

# Benefits and costs of native reforestation for breeding songbirds in temperate uplands

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## ABSTRACT

Global tree planting initiatives may benefit biodiversity depending on woodland type, but ecological effects must be understood when woodland replaces open habitats supporting characteristic wildlife. In the UK's temperate uplands, large-scale reforestation is replacing long-established open 'moorland' (heath, bog and grassland) supporting breeding bird communities of conservation importance. We quantified breeding bird species richness and abundance in 8–24 year-old native woodland plantations in Scotland and adjacent moorland and used bird densities to predict potential future abundance changes in woodland and moorland avian indicator species from recent national-level woodland creation policies. Bird species richness at point counts increased with increasing woodland cover, height and age and declined with increasing elevation. Differing abundances of bird species of conservation concern between woodland and moorland were related to their associations with vegetation measures, especially woodland cover and tree species composition. The creation of 54.9 km<sup>2</sup> of native woodland in Scotland across 2017 and 2018 predicts reduced Meadow Pipit *Anthus pratensis* (moorland indicator) abundance of 6214 individuals or 0.13% of current UK population, and increased Willow Warbler *Phylloscopus trochilus* (indicator of young woodland) abundance of 6040 individuals or 0.13% of current UK population. Native woodland plantations comprised c34% of new woodland creation and the projections should be extended to other woodland types in particular non-native commercial conifer forestry. Native reforestation of open ground offers net gains in bird species richness but could disbenefit open-ground birds including those of conservation concern. Where retention of open-ground species is desired, landscape-scale reforestation should consider both woodland and open-ground wildlife.

## 1. Introduction

Deforestation is associated with globally increasing atmospheric carbon and biodiversity loss (Hansen et al., 2013). Some governments including those of India (Green Future, 2016) and China (Climate Action, 2018) have developed national reforestation policies aiming to reduce environmental degradation (Bonn Challenge, 2019), primarily through large-scale tree planting.

The UK plans to expand woodland cover as current woodland area (13% of land area) (Forest Research, 2019) is lower than most European countries (Scottish Government, 2019); the Scottish Government aims to create up to 15,000 ha of new woodland annually to 2032 (Scottish Government, 2019). Much UK woodland expansion will continue to comprise non-native, commercial conifer plantations (Mason, 2007; Scottish Forestry, 2019). However, reforestation with native

species is also occurring through governmental (Scottish Government, 2019) and non-governmental initiatives (including “rewilding”) (Carrifran Wildwood, 2019; Trees for Life, 2019).

UK reforestation will lead to further large-scale replacement of open habitat with woodland, following earlier woodland planting during the latter half of the 1900s, especially in the uplands (Avery and Leslie, 1990). Reforestation with native trees is expected to benefit woodland biodiversity, including some taxa of conservation importance (Quine and Humphrey, 2010; Scridel et al., 2017). However, the potential or actual benefits of this large-scale habitat change have received little research attention.

Much UK woodland creation is expected on land of low agricultural value, for example unenclosed upland heathland, bog and grassland (Woodland Expansion Advisory Group, 2012). These largely treeless ‘moorlands’ are derived from historical tree removal for timber, wood

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fuel and agricultural clearance, with grazing (primarily sheep, cows and deer) (Fuller and Gough, 1999) and burning (Thompson et al., 2016) preventing woodland re-establishment (Thompson et al., 1995). Due partly to the long timescale since deforestation, moorlands now support wildlife of international conservation importance, including the bird community (Thompson et al., 1995) comprising species such as Eurasian Curlew *Numenius arquata* and Meadow Pipit *Anthus pratensis*, of which the UK supports notable breeding populations (Brown et al., 2015). Woodland creation is expected to negatively affect open-ground birds, through habitat replacement (Ratcliffe, 2007) and predation-mediated edge effects (Amar et al., 2011; Douglas et al., 2014a; Wilson et al., 2014). Understanding the ecological effects of woodland expansion on wildlife is crucial for informing how reforestation could be delivered whilst minimising negative impacts on important open-ground taxa and reconciling differing visions for upland areas (Defra, 2013; POST, 2016).

Here we use a representative UK upland landscape comprising existing plantations of native-dominated woodland of varying ages and sizes, and adjacent unplanted moorland. We test effects of native reforestation on species richness of breeding bird communities and abundance of individual species of woodland and moorland. For species of conservation concern, this informs conservation management through knowledge of how the structure and composition of new woodland and unplanted moorland influences species abundance. We focus on songbird communities because despite being typically widespread and numerous, effects of woodland creation on open-ground songbirds in this system are poorly studied relative to other groups including shorebirds and Galliformes (Amar et al., 2011; Douglas et al., 2014a; Scridel et al., 2017; Wilson et al., 2014). For common indicator species of moorland (Meadow Pipit; Vanhinsbergh and Chamberlain (2001)) and young woodland (Willow Warbler *Phylloscopus trochilus*; Fuller et al. (1999)), we predict future national abundance changes under scenarios of increasing native woodland cover on moorland.

## 2. Methods

### 2.1. Study site

The site encompassed approximately 700-km<sup>2</sup> in Highland Perthshire (Fig. 1). The main habitats are unenclosed open moorland (58%; dwarf shrub heath, bog and grassland, with some areas managed for livestock grazing and recreational Red Grouse *Lagopus lagopus scoticus* and deer shooting), woodland (mature deciduous woodland [3%], commercial conifer woodland [15%] and new ‘native woodland plantations’ [6%]; see detail below) and ‘farmland’ (17%; enclosed fields/dwellings/buildings/roads) (Scridel et al., 2017).

