

Restoring Mediterranean heathlands for declining birds: Initial responses to mosaic cutting and prescribed burning in the Natura 2000 LIFE program

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Abstract

1. Globally, loss and degradation of open habitats is causing biodiversity loss. Conserving important open habitats and the animal species that rely on them will require management interventions to reduce tree encroachment and to maintain open vegetation. Effectiveness of interventions will depend on knowledge of how species respond to the spatial and temporal configuration of treatments. Here, we assess short-term (5 years) responses of open habitat birds of conservation concern to mosaics of cutting and prescribed burning in a Mediterranean heathland Natura 2000 Special Area of Conservation (SAC) and Special Protection Area (SPA).
2. In the Pratomagno SAC (central Italy), vegetation structural characteristics and open habitat birds were surveyed from pre-treatment (only vegetation) to up to 4 years post-treatment. Birds were monitored each spring along fixed transects (7 reference, 19 treatment). First, we compared post-treatment trajectories of vegetation structure among treatment types. Then, we built non-linear mixed-effects models to assess changes in the abundance of singing individuals of open habitat birds (1) over time in treatment and reference areas; and (2) in response to the extent of treated vegetation within three age categories (<1 year, 1 year and >1 year since treatment).
3. Within 4 years of treatment, shrubby vegetation was regenerating on a trajectory towards that of untreated vegetation and reduced tree height was reduced. Abundance of the Dartford warbler (Natura 2000 target species)

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and cirl bunting declined significantly over time in control but not reference areas. Total abundance and that of the Dartford warbler, Moltoni's warbler and common stonechat declined significantly in response to the extent of vegetation <1 year since treatment, but not the extent of older age classes. The woodlark (also target species) and cirl bunting showed non-significant positive trends to the extent of vegetation >1 year and <1 year since treatment, respectively.

4. Synthesis and applications. Initial responses of open habitat birds indicate that mechanical cutting and prescribed burning in heathlands can maintain habitat to support open habitat bird species when applied in a mosaic approach. Vegetation treatments that resemble historic disturbance regimes (spatially and temporally staggered small-scale interventions) are recommended to regenerate vegetation, reduce tree encroachment and provide habitat for declining birds.

KEY WORDS

biodiversity conservation, European dry heaths, global change, integrated fire management, mastication, open habitat birds, prescribed fire, vegetation management

1 | INTRODUCTION

Open habitats throughout the world are declining in extent and condition due to widespread changes in land management and agricultural intensification, leading to biodiversity loss (European Environment Agency, 2020; Fagúndez, 2013; Jeanneret et al., 2021; Pywell et al., 2011; Stevens et al., 2017). Tree encroachment into open habitats drives changes in vegetation and faunal community structure and composition (Donovan et al., 2018; Zakkak et al., 2014), displacing specialist species that rely on open or shrubby habitats (Sirami et al., 2009; White et al., 2024). This phenomenon has been observed in open habitats across continents: including Africa (Sirami et al., 2009), North America (Andersen & Steidl, 2019), South America (Furtado et al., 2021) and Australia (Crowley et al., 2025).

In Europe, tree encroachment into open habitats has largely been driven by the abandonment of traditional land management practices, such as burning, harvesting grass or heather and grazing (Ascoli & Bovio, 2010; Webb, 1998). Accordingly, the conservation of open habitats, including dry heathlands (Habitat 4030), and the species that rely on them is a key objective of the European Union's (EU) biodiversity strategy, especially within the Natura 2000 network (Olmeda et al., 2020). To achieve this objective, management strategies and practices that limit tree encroachment while promoting regeneration of heathland vegetation are needed (Ascoli et al., 2013; Fogarty et al., 2020). However, a key knowledge gap remains regarding how heathland species assemblages respond to emerging management approaches, both globally and in Mediterranean areas (Puig-Gironès et al., 2025).

Tree encroachment in heathlands can have cascading effects on species assemblages, including birds that depend on open or shrubby habitat structure for nesting, foraging and shelter (Puig-Gironès et al., 2022; White et al., 2024). Global declines in open habitat birds (Rosenberg et al., 2019; White et al., 2024) are also evident in Europe

(Burns et al., 2021), prompting many species to be designated as priority species for conservation management (European Commission: Directorate-General for Environment & Sundseth, 2015). Best practices in habitat management, such as mechanical cutting, prescribed burning and/or grazing, can play a vital role in maintaining the open or shrubby structures required by many open habitat species, thereby supporting biodiversity, promoting ecological functionality and reducing wildfire risk (Ascoli et al., 2023). However, their effectiveness depends on locally relevant knowledge of how management actions influence the occurrence of species through space and time (Schmeller, 2008).

