15% of moss/litter depth consumed). For further information on fire management and characteristics see Dugan (2004) and Hancock et al. (2009). Later that year a fence was constructed at each block to exclude deer from one burnt and one unburnt plot. Fences did not exclude mountain hares *Lepus timidus* (maximum browse height ~0.7 m: Hodge and Pepper 1998) which were present but not abundant; studies under similar conditions have shown hare browsing impacts on Scots pine recruitment to be minor (Rao et al. 2003). Access within fences was also possible for black grouse *Tetrao tetrix*, which were present and can browse pines (Bocca et al. 2014). Treatment was randomised, with the proviso that, within each block, the

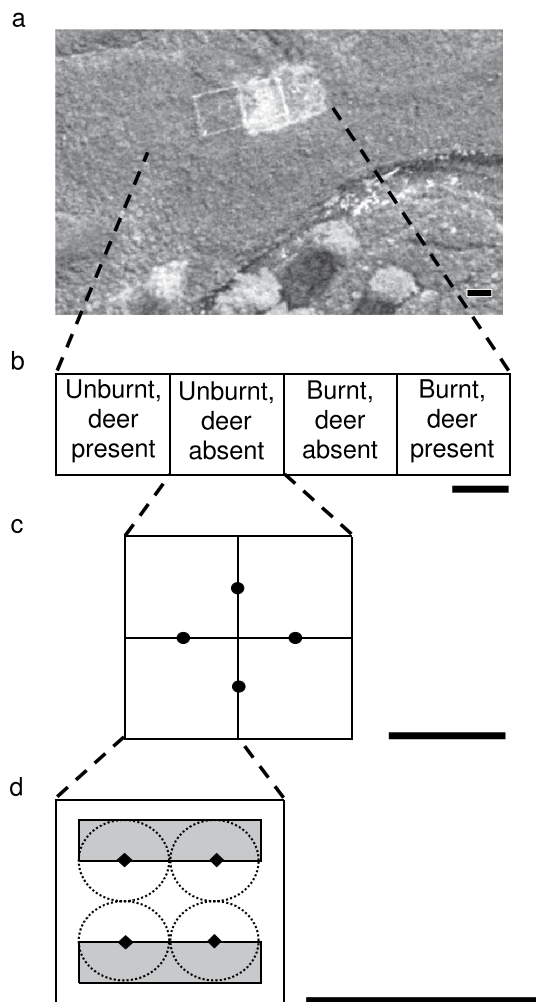


Fig. 1 The layout of an experimental block. **a** Aerial photograph of a block, showing nearby seed trees (bottom of photograph). The burnt area (pale vegetation) and fence can be seen. This photograph was taken in 2005, three years after burning. **b** Schematic diagram of a block. **c** One plot, showing the seed trap locations (black dots) and four quadrats. **d** One quadrat, showing the seedling search strips (grey shading), vegetation sample point centres (black diamonds) and vegetation cover score areas (dotted circles). A horizontal black 5 m scale bar is given in each Figure. Taken from Hancock et al. (2009)

two burnt plots and two fenced plots had to be adjacent to facilitate delivering the treatments.

Field monitoring

Each autumn in 2002, 2007, 2012 and 2017 (seasons 1, 6, 11, and 16 following burning) we carried out vegetation surveys, including searches for pine seedlings and saplings. Vegetation was surveyed in four, 1 m radius sample points per 5 m × 5 m quadrat (Fig. 1), with estimates made of plant top cover by species or species group. We searched for seedlings and saplings in two, 4 m × 1 m search strips per quadrat (Fig. 1), with approximately five minutes search time per strip. Seedlings or saplings were counted and their heights individually measured; if they had been previously browsed, that was noted. In every year from 2002 to 2009, and again in 2012 and 2017, seed-fall was measured, using four, 35 cm diameter seed-traps per plot. In each monitoring year, these were set up in April and checked for seeds in July and September. Pine seeds found were counted and cut open; those holding an endosperm were assumed to be viable.

Measures of young tree establishment

We used three different measures of establishment of young pine trees: stem density, cover, and maximum height. These measure different aspects of regenerating stands, each important in different ways. Stem density is the most commonly used measure for woodland establishment among practitioners and woodland grant funders in our region, with a long history of use by foresters. Woodland canopy cover has important ecological effects, for example on ground vegetation via shading (e.g. Parlane et al. 2006) and is widely used in remote sensing and biomass studies (e.g. Huang et al. 2009). Cover of established woodland exceeding 20% is used by UK forest agencies (see www.forestresearch.gov.uk) to define woodland for inventories, grants and targets. The maximum height of saplings partly reflects browsing influences and is an important characteristic of edge habitats between forests and open ground (Dodonov et al. 2013). It influences responses by fauna, such as birds typical of developing woodland (e.g. tree pipits *Anthus trivialis*: Kumstátová et al. 2004; black grouse: Roos et al. 2016) and affects microclimate (e.g. Geißler et al. 2012).