Native woodland plantations or ‘plots’, typically comprising Scots pine *Pinus sylvestris*, birches *Betula* spp. and/or rowan *Sorbus aucuparia* in varying proportions, had been established within the area, mainly under Government grants from 1988 to 2006, usually by erecting fencing on moorland to exclude mammalian herbivores with subsequent planting or natural regeneration. We delineated woodland plots from available GIS layers (Forestry Commission, 2012) and ground-truthed boundaries and species composition; although native-dominated, an estimated c20% of the tree cover comprised non-native trees, predominantly Sitka spruce *Picea sitchensis* assumed to have been planted. We identified 28 native woodland plots > 0.05 km<sup>2</sup> although additional smaller fragments were present. Twelve such native plots (mean area 2.68 ± 0.66 km<sup>2</sup>) were selected. These were a non-random subset where access permission was obtained and excluded small fragments (< 0.25 km<sup>2</sup>) which were logistically inefficient for sampling. Breeding bird communities were unknown when selecting plots. Approximate native woodland plot ages (8 to 24 years) were estimated by subtracting the median year of each woodland creation grant from the study year (2012) as per Scridel et al. (2017). Although woodland creation activities such as fencing and planting might coincide with the first year of a

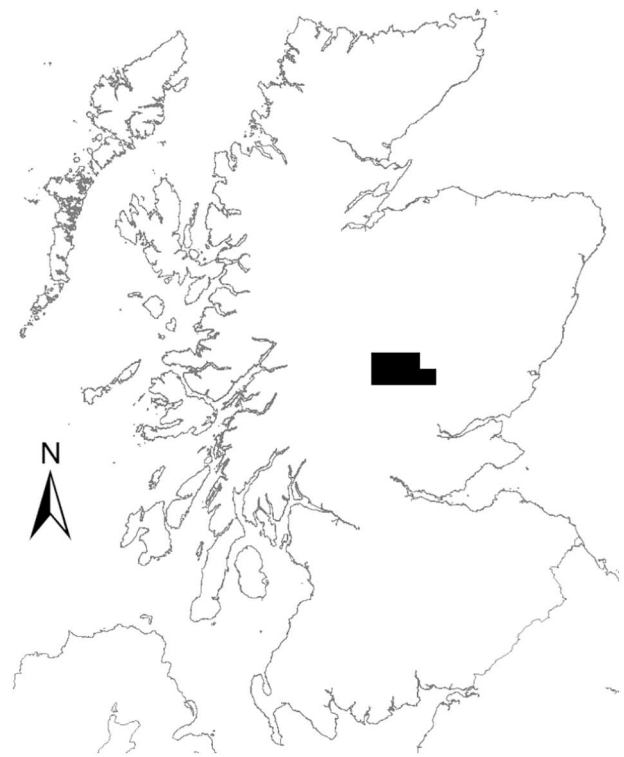


Fig. 1. Location of study area within the Scottish Highlands.

grant, this cannot be confirmed so median year yields a conservative plot age estimate.

### 2.2. Bird surveys

Bird surveys were point counts located 200 m apart along transects running between woodland and moorland, spacing transects by at least 500 m using national gridlines (Ordnance Survey, 2019). All transects specific to a plot were oriented on the same north-south or east-west axis though this varied between plots based on shape. Areas of unsafe (steep) terrain and patches of dense non-native conifers were avoided.

Woodland points were located from 3 m to 950 m inside plot boundaries and moorland points 1 m to 548 m outside plots, although 87% of the latter were within 300 m of woodland plot boundaries. Unsuitable sample points were trimmed when transects ran into dense non-native conifers, enclosed farmland, roads or water. In total 203 bird survey points were identified (145 woodland and 58 moorland) at elevations of 210-540 m, with 3–28 woodland points and 1–11 moorland points per plot.

Each point received an early (14 April–12 May) and late (14 May–20 June) breeding bird survey, commencing between 0600 and 1005 BST (GMT + 1) to target the morning period of greatest bird detectability (Bibby et al., 2000). Adverse weather (heavy or persistent rain or winds exceeding Beaufort scale force 4) was avoided as this could reduce bird activity or detection. On arrival at a point there was a 2-minute settling phase then a 10-minute bird survey, balancing false absences against multiple-recording of individual/s (Bonthoux and Balent, 2011). Birds were identified to species by sight and sound and all individuals recorded (excluding high-flying individuals assumed non-breeding) and assigned to distance bands of 0–50 m, 50–100 m and > 100 m for density calculations (Bibby et al., 1985). Birds knowingly detected from multiple points (e.g. singing from a prominent perch) were recorded only at the first encounter.

### 2.3. Habitat recording

From late June to July, habitat was measured at the 203 bird survey points. Using a cane marked with 1 cm wide bands at 5 cm intervals, three variables describing ground-layer vegetation height were measured as maximum height to the nearest 5 cm at two locations per point, holding the cane vertically to the ground at arm's length to either side of the observer. These were dwarf shrub height (pooling heather *Calluna vulgaris*, cross-leaved heath *Erica tetralix*, bell heather *Erica cinerea*, crowberry *Empetrum nigrum*, bilberry *Vaccinium myrtillus*, cowberry *Vaccinium vitis-idaea*), all grasses, and maximum height (any species); any relevant collinearity was addressed in analyses below. Ground-layer species richness comprised the number of plant species touched by a 1 m length of the cane lying horizontally to the ground, dropped randomly in front of the observer. Four tree variables (excluding shrubs e.g. gorse *Ulex* sp.) were estimated visually: within a 10 m radius of each point, categorical tree height index was either no trees, all < 3 m, mixed heights < 3 m and > 3 m or all > 3 m; the number of native and non-native tree species was counted separately; within a 100 m radius, percentage tree cover was estimated to the nearest 5%. At each point, slope and elevation were derived from 50-m gridded data (Panorama, Ordnance Survey UK) and linear distance to nearest woodland plot boundary was calculated using GIS to examine woodland edge effects on bird abundance.

### 2.4. Analyses

Analyses were conducted in R 3.5.2 (R Core Team, 2018).

### 2.5. Correlates of bird species richness in woodland and moorland

We used bird registrations within 50 m of points as a typical distance for reliable detection of most birds within woodland and scrub (Bibby and Buckland, 1987). A response variable of bird species richness per point was created by summing the number of species across both visits and modelled against fourteen environmental correlates (Table 1a). As initial modelling detected residual spatial

**Table 1**

Correlates of bird species richness at native woodland ( $n = 145$ ) and moorland ( $n = 58$ ) point counts using GLMMs with spatial autocorrelation term.