In European heathlands, where species have evolved alongside a long history of frequent small-scale disturbances, management approaches that resemble historical disturbance regimes have great potential to achieve desirable conservation outcomes for declining specialist species (Ascoli et al., 2009; Newton et al., 2009). Spatially and temporally staggering disturbances in a mosaic approach should help meet the needs of diverse species and maintain resilient bird communities through time (Bradstock et al., 2005; Pons, Lambert, et al., 2003). Specifically, implementing small-scale disturbances in a landscape mosaic approach is hypothesized to help conserve heathland communities by controlling tree encroachment and maintaining a diversity of vegetation (habitat) structures, which will enable diverse species to persist in the landscape during post-disturbance successions (Thompson et al., 2016). For example, species that forage in recently disturbed areas (Hawkes et al., 2019) and those that prefer an established shrub layer (Chiatante, 2014) should be able to coexist in a landscape characterized by a mosaic of spatially discrete patches of different post-disturbance stages (Hovick et al., 2015). In particular, mechanical cutting and prescribed burning have emerged as promising techniques for maintaining open habitats (Ascoli et al., 2013; Cadenas et al., 2024; Davies et al., 2016; Fernández et al., 2015).

In other heathland ecosystems around the world (e.g. in Australia and South Africa), disturbances such as fire drive rapid and pronounced ecological changes and have been used to manipulate vegetation structural dynamics (e.g. through prescribed burning) to achieve conservation objectives for birds (Chalmandrier et al., 2013; Rainsford et al., 2022). However, prescribed burning is still a relatively underexplored and sometimes contentious technique in Europe, underscoring the need for research into its effects on ecosystem dynamics (Puig-Gironès et al., 2025). Understanding how mosaics of cutting and prescribed burning can help to conserve open habitats and support heathland bird species is a critical step towards developing sustainable management practices within the EU's Natura 2000 network.

This study was part of the LIFE Granatha project (<https://www.lifegranatha.eu/en/>), an initiative that aimed to enhance conservation of declining open habitat bird species by regenerating vegetation and reducing tree encroachment in heathlands in central Italy. The study area belongs to the Natura 2000 target habitat 4030, 'European dry heaths', which is characterized by the prevalence of tree heather (*Erica arborea*). The LIFE Granatha project employed a mosaic approach to heathland management, incorporating both mechanical cutting and prescribed burning to encourage shrub and grass persistence while limiting tree encroachment. This strategy aimed to create a dynamic, resilient ecosystem that meets the needs of open habitat bird species of conservation concern. Here, our primary objective is to evaluate the initial responses of bird species to mosaics of vegetation management interventions. Specifically, we aimed to address three main research questions:

1. How do cutting and burning treatments affect vegetation structural attributes over time?
2. How do populations of open habitat bird species fluctuate over time in areas subjected to cutting and burning treatments?
3. How do spatio-temporal mosaics of cutting and burning influence populations of open habitat bird species?

To address these questions, we used empirical data collected during field surveys over 5 years and built statistical models to assess, first, the post-treatment dynamics of vegetation structure (an indication of habitat structural dynamics) and, subsequently, the distribution of open habitat bird species in response to treatment mosaics.

2 | METHODS

2.1 | Study area

This study was conducted in the Natura 2000 SAC-SPA IT5180011—'Pascoli montani e cespuglieti del Pratomagno' located in Tuscany, central-northern Italy, within the Mediterranean biogeographical region at an altitudinal range of ~580 to ~1600 m a.s.l. (Figure 1a). Average daily temperature in the study area ranges from 14°C in

the summer to 2.5°C in the winter. Average monthly precipitation ranges from 47 mm in July to 152 mm in November (<https://www.cfr.toscana.it>).

The focus of the study was 'European dry heaths—habitat type 4030' in the EU Habitats Directive (European Commission: Directorate-General for Environment & Sundseth, 2015), which covers ~450 ha within the study area. The heathland vegetation in Pratomagno is dominated by heathers (*Erica arborea*, *E. multiflora*), which form dense formations from lower foothills to submontane areas. Within the heathlands, broad-leaved tree species are often patchily distributed, creating a heathland/forest mosaic. The conservation status of dry heaths within the study area is considered 'Unfavourable-Inadequate' due to pressures from tree encroachment leading to transformations from heaths to woodland, especially in the most fertile areas (European Commission: Directorate-General for Environment & Sundseth, 2015).

The study area consisted of four blocks (total 308 ha)—two reference blocks that received no treatments and two treatment blocks that, each year, were subjected to a mosaic of mechanical cutting (i.e. mastication), hand cutting, hand cutting plus pile burning and prescribed burning applications (Table 1; Figure 1). The reference and treatment areas were selected based on private landowners' availability to support the Granatha Life project, the suitability of vegetation for broom production (a traditional use of harvested heather) and strategic fuel management for fire hazard reduction (Ascoli et al., 2023). For these reasons, reference and treatment areas were not interspersed in a true blocked and balanced design (Figure 1), which is a typical constraint faced by investigations into real-world management programs, such as the EU LIFE program. The reference areas were selected based on having similar characteristics (vegetation type and structure, altitude, topography, climate) as the treatment areas.