For estimates and analyses of stem density we defined “saplings” as young pines at least 25 cm in height, a size threshold used to define saplings in some other studies (e.g. Kobe 1996; Lichstein et al. 2004; Elenitsky et al. 2020). At this height, young trees are around the typical height of dominant dwarf shrub vegetation in our study area (see Results), used as an inclusion threshold in related studies

(Palmer and Truscott 2003) and treated by local practitioners as a key establishment milestone (Gullett et al. 2023). Young trees at or above the height of surrounding vegetation are easily detectable using search methods such as those used here. This simplifies data analysis, since it avoids the need to compensate for differences in detection between treatments. Supporting this idea, simple linear extrapolation from our earlier seedling detection trials would imply that detection should reach 100% for young trees that are over 23 cm tall (from Hancock et al. (2009), using detection estimates of 28% and 55% at median seedling heights of 2.5 and 10 cm respectively).

For analyses of cover and maximum height, we included all young trees observed, regardless of height. However, although some smaller seedlings were recorded in these data, the taller young trees (many over 25 cm and some as tall as a few m) tended to have a strong influence on plot level means, which were the focus of interpretation. For simplicity henceforth we refer to all young trees, defined as above for each of the three analyses, simply as “saplings”.

Data analysis

Statistical analyses were restricted to data from the final year of the study (2017, 16 growing seasons after treatment), to obtain formal estimates of treatment effects on final focal outcomes at the end of the study. By this time also, field-layer vegetation heights were broadly similar between treatments (Results) reducing between-treatment biases in sapling apparency. Data from earlier years are simply presented graphically, to help describe the development of these young pine stands and other vegetation. To analyse final-year treatment effects we fitted three statistical models, one for each of our three measures of sapling abundance: density, cover and height.

For the density analysis, the *y*-variable (i.e. response variable) was the total number of saplings at least 25 cm tall, observed across all search strips (32 m² in total) in each plot in 2017. These count data were modelled in a Generalised Linear Model which had a Poisson error distribution and log link, and included a dispersion parameter to model any overdispersion in the data. For the cover analysis, the *y*-variable was the mean percentage top cover of pine seedlings and saplings at the plot level in 2017, averaged across all vegetation quadrats in each plot, and square-root transformed to reduce skew. This was analysed using a General Linear Model (i.e. with a normal error distribution). For the maximum height analysis, the *y*-variable was the maximum height of any seedling or sapling in the plot, found in the search strips in 2017. As for cover, height was square-root transformed to reduce skew and analysed with a General Linear Model. If no young trees were found (8 out of 40

plots) height was set to zero. For all models, we included both “treatment” (specified as two, two-level treatment factors: “burnt” and “fenced”, and their interaction) and “experimental block” as categorical fixed effects, consistent with previous analyses of this experiment (Hancock et al. 2009), and carried out planned pairwise comparisons between all treatment combinations. All models were fitted in the GENMOD procedure in SAS (www.sas.com), and in each case residuals were checked graphically for normality and homoscedasticity.

To quantify how experimental blocks compared in terms of their relative abundance of Scots pine seed-fall, we calculated, in each year for each block, the proportion of that year’s recorded seed-fall that was recorded in that block. For each block, we then took the average of these proportions, across all years, as an estimate of the relative abundance of falling seed in that block, referred to here as the “study-wide mean proportion of seed-fall” for that block. We also considered a different approach, modelling seed-fall as a

function of block, year and their interaction, and using this to derive block-level estimates of mean seed-fall, but this was not possible due to large numbers of block-years with zero values.

Results

Descriptive results across the whole study period

In the first season following treatments (2002), the field-layer vegetation differed markedly between unburnt and recently burnt plots (Fig. 2a). Unburnt plots were dominated by live heather (~70% top cover). With this being the main flammable plant in this habitat, its cover was much lower in freshly burnt plots (~4%), which were instead dominated by exposed substrate (~62% cover). Similarly, unburnt plots had much taller live vegetation (~30 cm) than burnt plots (~5 cm) (Fig. 2b). The field-layer vegetation gradually