Term	Slope	SE	Wald	P
<i>(a) Univariate tests</i>	<i>(b)</i>	<i>(c)</i>	<i>(d)</i>	<i>(e)</i>
Woodland cover within 100 m	0.0114	0.00146	7.81	< 0.0001
Age of woodland plot	0.0478	0.0196	2.44	0.035
Area of woodland plot	-0.062	0.0393	1.58	0.146
Dwarf shrub height	-0.00448	0.00302	1.48	0.1394
Ground-layer plant species richness	-0.00114	0.0313	0.04	0.9711
Grass height	0.00215	0.0033	0.65	0.5148
Maximum ground-layer height	-0.00468	0.00319	1.47	0.1442
Native tree species richness	0.273	0.0504	5.41	< 0.0001
Non-native tree species richness	0.443	0.125	3.56	< 0.0001
Distance from plot boundary	-0.0000926	0.000283	0.33	0.7437
Tree height index			7.49	< 0.0001
Plot type (w)	0.510	0.113	4.52	< 0.0001
Gradient	0.021	0.0135	1.56	0.1209
Elevation	-0.00463	0.000871	5.32	< 0.0001
<i>(f) Minimum Adequate Model</i>	<i>(g)</i>	<i>(h)</i>	<i>(i)</i>	<i>(j)</i>
Woodland cover within 100 m	0.00537	0.00178	3.03	0.0028
Age of woodland plot	0.0350	0.0152	2.31	0.0439
Tree height index			3.34	0.0010
Elevation	-0.00325	0.000758	4.29	< 0.0001
<i>Non-significant terms deleted</i>				
Non-native tree species richness	-0.0809	0.136	0.59	0.5527
Plot type (w)	0.0695	0.121	0.58	0.5651
Native tree species richness	0.0962	0.0653	1.47	0.1428

autocorrelation (Moran's  $I > 0.1$ ) in SAS 9.4 (SAS, 2012) up to 1-km between points that could compromise inference (Ryan et al., 2004; Kraan et al., 2009), we used a Generalised Linear Mixed Model (GLMM) using the glmmPQL function in package MASS with Poisson errors, log-link, 'plot identity' random term and spatial correlation term, the latter selected from those within glmmPQL (Exponential, Gaussian, Linear, rational quadratic, spherical) by first fitting an intercept-only model to the response variable, fitting each correlation structure separately and selecting the term with the smallest residual sum of squares (linear; glmmPQL does not produce AIC values, Scridel et al. (2017)).

Important correlates of bird species richness were identified following Pearce-Higgins et al. (2009) who validated this approach. We first fitted univariate tests and retained variables with  $P < .1$ . The glmmPQL approach does not provide likelihood-ratio tests of fixed terms, so we used Wald t-statistics and associated  $P$ -values which approximate to  $P$ -values from likelihood-ratio tests (Scridel et al., 2017). We checked for collinearity which could distort model estimation ( $r > 0.7$ , Dormann et al., 2013) using pairwise correlations between pairs of retained variables and none was found. We then fitted a multivariate model of retained correlates and produced a MAM (Minimum Adequate Model) of terms significant at  $P < .05$  using stepwise deletion.

### 2.6. Correlates of bird abundance in woodland and moorland

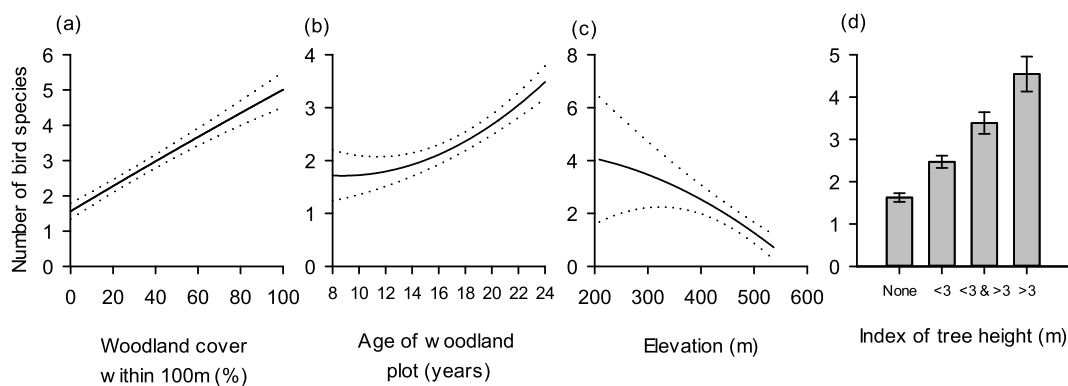
For bird species occurring at  $\geq 5\%$  of points in either habitat (Table 1b), we examined habitat-specific breeding abundances between plot-types (woodland and moorland) using glmmPQL models per species with response variable of maximum abundance per point within 50 m across the two visits, Poisson errors, log-link, plot identity random term, spatial correlation structure identified per species as above and plot-type factor.

Three bird species occurred in  $\geq 5\%$  of points in at least one habitat, showed significant or near-significant ( $P \approx 0.06$ ) differences in abundance between woodland and moorland and are of conservation concern in the UK (Amber or Red-listed; Eaton et al. (2015) and/or internationally (Birdlife International, 2018); Meadow Pipit, Willow Warbler and Common Redpoll *Acanthis flammea*. For these, we tested whether point-scale variation in abundance was related to habitat and topographic correlates (Table 1a). We used glmmPQL structures and the variable selection process above to derive MAMs.

### 2.7. Predicting changes in bird abundance from native woodland creation

Two abundant species (Meadow Pipit and Willow Warbler) showed contrasting abundances between plot-types (Table 1b) and are useful examples for predicting medium-term (< 25 years) abundance changes following native woodland creation on moorland in Scotland. We focus on 25 years as longer-term woodland impacts are harder to predict due to the potential influence and unknown timescales of management such as restructuring or felling.

The Meadow Pipit is a functionally important moorland indicator species as i) it is frequently the most abundant passerine in open upland habitats in the UK (Vanhinsbergh and Chamberlain, 2001; Balmer et al., 2013); ii) it is a crucial species in upland food webs – a major prey of raptors of conservation concern (Hen Harrier *Circus cyaneus* and Merlin *Falco columbarius*, Amar et al. (2008), Eaton et al. (2015)) and numerically important host for the brood-parasitic (UK Red-listed, Eaton et al., 2015) Common Cuckoo *Cuculus canorus* (Denerley et al., 2018); iii) its abundance varies predictably with key moorland land uses including grazing (Evans et al., 2015); iv) it is of UK, European and global conservation concern (Table 3). The Willow Warbler is an indicator species of young (< 25 years) upland woodland as i) it is positively associated with the early stages of woodland and scrub development (Fuller et al., 1999; Sim et al., 2016); ii) its distribution is increasingly shifting to the north and west of the UK and lower/mid-elevations of



**Fig. 2.** Bird species richness at sample points in native woodland plantation ( $n = 145$ ) and moorland ( $n = 58$ ) increases with increasing woodland cover (a) and age (b), declines with increasing elevation (c) and increases with increasing tree height index (d). Graphs show fitted relationships  $\pm$  95% CI derived from multivariate GLMM with spatial autocorrelation term.

the Scottish Highlands are among the areas of highest density (Balmer et al., 2013; Morrison et al., 2016); iii) its abundance varies predictably with major influences on woodland condition such as understorey deer browsing (Newson et al., 2012); iv) it is of UK conservation concern (Table 3); v) it is already used as a woodland indicator species (Defra, 2019).

We quantified representative breeding densities of both bird species in native-dominated woodland and moorland. We firstly calculated densities (D) from our study using Bibby et al. (1985):

$$D = \log_e(n/n_2) \times (n/m \pi r^2)$$

where  $n$  = total birds detected,  $n_2$  = number outside the pre-selected radius ( $r$ ) and  $m$  = number of points. Assumptions include random distribution and stationarity of birds during counts; detection probability declines with distance according to a half-normal function (and is one at distance 0); no multiple-counting; allocation to the correct distance class without error and this approach allows for biases due to different detectabilities by species or habitat which affect bird census techniques.

To provide representative densities across comparable habitats, we collated a minimum of two additional densities per species and habitat from available literature, using Scotland-focused studies where possible (Appendix 2a). Woodland estimates focussed on native woodland for consistency with our study and because the aim is to assess changes in bird abundance as native woodland replaces moorland.

We derived mean densities (birds  $\text{km}^{-2}$ ) across collated estimates per species/habitat using a 10,000-iteration resampling procedure with replacement, setting length = 3 to calculate mean across three sampled densities per iteration (the minimum number of density estimates per species/habitat, Appendix 2a).

We subtracted moorland breeding density from that in woodland to quantify the effect of creating  $1\text{km}^2$  of native woodland on moorland. In 2017 the Scottish Government published new targets for annual woodland creation area (Scottish Government, 2017). We used the most recently available data (November 2019, Scottish Forestry, 2019) to examine claimed areas of native woodland creation for 2017 and 2018. We extrapolated bird density changes per  $\text{km}^2$  of woodland to annual areas created nationally to calculate bird abundance changes. Simplifying assumptions are that changes in breeding abundance are unaffected by other factors, open-ground birds displaced by woodland are lost to the population and habitat-specific densities remain constant with respect to variables such as distance from woodland (modelling above showed no association [ $P > .8$ ] between abundance and distance from woodland plot boundary). We express predicted changes in abundance as approximate percentages of UK population estimates (Musgrove et al., 2013), converting from pairs or territories to mature individuals by doubling following Musgrove et al., 2013; (BirdLife

International, 2018); the methods used to derive population estimates in Musgrove et al. (2013) and the current study are not directly comparable and provide approximate percentage changes.

### 2.8. Habitat structure and composition in woodland and moorland

To aid interpretation of bird-habitat associations, we examined how four significant point-scale habitat correlates of bird species richness or abundance (percentage woodland cover within 100 m, tree height index and species richness of native and non-native trees) differed in relation to three explanatory variables (plot-type, woodland plot age and elevation) fitted simultaneously to each response variable.

Percentage woodland cover was rescaled to a proportion, logit-transformed to normalise after adding 0.01 to values (following Douglas et al., 2015) and analysed using glmmPQL with Gaussian errors, identity-link and plot identity random term, selecting a spatial correlation structure (linear) as above and then adding the three explanatory variables above to the model. Tree height index was analysed using an ordinal cumulative link mixed model using the function clmm2 in package “ordinal” with a factor of plot identity. Native and non-native tree species richness were analysed separately using glmmPQL with Poisson errors, log-link, plot identity random term and the best-fitting spatial correlation structures which achieved convergence (native = spherical; non-native = rational quadratic).

## 3. Results

### 3.1. Correlates of bird species richness in woodland and moorland

In univariate tests, plot-type was a strong predictor of breeding bird species richness (Table 1a), with higher mean species richness in woodland ( $2.76 \pm 0.07$ ) than moorland ( $1.77 \pm 0.07$ ). This term dropped out during multivariate modelling because point- or plot-specific variables were stronger correlates of species richness (Table 1b). In the Minimum Adequate Model (MAM), bird species richness increased with increasing woodland cover, age and index of tree height and decreased with increasing elevation (Table 1b, Fig. 2).

### 3.2. Correlates of bird abundance in woodland and moorland

Fourteen bird species occurred at  $\geq 5\%$  of points in either woodland or moorland (Table 2). Abundances of eight species were significantly or near-significantly ( $P \approx 0.06$ ) higher in woodland with one (Meadow Pipit) more abundant on moorland (Table 2). Three of these species are of UK conservation concern and Willow Warbler and Common Redpoll were more abundant in woodland and Meadow Pipit more abundant in moorland (Table 3).



**Table 2**  
 Occurrence and abundance of breeding bird species recorded at  $\geq 5\%$  of points in native woodland plantations (n = 145 points) and adjacent moorland (n = 58). 'Conservation status' denotes status within UK (UK, R = Red, A = Amber; Eaton et al., 2015), Europe (EU, NT = Near-threatened; IUCN, 2015) or globally (GL; IUCN, 2019). 'Mean abundance' is model-derived mean counts of individuals within 50 m radius of point counts. 'Correlates of species abundance' were analysed for three species (in bold) showing significant or near-significant ( $P \approx 0.06$ ) differences in abundance between woodland and moorland and which have adverse UK conservation status (Red or Amber; Eaton et al., 2015); correlates shown are multivariate Minimum Adequate Model (MAM) per species from GLMM with spatial autocorrelation term; symbols denote positive (+) or negative (–) direction of relationships, asterisks denote significance level of each term in MAM (\* $P < .05$ , \*\* $P < .01$ , \*\*\* $P < .001$ , \*\*\*\* $P < .001$ ).