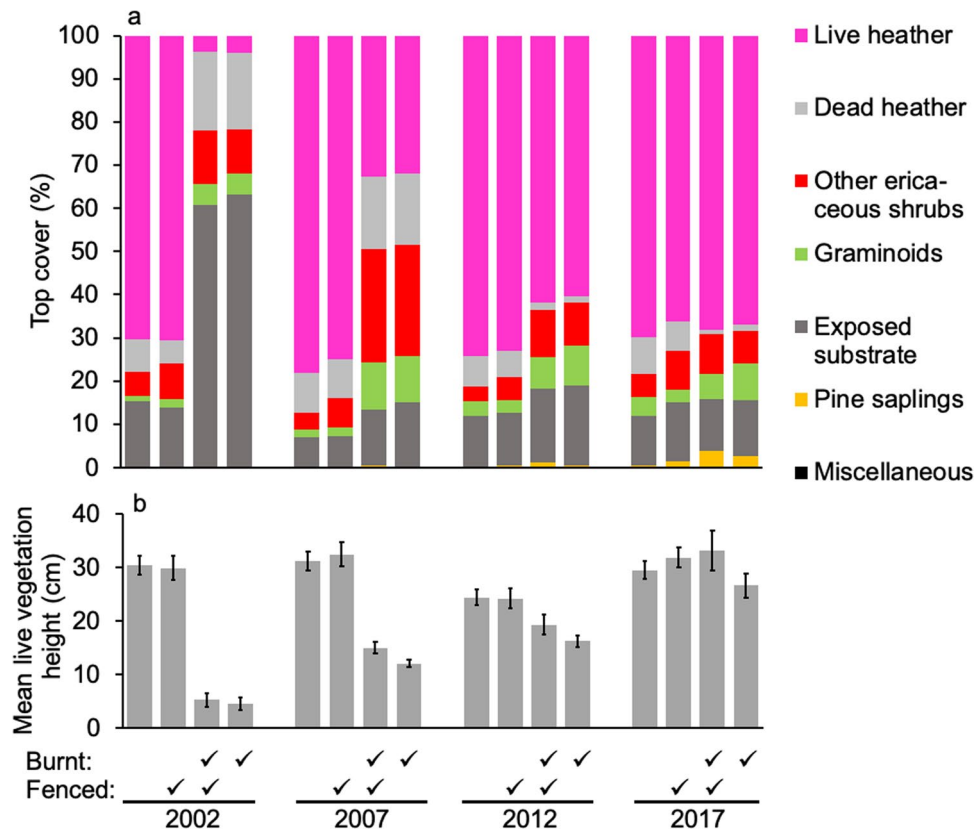


Fig. 2 The vegetation of the study plots by treatment and year, averaged across the 10 replicates for each treatment type: **a** top cover by vegetation categories; **b** live vegetation height. For Fig. 2a, vegetation categories were defined as follows: (i) live heather: live *Calluna vulgaris*; (ii) dead heather: *Calluna vulgaris* that is standing but brown (freshly dead), grey (long dead) or burnt, rather than green; (iii) other ericaceous shrubs: other dwarf shrubs of the family Ericaceae, principally *Vaccinium* and *Erica* species; (iv) graminoids: grasses Poaceae, sedges Cyperaceae and rushes Juncaceae; (v) exposed substrate:

exposed moss (live or dead), litter or bare ground; (vi) pine saplings: any Scots pine saplings or seedlings contributing to top cover; (vii) miscellaneous: anything else. For Fig. 2b, vegetation heights were calculated as the mean average for each species or species group (measured at 16 sample points per plot), weighted by percentage top cover to calculate a single average height per plot, which was then averaged across the 10 replicates per treatment in each year. Note that burning and fencing treatments took place in spring 2002, prior to the first vegetation survey in autumn 2002

developed during the study period, with heather recovering its dominance. At the end of the study, 16 growing seasons after burning, the field-layer vegetation composition and height were broadly similar in burnt and unburnt plots, although burnt plots tended to have relatively less dead heather, and more graminoids (Fig. 2a).

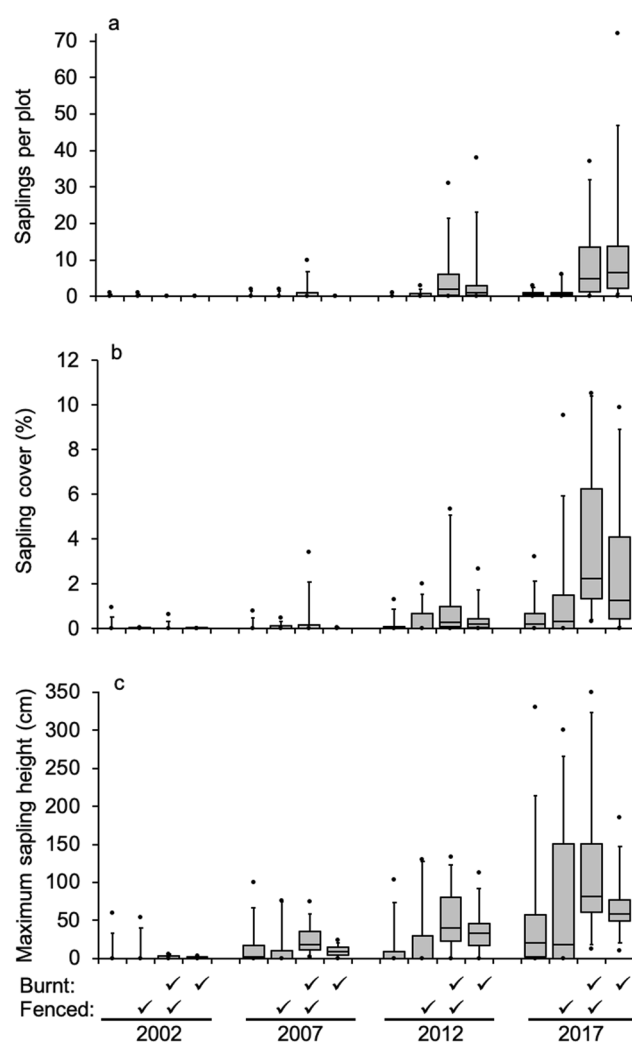


Fig. 3 Observed patterns in sapling establishment during the experimental period: **a** density; **b** cover and **c** maximum height. Boxplots show the median (central line) and upper and lower quartiles (box); 5% and 95% percentiles (whiskers) and minimum and maximum values (outlier points), in each year for the 10 replicates of each treatment. The data shown are based on autumn surveys at five-year intervals; treatments (burning, fencing) took place in spring 2002, prior to the first survey. Density values (Fig. 3a) indicate the number of saplings at least 25 cm tall, found in the eight, 4 m² search strips in each plot (total search area per plot: 32 m²). Hence, multiplying these values by 312.5 gives the estimated number of saplings per ha. Cover estimates (Fig. 3b) are based on the mean top cover of young pine trees for each plot, using 16 vegetation sample points per plot, each of 3.14 m² radius. Maximum height estimates (Fig. 3c) are based on the largest young pine tree found in each plot within the 32 m² of search strips. Where no young pines were present in a plot (30, 13, 18 and 8 out of 40 plots in 2002, 2007, 2012 and 2017 respectively), this was set to zero

In some years, fenced plots held slightly taller vegetation and/or somewhat more abundant ericaceous shrubs other than heather (principally *Vaccinium* and *Erica* species) (Fig. 2). However, compared to burning, the effect on the field-layer vegetation of the other treatment factor – deer exclusion by fencing – was minor.