	% points recorded				Mean abundance $\pm$ SE				Correlates of species abundance					
	Conservation		Wood- Moor-		Woodland		Moorland		Woodland cover within 100 m (%)		Number of non-native tree species		Number of native tree species	
	Status	land	land	All	Woodland	Woodland	Moorland	t	P	Woodland cover within 100 m (%)	Number of non-native tree species	Number of native tree species	Elevation	
Meadow Pipit <i>Anthus pratensis</i>	UK-A; EU, GL-NT	62.8	82.8	68.5	1.42 $\pm$ 0.06	2.41 $\pm$ 0.06	4.35	< 0.0001	-.***	-.**	-.*			
Willow Warbler <i>Phylloscopus trochilus</i>	UK-A	44.8	8.6	34.5	0.68 $\pm$ 0.02	0.31 $\pm$ 0.00	2.31	0.0217	+.***	+.*				
Chaffinch <i>Fringilla coelebs</i>		24.8	6.9	19.7	0.47 $\pm$ 0.07	0.12 $\pm$ 0.01	2.88	0.0044						
European Robin <i>Erithacus rubecula</i>		24.1	5.2	18.7	0.27 $\pm$ 0.03	0.05 $\pm$ 0.00	3.21	0.0016						
Coal Tit <i>Periparus ater</i>		19.3	1.7	14.3	0.32 $\pm$ 0.06	0.02 $\pm$ 0.00	2.89	0.0043						
Eurasian Siskin <i>Spinus spinus</i>		15.9	6.9	13.3	0.23 $\pm$ 0.01	0.11 $\pm$ 0.00	1.57	0.1192						
Common Redpoll <i>Acanthis flammea</i>	UK-R	14.5	3.4	11.3	0.21 $\pm$ 0.00	0.05 $\pm$ 0.00	1.89	0.0608				+.***		
Goldcrest <i>Regulus regulus</i>		14.5	1.7	10.3	0.16 $\pm$ 0.01	0.03 $\pm$ 0.00	2.09	0.0383						
Eurasian Wren <i>Troglodytes troglodytes</i>		11	5.2	9.4	0.13 $\pm$ 0.18	0.04 $\pm$ 0.01	1.93	0.0554						
Duncock <i>Prunella modularis</i>	UK-A	6.2	3.4	5.4	0.07 $\pm$ 0.00	0.05 $\pm$ 0.00	0.5	0.6186						
Common Woodpigeon <i>Columba palumbus</i>		5.5	3.4	4.9	2.40 $\pm$ 1.52	2.07 $\pm$ 0.63	38.28	< 0.0001						
Red Grouse <i>Lagopus lagopus scoticus</i>	UK-A	2.1	6.9	3.4	0.03 $\pm$ 0.00	0.09 $\pm$ 0.00	1.14	0.1588						
Eurasian Skylark <i>Alauda arvensis</i>	UK-R	0	5.2	1.5	Model did not converge	0.00 $\pm$ 0.00								
Northern Wheatear <i>Oenanthe oenanthe</i>		0	5.2	1.5	0.00 $\pm$ 0.00	0.07 $\pm$ 0.01	< 0.01	0.9998						

**Table 3**

Vegetation differences between sample points in native woodland plantations ( $n = 145$ ) and moorland ( $n = 58$ ). Separate multivariate models were per response variable, using the three explanatory variables elevation, plot age and two-level plot-type factor woodland/moorland. Symbols denote positive (+) or negative (-) relationships and asterisks denote significance level of each term (\* $P < .05$ , \*\* $P < .01$ , \*\*\* $P < .001$ ). The two final columns denote overall mean  $\pm$  SE values of each response variable in woodland and moorland points.

Response variable	Explanatory variables				Woodland	Moorland
	Plot	Plot	Plot	Plot		
Woodland cover within 100 m (proportion)	Elevation	Age	Type		Mean	Mean
Number of native tree species	—***	+***	***		$0.28 \pm 0.00$	$0.15 \pm 0.00$
Number of non-native tree species	—***	ns	***		$0.83 \pm 0.04$	$0.05 \pm 0.00$
Tree height	ns	+*	**		$0.18 \pm 0.02$	$0.02 \pm 0.00$
	—***	+***	***			

A further 24 species occurred at  $< 5\%$  of points (Appendix 1) of which 12 are of UK conservation concern (9 Red and 3 Amber). Habitat-specific abundances were not formally analysed due to low occurrences at point counts but in a qualitative comparison 8 out of 12 were recorded more frequently at woodland than moorland point counts.

Of the three species of conservation concern for which habitat associations were analysed (Table 2), Meadow Pipit abundance decreased with increasing woodland cover and increasing non-native tree species richness (Fig. 3a-b). Willow Warbler abundance increased with increasing woodland cover, number of native tree species at a point and peaked at elevations around 350 m (Fig. 3c-e). Abundance of Common Redpoll peaked at an intermediate value of native tree species richness (around 2 species per point) (Fig. 3f).

### 3.3. Predicting changes in bird abundance from native woodland creation

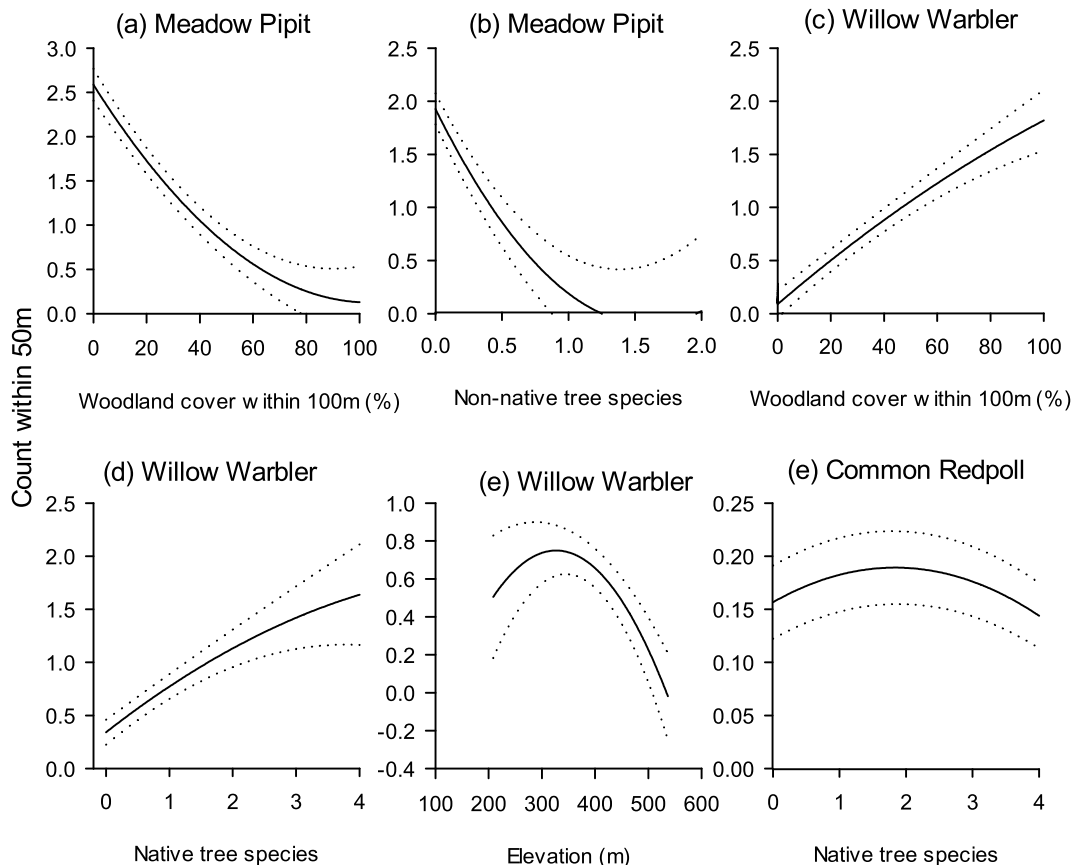
Meadow Pipit breeding densities were estimated as mean 116.7

individuals  $\text{km}^{-2}$  in young native woodland and  $230.0 \text{ km}^{-2}$  on moorland. The creation of  $54.9 \text{ km}^2$  native woodland in Scotland across 2017 and 2018 is predicted to result in 6213 fewer Meadow Pipits or 0.13% of the UK population estimate of 4,000,000 individuals (Musgrove et al., 2013).

Willow Warbler breeding densities were estimated as 117.0 individuals  $\text{km}^{-2}$  in young native woodland and  $6.9 \text{ km}^{-2}$  on moorland. Creation of  $54.9 \text{ km}^2$  native woodland in Scotland across 2017 and 2018 is predicted to result in 6040 more individuals, representing 0.13% of UK population estimate of 4,800,000 individuals.

### 3.4. Habitat structure and composition in woodland and moorland

Woodland cover at a point increased with increasing woodland plot age, declined with increasing elevation and was overall higher in woodland than moorland plots (Table 3, Fig. 4a-b). Native tree species richness declined with elevation (Table 3, Fig. 4c) and was higher in



**Fig. 3.** Correlates of individual species abundance at sample points in native woodland plantation ( $n = 145$ ) and moorland ( $n = 58$ ). Graphs show fitted relationships  $\pm$  95% CI derived from multivariate GLMM with spatial autocorrelation term.

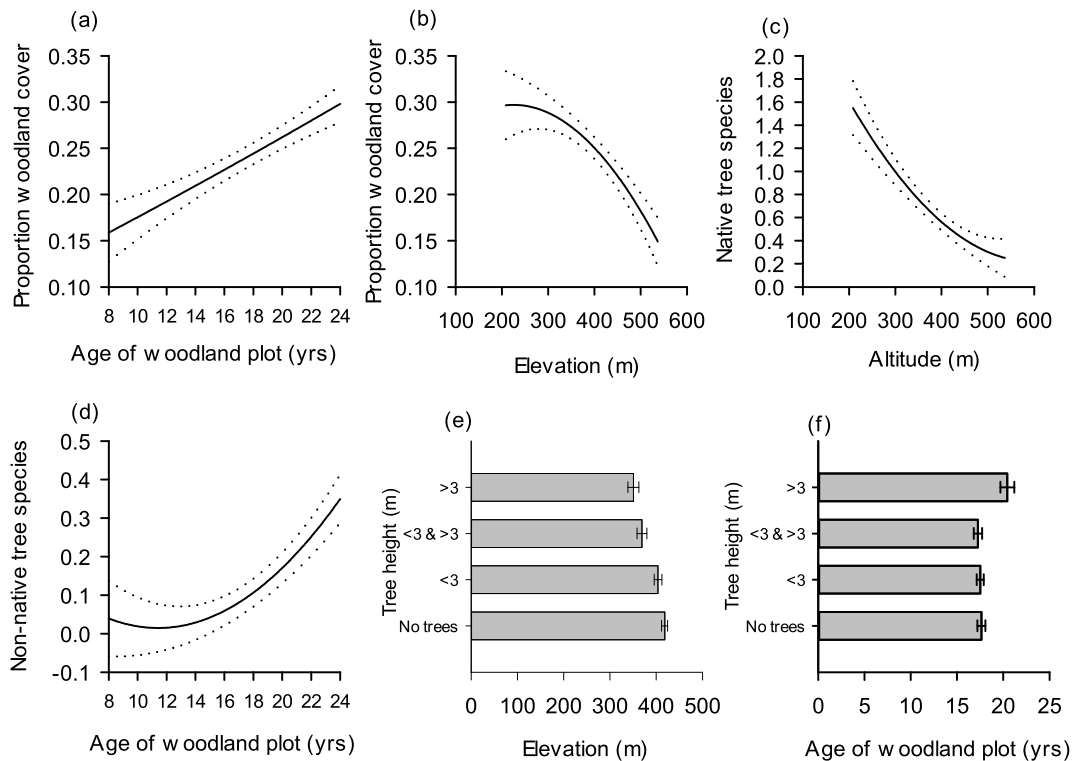


Fig. 4. Correlates of habitat measures at sample points in native woodland plantations ( $n = 145$ ) and moorland ( $n = 58$ ). Graphs show fitted relationships  $\pm$  95% CI derived from multivariate GLMMs with spatial autocorrelation term.

woodland than moorland but did not differ with woodland plot age (Table 3). Non-native tree species richness increased with increasing woodland age and was higher in woodland than moorland, but did not differ with elevation (Table 3, Fig. 4d). The tree height index was lower at higher elevation, higher with increasing woodland plot age and was higher in woodland than moorland (Table 3, Fig. 4e–f).