Young pine trees gradually established during the study period, and tended to occur at higher densities, cover and heights in the burnt plots (Fig. 3). By the end of the study, median sapling densities in burnt plots were between 5.0 and 6.5 per plot, equivalent to ~1500–2000 stems ha⁻¹, around 12 times greater than unburnt plots (Fig. 3a). In burnt plots, the maximum densities reached 72 saplings per plot (~22,500 ha⁻¹), compared to a maximum of only 6 per plot (~1900 ha⁻¹) in unburnt plots. Cover and maximum height showed a similar pattern of greater values in burnt plots. Cover reached median values between 1.3 and 2.3% in burnt plots, averaging around six times greater than in the unburnt plots (Fig. 3b). Maximum sapling heights in burnt plots had median values between 58 and 81 cm (depending on fencing), which were around three to five times greater than corresponding unburnt plots (Fig. 3c). The highest values for pine sapling cover and maximum height were 10.5% and 350 cm respectively, both recorded in a plot that was burnt and fenced.

Deer exclusion by fencing appeared to have a relatively more modest or varied influence on pine sapling measures than burning (Fig. 3). There was little sign that deer exclusion consistently increased sapling density (Fig. 3a). In fact, interestingly, on burnt plots, at the end of the study (2017), maximum sapling densities were found outside fences, where the maximum value was around double that found inside fences. Median density was also relatively higher on the burnt plots that were outside fences. By contrast, in burnt plots at the end of the study, both cover (Fig. 3b) and maximum height (Fig. 3c) had maximum and median values that were lower outside fences.

Analytical results from the final year, 16 years after treatments

Analyses of the 2017 data, gathered 16 years after treatments, emphasised the positive effect of burning on all three measures of sapling establishment: for every measure, burnt and unburnt plots differed significantly ($P < 0.005$; Table 1; Fig. 4). In unfenced plots, burnt plots had a mean sapling density that was 16.9 times higher than that of unburnt plots (95% confidence intervals 5.8 to 49) (Fig. 4a). This factor was lower inside fences, though still large: burnt plots here, had 6.6 times more saplings than unburnt ones (95% CLs 2.9 to 16). Similarly, fitted mean sapling cover at the end of the study was higher in burnt than unburnt plots, by

Table 1 Results of analyses of the effects of burning and fencing treatments on three measures of Scots pine sapling abundance: density, cover and maximum height. The units of measurement are given in the column headers but the estimates are presented in the scales of analyses, and therefore reflect either the link function (\log_e , for the density analysis) or the transformations (square-root, for the cover and height analyses) that were used for analysis

| | | y-variable | | | | | | | | |
|--|------------------|---|----------------|---------|-------------------|----------------|---------|-----------------------------|----------------|---------|
| | | Sapling density (stems recorded per plot) | | | Sapling cover (%) | | | Maximum sapling height (cm) | | |
| | | Estimate | Standard error | P-value | Estimate | Standard error | P-value | Estimate | Standard error | P-value |
| <i>Variables in the model:</i> | | | | | | | | | | |
| Intercept | | 2.26 | 0.32 | <0.001 | 2.74 | 0.27 | <0.001 | 16.06 | 2.04 | <0.001 |
| Experimental block | | See Fig. S2 | | <0.001 | See Fig. S2 | | <0.001 | See Fig. S2 | | 0.001 |
| Burning | Burnt | 1.74 | 0.18 | <0.001 | 1.59 | 0.10 | <0.001 | 9.04 | 0.80 | 0.004 |
| | Unburnt | -0.62 | 0.36 | | 0.69 | 0.10 | | 5.61 | 0.80 | |
| Fencing | Fenced | 0.64 | 0.26 | 0.639 | 1.30 | 0.10 | 0.031 | 8.11 | 0.80 | 0.168 |
| | Unfenced | 0.48 | 0.31 | | 0.97 | 0.10 | | 6.54 | 0.80 | |
| Burning \times Fencing | | See Fig. 4 | | 0.161 | See Fig. 4 | | 0.775 | See Fig. 4 | | 0.538 |
| <i>Pairwise treatment comparisons:</i> | | | | | | | | | | |
| Unburnt & unfenced vs | | | | | | | | | | |
| | Unburnt & fenced | -0.63 | 0.66 | 0.340 | -0.28 | 0.21 | 0.172 | -0.88 | 1.60 | 0.582 |
| Unburnt & unfenced vs | | | | | | | | | | |
| | Burnt & unfenced | -2.83 | 0.55 | <0.001 | -0.86 | 0.21 | <0.001 | -2.72 | 1.60 | 0.088 |
| Unburnt & unfenced vs | | | | | | | | | | |
| | Burnt & fenced | -2.52 | 0.55 | <0.001 | -1.23 | 0.21 | <0.001 | -5.00 | 1.60 | 0.002 |
| Unburnt & fenced vs | | | | | | | | | | |
| | Burnt & unfenced | -2.20 | 0.41 | <0.001 | -0.58 | 0.21 | 0.006 | -1.85 | 1.60 | 0.248 |
| Unburnt & fenced vs | | | | | | | | | | |
| | Burnt & fenced | -1.89 | 0.42 | <0.001 | -0.94 | 0.21 | <0.001 | -4.12 | 1.60 | 0.010 |
| Burnt & unfenced vs | | | | | | | | | | |
| | Burnt & fenced | 0.31 | 0.20 | 0.119 | -0.37 | 0.21 | 0.077 | -2.27 | 1.60 | 0.155 |