#### 4. Discussion

The higher breeding bird species richness in native woodland plantations relative to open moorland is consistent with previous patterns of species richness, although the specific types of woodland and open ground differ between studies (e.g. Calladine et al., 2013; Goetz et al., 2014). Increasing bird species richness with increasing woodland cover, age and tree height index suggest positive associations with woodland maturation, as woodland cover and tree height were highest in areas where woodland was longest established. Other studies have shown general patterns of increasing bird species richness with maturation of native woodland subject to varying management (Winkler, 2005; Bergner et al., 2015). Calladine et al. (2013) however found that younger woodland had higher bird species richness than older woodland, although the predominantly non-native commercial plantations of Calladine et al. (2013) become increasingly dense with age and canopy closure which can disbenefit some birds including Black Grouse (Pearce-Higgins et al., 2007; Pearce-Higgins et al., 2016). The decline in bird species richness with increasing elevation we found is well known (Hortal et al., 2013; Kim et al., 2018); some studies find that species richness peaks at mid-elevation before declining at higher elevation, although we found a more linear decline in species richness with increasing elevation within the elevational range of our study. Woodland cover, tree height index and native tree species richness declined with increasing elevation and may help explain elevational declines in bird species richness in our study.

Despite comprising predominantly open-ground, the moorland in our study contained some tree cover which increased with increasing

age of the adjacent woodland plot. Moorland in our study was within 550 m of woodland plots and this suggests that over time trees establish beyond the boundary of woodland plots, for example through self-seeding. Bird species richness can be highest at the woodland-open-ground interface (Calladine et al., 2013; Terraube et al., 2016), although we found no significant association between species richness and proximity to woodland edge. Native woodland plantations in our study included up to 20% open-ground area when created (Forestry Commission, 2003), so might present a less clearly-defined interface between woodland and moorland and may therefore induce weaker edge effects on bird distributions.

Abundance of most bird species, including many species of conservation concern, was generally higher in native woodland than moorland, with only Meadow Pipit more abundant on moorland. Similarly, Terraube et al. (2016) found that a bird conservation value index was higher in temperate forest than adjacent open habitats in France. Woodland in our study area was predominantly young (< 25 years) native-dominated woodland and precludes a within-study comparison of bird species richness and abundance between woodland types e.g. native versus non-native (commercial conifer plantations). However, in climatically-similar Ireland, Sweeney et al. (2010) found that bird species richness was higher in native woodland than non-native plantation forestry.

Our model predictions suggest contrasting fortunes for two abundant indicator species in response to native woodland creation. In the initial two years (2017 and 2018) since Scottish Government published new targets for woodland creation to 2032 (Scottish Government, 2017), our predictions suggest an increase in Willow Warbler of about 0.13% of current UK population size and decline in Meadow Pipit of about 0.13% of current UK population size. These changes are modest but reflect only two years of native woodland creation against long-term aspirations to deliver more woodland of a range of types (Scottish Government, 2017). In 2017–2018, native woodland comprised a minimum of around 35% of new woodland (Appendix 2), with a large proportion of the remainder being non-native commercial conifer

plantations (Scottish Forestry, 2019). Our predictions should be extended to other woodland types to enable an evidence-based assessment of the effects on bird communities of reforestation with other woodland, in particular the large areas of non-native commercial conifers. Crucially, if bird densities differ between woodland types (in particular native and non-native), the effects of large-scale woodland creation on bird abundance will be strongly dependent on the woodland type created. Therefore, although our aim was not to compare predicted changes in bird abundance under the alternative scenarios of native and non-native (commercial) woodland creation on open ground, such a comparison would be valuable for understanding future biodiversity responses to woodland creation policy. In tropical systems, native trees in human-modified landscapes are associated with greater benefits for birds than non-native trees (Douglas et al., 2014b).

Our moorland indicator species, the Meadow Pipit, in addition to having an adverse conservation status (Table 3), is a crucial species of upland food webs, being a major prey item of threatened raptor species such as Hen Harrier and Merlin (Amar et al., 2008; Eaton et al., 2015) and a numerically important host species for the declining (Eaton et al., 2015) Common Cuckoo (Denerley et al., 2018). This study suggests that replacement of long-established open-ground through woodland expansion could have far-reaching implications for upland food webs through reduction in prey and host abundance, with negative effects for open-ground bird species.

This study mainly focussed on the breeding songbird community. Effects of woodland creation on open ground on other birds such as Galliformes (e.g. Black Grouse *Lyrurus tetrix*) vary from positive to negative, depending on woodland type and/or age (Pearce-Higgins et al., 2007; Scridel et al., 2017; Pearce-Higgins et al., 2016), and for shorebirds are overwhelmingly negative (Amar et al., 2011; Douglas et al., 2014a; Wilson et al., 2014).

Globally, in response to, or to compensate for, widespread deforestation (Hansen et al., 2013), many countries are undertaking large-scale reforestation programmes (Bonn Challenge, 2019). Our study provides an example of the ecological effects of native reforestation in

the temperate zone, in an area subject to long-term tree loss, and shows how use of sample densities can enable predictions of wildlife abundance changes from reforestation. The restoration of native woodland in temperate uplands should have net gains for overall bird species richness. Areas that have been treeless in the long-term can however support characteristic fauna adapted to open ground. If the retention of important open-ground wildlife is desired, the spatial delivery of landscape-scale reforestation should account for both woodland and open-ground wildlife.

#### CRediT authorship contribution statement

**David J.T. Douglas:** Conceptualization, Methodology, Validation, Formal analysis, Writing - original draft, Visualization, Supervision, Project administration, Funding acquisition. **Jonathan D. Groom:** Methodology, Investigation, Data curation. **Daive Scridel:** Formal analysis, Writing - review & editing.

#### Declaration of competing interest

The authors declare they are not aware of any conflict of interest arising from this work.

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**Appendix 1. Species recorded at  $\leq 5\%$  of sample points in native woodland plantations ( $n = 145$  points) or moorland ( $n = 58$ ). Occurrence is shown within 50 m of point count locations. ‘Conservation status’ denotes conservation status within UK (R = Red, A = Amber; Eaton et al., 2015), Europe (EU, NT = Near-threatened; IUCN, 2015) or globally (GL; IUCN, 2019)**

	Conservation status	% points recorded		
		Woodland	Moorland	All
European Stonechat <i>Saxicola rubicola</i>		4.1	1.7	3.4
Eurasian Blue Tit <i>Cyanistes caeruleus</i>		3.4	0.0	2.5
Great Tit <i>Parus major</i>		3.4	0.0	2.5
Barn Swallow <i>Hirundo rustica</i>		2.8	3.4	3.0
Black Grouse <i>Lyrurus tetrix</i>	UK-R	2.1	0.0	1.5
Tree Pipit <i>Anthus trivialis</i>	UK-R	2.1	0.0	1.5
Eurasian Curlew <i>Numenius arquata</i>	UK-R; EU, GL-NT	1.4	3.4	2.0
Whinchat <i>Saxicola rubetra</i>	UK-R	1.4	3.4	2.0
Common Snipe <i>Gallinago gallinago</i>	UK-A	1.4	1.7	1.5
Common Crossbill <i>Loxia curvirostra</i>		1.4	0.0	1.0
Common Grasshopper Warbler <i>Locustella naevia</i>	UK-R	1.4	0.0	1.0
Greylag Goose <i>Anser anser</i>	UK-A (not feral)	1.4	0.0	1.0
Mallard <i>Anas platyrhynchos</i>		0.7	3.4	1.5
Common Blackbird <i>Turdus merula</i>		0.7	0.0	0.5
Great Spotted Woodpecker <i>Dendrocopos major</i>		0.7	0.0	0.5
Hen Harrier <i>Circus cyaneus</i>	UK-R	0.7	0.0	0.5
Eurasian Jay <i>Garrulus glandarius</i>		0.7	0.0	0.5
Mistle Thrush <i>Turdus viscivorus</i>	UK-R	0.7	0.0	0.5
Common Reed Bunting <i>Emberiza schoeniclus</i>	UK-A	0.7	0.0	0.5
Common Redstart <i>Phoenicurus phoenicurus</i>	UK-A	0.7	0.0	0.5
Eurasian Treecreeper <i>Certhia familiaris</i>		0.7	0.0	0.5
Eurasian Woodcock <i>Scolopax rusticola</i>	UK-R	0.7	0.0	0.5
Carrion Crow <i>Corvus corone</i>		0.0	3.4	1.0
Grey Wagtail <i>Motacilla cinerea</i>	UK-R	0.0	1.7	0.5



## Appendix 2. Predicting abundance changes for meadow pipit and willow warbler from native woodland creation

### (a) Breeding densities per species in woodland and moorland

Estimates from woodland focussed on native woodland < 25 years old for consistency with this study (excluding closed-canopy/post-thicket woodland where the age was not stated). If densities in a study were presented using more than one calculation method, we used the one closest to [Bibby et al. \(1985\)](#) for consistency with the current study. Published Willow Warbler densities on moorland in Scotland were limited so we included estimates from comparable moorland studies elsewhere in the UK.

Species	Broad habitat	Habitat details	Study location	Density (birds km <sup>-2</sup> )	Density calculation method (additional notes)	Reference
Meadow pipit	Moorland	Moorland < 550 m from NWP*	C Scotland	281.4	BIBBY	Current study
		Moorland	S Scotland	201.0	EMLEN (utilised seasonal median 0600-0900 counts)	<a href="#">Thirgood et al., 1995</a>
		Moorland < 1 km of woodland	S Scotland	287.9	BIBBY	<a href="#">Calladine et al., 2014</a>
		Moorland > 200 m from woodland	S Scotland	290.8	DISTANCE	<a href="#">Buchanan et al., 2006</a>
		Moorland	N/NE Scotland	89.0	SIMPLE (extrapolated from 0.89 ha <sup>-1</sup> )	<a href="#">Fuller et al., 1999</a>
Meadow pipit	Woodland	Woodland/moorland fringe NWP* < 25 years	S Scotland	171.9	BIBBY	<a href="#">Calladine et al., 2014</a>
		Young birch woodland < 25 yrs	C Scotland	173.3	BIBBY	Current study
			N/NE Scotland	3.5	SIMPLE (extrapolated 0.07, 0 per ha = mean 0.035)	<a href="#">Fuller et al., 1999</a>
					Excluded pine scrub which included closed canopy	
Willow warbler	Moorland	Moorland < 550 m from NWP*	C Scotland	23.9	BIBBY	Current study
		Moorland	N Scotland	0.0	SIMPLE (count 0 in 38.2 km <sup>2</sup> )	RSPB, unpubl. Data. Methods in <a href="#">Sansom et al. (2016)</a> . Utilised two pre-construction baseline years
		Moorland < 1 km of woodland	S Scotland	6.4	SIMPLE (estimate using BIBBY was NA)	<a href="#">Calladine et al., 2014</a>
		Moorland	N/NE Scotland	10.0	SIMPLE (extrapolated 0.2, 0 birds ha <sup>-1</sup> = mean 0.1)	<a href="#">Fuller et al., 1999</a>
		Moorland	N Wales	0.7	SIMPLE	<a href="#">Warren and Baines, 2012</a>
		Moorland	N England	0.4	SIMPLE (count 182 in 503 km <sup>2</sup> )	<a href="#">Carr and Middleton, 2004</a>
Willow warbler	Woodland	NWP* < 25 years	C Scotland	59.9	BIBBY	Current study
		Woodland/moorland fringe	S Scotland	179.7	BIBBY	<a href="#">Calladine et al., 2014</a>
		Young birch woodland < 25 yrs	N, NE Scotland	111.5	SIMPLE (extrapolated 1.3, 0.93 birds ha = mean 1.115)	<a href="#">Fuller et al., 1999</a>

\*NWP = Native woodland plantation.

Density calculation methods:

BIBBY: [Bibby et al. \(1985\)](#) - assumes common detection function.

EMLEN: Method from [Emlen \(1971\)](#).

DISTANCE: Distance sampling ([Thomas et al., 1998](#)).

SIMPLE: Simple bird density: individuals/area.

Woodland fringe habitats from [Calladine et al. \(2014\)](#) were included here as native woodland, as the native species' defined as shrub by [Calladine et al. \(2014\)](#) (birch, rowan, willow) were more frequent than non-native species (sitka spruce or lodgepole pine).

### (b) Areas of native woodland created in Scotland

We used areas claimed for payment in 2017 and 2018 on the assumption that these areas have been created ([Scottish Forestry, 2019](#)).

Woodland type	2017 area (ha)	2018 area (ha)
Conifer option	3384	5024
Diverse conifer	338	980
Broadleaves	377	192
Native broadleaves*	612	1336
Native Scots pine*	296	1248
Native upland birch*	419	826
Small or farm woodlands	111	91
Broadleaves in Northern and Western Isles	8	4

Native low density*	42	195	
Natural regeneration*	514	0	Grand total
Total	6101	9896	15,997
Native	1883	3605	5488

\* Woodland types included in our total area of native woodland created. Some native woodland might potentially be included other woodland types but areas are unknown.

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