similar factors outside and inside fences: 6.7-fold and 4.6-fold respectively (Fig. 4b). Fitted maximum sapling height (Fig. 4c) was also higher in burnt than unburnt plots, by factors of 2.3 (outside fences) and 2.8 (inside fences).

The effect of deer exclusion by fencing was much weaker than that of burning. For sapling density and maximum height, the overall fence effect was non-significant ($P=0.64$ and 0.17 respectively; Table 1; Fig. 4). There was a modest positive effect of fencing on pine sapling cover ($P=0.03$); fitted mean cover was 1.6 and 2.3 times greater inside fences than outside, in burnt and unburnt plots respectively. There was no significant interaction between fencing and burning (Table 1).

Irrespective of treatment, all sapling measures varied significantly between experimental blocks ($P \leq 0.001$; Table 1). These differences were marked: the highest and lowest block means differing by factors of 38 (density), 72 (cover) and 21 (maximum height). Between these extremes, the ranked block means tended to form an approximate geometric series, i.e. they fell in a roughly linear sequence on a log scale (Fig. S2). The burnt plots strongly influenced block means, reflecting their much greater abundance of pine saplings than unburnt plots. When block means were estimated for burnt plots alone, these were strongly correlated with those from the full dataset: for density, cover and

height, correlations were 0.99, 0.99 and 0.78 respectively ($N=10$).

Seed-fall, browsing and photography

Seed-fall varied markedly between study years and experimental blocks (Fig. S3a, b). Year totals from the 10 years with data showed a 44-fold range of variation; the 2006 mast year was a clear outlier, having six times the seed-fall of the next highest year, and accounting for 60% of all recorded seed-fall during the study. Recorded seed-fall totals from the 10 experimental blocks varied more modestly but still showed an 8.5-fold range of variation. Across the study, an estimated mean of ~ 3.3 seeds fell per m^2 per year, or around 33,000 per ha per year. More than half the variation in fitted block means for sapling density was explicable in terms of variation between blocks in their study-wide mean proportion of seed-fall ($R^2=53\%$). Similarly, approximate counts ($\log_e[x+1]$ transformed) of mature trees within 25, 50 and 100 m of block centres explained, respectively, around 39%, 26% and 26% of variation in fitted block means of sapling density. These counts were also weakly correlated with block-level seed-fall for lower distance bands ($r=0.21$, 0.30 and -0.14 respectively; $N=10$); the relationship between

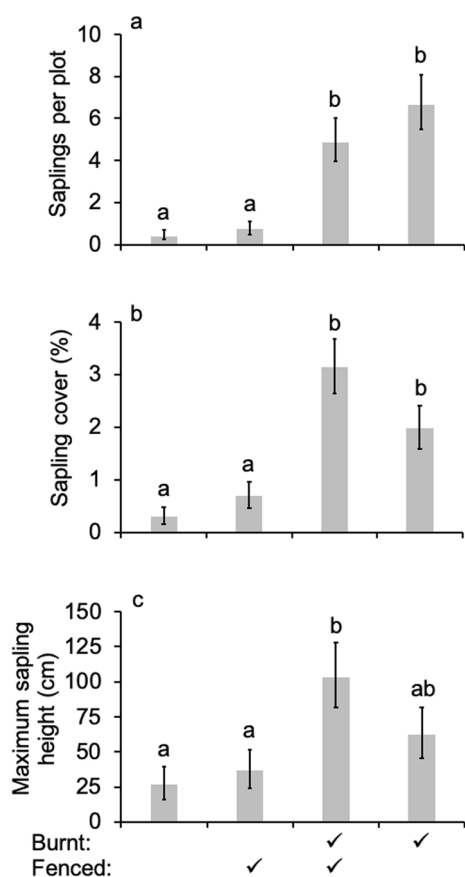


Fig. 4 Fitted treatment means for measures of sapling establishment at the end of the study (2017), 16 growing seasons after treatment: **a** density; **b** cover and **c** maximum height. Error bars show standard errors. Means as plotted are derived by back-transforming results of analyses, which used a \log_e link-function (density) or square-root transformation (cover and height). Letters indicate treatment means that differed significantly at $P < 0.05$. Exact P -values, estimates and standard errors are shown in Table 1. As for the observed raw data (Fig. 3), saplings per plot (Fig. 4a) can be converted to estimates of seedlings per ha, by multiplying by 312.5

seed-fall and mature trees in the 50 m distance band is shown in Fig. S3c.

Saplings at least 25 cm tall in the final year of the study sometimes showed some evidence of past browsing, averaging between 23 and 80% of saplings affected, depending on treatment (Fig. S4), although error bars were wide, indicating much variation between blocks. Some past browsing evidence was recorded inside fences, though this was less than half (~43%) of browse rates outside fences. With deer excluded by the fences, this within-exclosure browsing was likely due to smaller browsers like mountain hares and black grouse, which could pass through or over fences, and from which faeces were sometimes found.

In the Supplementary Material we present aerial photographs of each experimental block at the start and end of the study (Fig. S5) and examples of ground-based photographs

of vegetation development over the study period, in the different treatments (Fig. S6).

Discussion

Key results

This study provides further evidence that prescribed burning can markedly increase Scots pine recruitment in similar contexts, i.e. formerly forested open heathland near to seed trees. Building on our earlier studies at the seedling stage (Hancock et al. 2005; 2009) and similar seedling studies (i.e. carried out in the first few years post-germination) in other regions (Hille and den Ouden et al. 2004), we have shown here that, after 16 years, where deer were present at $\sim 6\text{--}7 \text{ kg ha}^{-1}$, burning led to a ~ 17 -fold increase in density of pine saplings. Similarly, in the presence of deer, on burnt plots, pine sapling cover was 6.7 times greater, and maximum height 2.3 times greater, compared to unburnt plots. Thus, all three measures of sapling abundance showed a strong increase following burning. Hence our results are consistent with a general tendency for disturbance events such as fires to facilitate sapling recruitment in small-seeded trees, and illustrate how marked such facilitation can be.

We believe that the main mechanism by which fire enhanced pine recruitment in our study system was via its influence on the moss and litter substrate. In our earlier papers (Hancock et al. 2005, 2009) we showed that slower moving fires, that consumed more of the moss and litter substrate, had greater seedling establishment rates. However, a wide range of processes, both abiotic (e.g. light, moisture, nutrients, frost) and biotic (e.g. browsing, competition, seed or seedling predation, allelopathy, microbial and fungal interactions) might influence seedling and sapling establishment, and be influenced by fire (see e.g. references in Hancock et al. 2005). A more detailed understanding of the relative importance of different mechanisms requires studies that manipulate potential mechanistic factors experimentally: see for example, Castro et al. (2002) who used this approach to demonstrate that the depth of the herbaceous layer, and seed predation, were the main mechanisms explaining low Scots pine seedling establishment in Mediterranean mountain meadows.

Intriguingly, at our study site with its relatively low deer densities, results hint that effects of burning on sapling density could even be enhanced by the presence of deer. Where deer were excluded, we only observed a 6.6-fold increase in sapling density after burning. Deer might preferentially browse competing vegetation, assisting the growth of young trees (Tercero-Bucardo et al. 2007), or—consistent with the substrate-disturbance mechanism discussed above—they

might create additional microsites for regenerating trees (Castro et al. 2002; Reimoser and Putman 2011). Although vulnerable to deer browsing, Scots pine is considered one of the less palatable trees in Scotland (<https://forestry.gov.scot/woodland-grazing-toolbox>). In general, fire and mobile ungulates can interact strongly in their influences on vegetation (Holdo et al. 2007). However, high variation in our results meant that any interactions associated with deer exclusion (i.e. the burn \times fence interaction terms in analyses) were not statistically significant. Also, unlike their possible positive effect on sapling density, deer did tend to reduce pine sapling cover. But in general, contrasting with the marked effects of fire, deer effects were relatively minor. This may partly reflect low deer numbers (by Scottish standards) at our study site, where estimates suggested around $\sim 6\text{--}7$ kg deer biomass per ha during this study. Here, intensive deer culling has been carried out for decades to encourage woodland expansion by natural regeneration, while recognising that red and roe deer are native species, and if not too abundant, could sometimes assist tree recruitment by creating regeneration niches (Gullett et al. 2023). It is well established that where there are high numbers of deer or other ungulates, these often prevent Scots pine regeneration; this is revealed when they are reduced, as shown in past work at our study site (Beaumont et al. 2005), our landscape partnership (Gullett et al. 2023), similar sites in our region (Rao 2017), other British heathland sites with Scots pine seed trees (e.g. Darwin 1859: Chapter 3) and other ecosystems with Scots pine (e.g. Zamora et al. 2001). However, where ungulate numbers are low, as during this study, then other factors such as seed-bed conditions may start to have relatively more significant effects on pine regeneration; some such factors are influenced by disturbances such as fire.

We could find no comparable studies that used a replicated experiment to study the effects of prescribed fire on Scots pine sapling recruitment. However, more broadly, fire experiments studying Scots pine at the seedling stage (Hille and den Ouden 2004) or recruitment in other pine species (e.g. Shelton and Wittwer 1991; Perkins 2015; Edwards et al. 2015), often showed similar results, with much greater recruitment after fire. Observational studies of Scots pine, and other pines sharing a similar fire regime (e.g. *P. ponderosa*, *P. nigra*: Pausas 2015), which have measured recruitment after management burning or wildfire, have given more varied results. Some studies found greater seedling densities in burnt areas (Lehto 1956; Sykes and Horrill 1981; Tardós et al. 2019), but others found no fire effect (Ouzts et al. 2015; Rao et al. 2017; Przybylski et al. 2022). These unreplicated or less formally designed studies perhaps illustrate the importance of site-specific factors such

as vegetation type or browsing effects, in influencing pine recruitment after fire.

Related to such site-specific factors, our own study showed that all three measures of sapling recruitment (density, cover, and maximum height) varied strongly ($\sim 20\text{--}70$ -fold) across our 10 experimental blocks. Other studies have also found very high variability in pine sapling densities after fire (e.g. Pausas et al. 2004; Turner et al. 2004). The pattern we found, of a geometric series in ranked post-disturbance sapling densities, has also been found elsewhere e.g. in *Nothofagus* forest (Coomes and Allen 2007). In our study, about half of the variation in sapling density (averaged across treatments within each block) was associated with variation in seed-fall. The remaining variation in this study may reflect a range of factors influencing tree demography between viable seed-fall and sapling establishment, such as seed predation, germination, and seedling establishment and survival, influenced for example by herbivory by invertebrates or small mammals (Munier et al. 2010; Nystrand and Granström 2000) or microclimatic effects (Vacchiano et al. 2015; Domisch et al. 2017). These results imply that such factors can vary markedly, even among replicates at one study site, despite these holding similar vegetation at the start of the study, and receiving similar prescribed burning treatments. This strong spatial variation within the study site supports our decision to use a blocked experimental design: such designs tend to be relatively efficient in this context (Quinn and Keough 2002).

High variability of natural regeneration density does not fit easily with definitions of “woodland” as “more than x stems per ha”. Densities that are both very much lower, and very much higher than commonly used thresholds appear to be an important part of the character of naturally regenerating pine woodland under our conditions (see also Gullett et al. 2023). Very low density stands, containing only scattered trees (a few per ha) nevertheless have important ecological functions, helping maintain woodland connectivity, supporting some characteristic species, and acting as nuclei for woodland expansion (Manning et al. 2006). One woodland definition used in the UK for allocating funding, is 400 stems per ha (UK Woodland Carbon Code www.woodlandcarbon-code.org.uk; this density was chosen as being likely to meet the 20% canopy cover definition of woodland used by the UK government (www.forestresearch.gov.uk)). Our study plots will require some years to become fully established forest stands. However, for now, this woodland density criterion was met with Scots pine saplings at least 25 cm high at 16 out of 20 burnt plots at the end of the study, contrasting with only 4 out of 20 unburnt plots. Hence for restoring young woodland, defined by this density threshold, sapling size threshold and study time-frame, prescribed burning was four times more effective than leaving areas unburnt.

Caveats and further research priorities

Although reasonably well replicated in space, our study was not replicated in time: all the fires took place in a single year (2002). Hence our results are contingent on the particular time period used. Aspects of that time period which could have influenced results included major heather die-back in 2003 (Hancock 2008); such events can be associated with tree colonisation (Marrs 1986). Our study also included a very high seed year in 2006, which produced 60% of all recorded seed-fall (Results; Hancock et al. 2009). Other studies show how integrating time-varying effects e.g. of herbivory on pine saplings, across multiple years, can yield more robust results (Herrero et al. 2016). For future experimental work, application of treatments across a number of years would improve generality, although results would then of course take longer to determine.

In any experiment, it is not possible to manipulate all factors of interest. And yet, various other considerations are of interest, which could affect how prescribed burning influences Scots pine recruitment, for example, patch size, vegetation community and season (spring or autumn) of prescribed burning. More broadly in the restoration of woodlands in our region, a range of other, related questions have been raised around how we might assist regeneration in practice. Can the interactions of deer (and potentially other mammals) with fire be better measured, for example using camera traps (Soyumert et al. 2020)? Can other techniques, like mowing or cattle grazing/trampling, have similar benefits (see below)? Does prescribed burning or other disturbance increase sapling recruitment for other small-seeded tree species, which are also the focus of restoration efforts, such as birches *Betula* spp. and aspen *Populus tremula* (Lankia et al. 2012; Parro et al. 2015)? Broadleaves like these are markedly under-represented at Abernethy due to past silvicultural management and formerly high deer numbers (Summers 2018). Some such questions are the focus of later experiments in the Cairngorms Connect area, to be reported separately (Wardle 2023; Gullett et al. in press); there are also ongoing trials at other nearby sites. In general, we consider there is a strong case for making better use of opportunities in nature conservation management to set up experiments to answer such questions (Ockendon et al. 2021; Tinsley-Marshall et al. 2022).

Management implications

The dramatic boost in Scots pine sapling recruitment we found here, lends strong justification to using this approach in similar contexts, e.g. where Scots pine woodland adjoins successional heathland dominated by heather. A 17-fold increase in recruitment is a very strong change, compared to

typical differences between alternative nature conservation management interventions. Indeed, following our earlier experimental results (Hancock et al. 2005; 2009), prescribed burning was widely used at Abernethy over a ~10-year period, to promote pine regeneration both at the forest edge and in forest gaps, with an average of ~2.5 ha burnt annually during 2004–10 (unpublished data and Summers 2018, p150). The technique can be quite costly: Roberts (2010) estimated costs of prescribed burning at Abernethy in or near woodland at around £800 per ha. Prescribed fires can sometimes escape from control, though if burning is well resourced and carefully applied, as at Abernethy during this period (Dugan 2004), these risks can be minimised. Given the costs, use of this approach might be most appropriate where a very high boost in tree recruitment was desired, at more challenging locations, e.g. distant from seed sources – in effect, zoning levels of intervention according to expected seed-fall. Costs could be reduced by scaling up, with prescribed burning of larger areas. This could explain why cost estimates in the US are much lower, at around £150 ha⁻¹ (see Cleaves et al. 1999, Table 1, management-ignited forest burning; perhaps ~£200 ha⁻¹ at 2010 prices).

However, in recent years there has been a move away from prescribed burning at Abernethy, reflecting cost considerations and increasing concern (see Holland et al. 2022) over the use of prescribed fire on peaty and organo-mineral soils, which are typical of much of the regeneration zone at this site and others in Scotland. Hence, as in other regions (Lucas-Borja et al. 2016) there has been increasing interest in other techniques that remove vegetation and disturb the substrate. Silvicultural approaches such as scarification have been effective in boosting pine and birch regeneration at nearby Mar Lodge estate (Mason et al. 2024). Within-forest trials of cultivation dating back to the 1930s in nearby Glenmore showed 3.9-times more recruitment than controls after 60 years (weighted mean of all treatments); however, the sparser regeneration in control plots also developed well (Edwards and Rhodes 2006). At Abernethy, interest has focussed on approaches such as pulses of cattle grazing and trampling, or mowing using tractor-mounted swipes or remote-controlled “robocutters”. Costs of machine cutting were estimated at around one third those of prescribed burning (Roberts 2010). Both cattle and mowing delivered similar benefits to prescribed burning, when the focus was field-layer management for capercaillie *Tetrao urogallus* (Hancock et al. 2023). A key question is whether these approaches can deliver a similar boost in regeneration of pine or other small-seeded tree species (Gullett et al. in press). This will partly reflect the extent to which unique characteristics created by fires, such as heat, ash, smoke and charcoal—known to have some ecological effects—play critical roles in seedling recruitment (Reyes and Casal 2004;

Pluchon et al. 2014; Keeley et al. 2011). Formal comparisons of burning and mowing are needed to help elucidate this (Wardle 2023). If proven, ideally through field trials like this one, then approaches like mowing may be highly practical for UK conditions. Ultimately, timescales are crucial to discussions around how much to intervene; considerable progress has been made with woodland expansion in our area over 30 years, with deer reduction being the only intervention in much of the area (Gullett et al. 2023). Disturbance management and other forms of “assisted regeneration” (Gullett et al. in press) are perhaps most relevant if we seek to markedly accelerate woodland expansion, particularly in challenging areas like those further from seed trees. To inform these discussions, even though some landowners like RSPB no longer use prescribed burning, it remains valuable to learn from earlier trials such as this one.

The strong boost in Scots pine sapling recruitment after fire found here, does raise the question as to whether fire and other disturbances are important in maintaining pine dominance in Scottish native pinewoods. Such disturbances characterise many woodlands with pine across Eurasia (Shorohova et al. 2009). A roughly 100-year fire return interval has been suggested as part of the natural disturbance regime for Scots pine woodland in Scotland (Mason and Alía 2000). In south-west Norway under a similar climate to Abernethy, Rolstad et al. (2017) found a ~73-year fire return interval in near-natural Scots pine forest. In western Scotland, under wetter climates than the main Scottish native pine-wood areas, sessile oak *Quercus petraea* and downy birch *Betula pubescens* tend to take over from pine as dominant native woodland species (Towers et al. 2004). Elsewhere in Europe, periods without fire or other disturbance have been linked to a shift away from Scots pine dominance, e.g. towards broadleaves such as oak *Quercus* spp. (Adámek et al. 2016; Jaroszewicz et al. 2019; Spînu et al. 2020). Even if fire is not needed to maintain pine, it can add to structural diversity (e.g. Kuuluvainen and Rouvinen 2000): our results support this by suggesting that young pine stands in burnt and unburnt areas can be very different in character.

At the outset of this study, concerns were raised that deer would target post-burn sites and reduce seedling recruitment. Rao et al. (2017) considered that this mechanism, likely linked to increased abundance of the tall and dense grass species *Molinia caerulea* (initially colonising the wet heath fire site from the seedbank), explained the lack of pine recruitment following wildfire on Mar Lodge estate in the eastern Cairngorms, only ~20 km from our study site. Nevertheless, our results imply that in similar contexts to this study, i.e. dry heaths with heather dominance and little *Molinia*, deer at low densities may have neutral or even weakly positive effects on pine sapling densities after burning. This would support the approach used in Cairngorms

Connect (Gullett et al. 2023), and at Mar Lodge (Rao 2017; Painting 2021), of seeking woodland restoration in the presence of deer. In the right contexts, our work shows that prescribed burning can play a valuable role in such restoration.

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Author contributions MHH led the study, with support from NRC. SJR contributed to the study design. SJR, JW, GM, MC, PG and MHH carried out data collection in different years (with assistance as acknowledged), as well as data collation, and initial stages of analysis and reporting. MHH completed the analyses and prepared the initial draft of this manuscript with support from PRG and NRC. All authors reviewed, revised and finalised the manuscript.

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Data availability The data that support the findings of this study are available from the authors upon reasonable request.

Declarations

Conflict of interest The authors declare no competing interests.

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