2.2 | Description of treatments

Each year from 2018 to 2022, the heathland vegetation was treated to achieve three main objectives: (1) to enhance conservation of open habitat bird species by reducing tree encroachment and regenerating heathland vegetation; (2) to harvest heather for broom making; and (3) to reduce wildfire hazard through fuel reduction. Treatments were implemented by the local land management agency according to their protocols and targets and therefore were not randomly or uniformly implemented across the study area. Within the Pratomagno region, a total of 172 ha of vegetation was treated over the project (noting that not all vegetation within treatment blocks was treated and a given area was only treated once during the period). Within the area sampled for birds, there was a total of 74 individual interventions (66x mechanical cutting; 6x prescribed burn; 1x cut+burn; 1x hand cut). A total of 87.8 ha (29% of the total sampled area) was treated—75.1 ha were treated by mechanical cutting, 8.5 ha using prescribed burning, 3.0 ha by hand cutting and 6.1 ha by cut+burn (Table 1; Figure 1d,e). Interventions ranged from 0.1 to

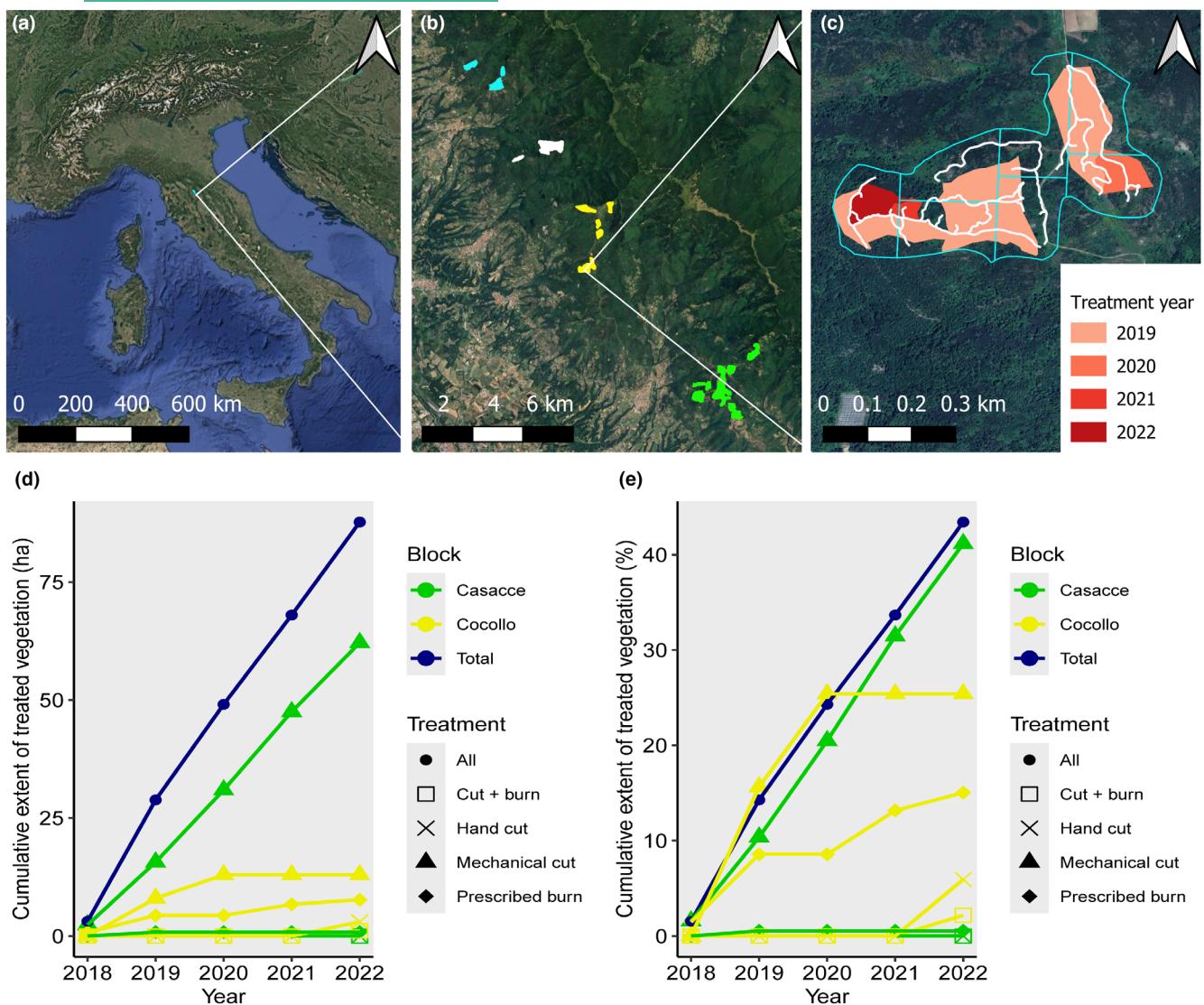


FIGURE 1 (a) Location of study area in Italy. (b) Location of blocks within the study area: Light blue = Massanera (reference); white = Poggio della Regina (reference); yellow = Cocollo (treated, reference); green = Casacce (treated). (c) Sampling units in the Cocollo block: Teal lines indicate sampling unit boundaries, shades of red indicate treatment year, white lines indicate bird survey transects. Arrows in top right of all plots point north. (d, e) The cumulative extent of treated vegetation within the bird sampling units over the study period (2018–2022) calculated as hectares (d) and percentage of the block (e) for Casacce (yellow) and Cocollo (green). Navy blue lines represent the total summed (d) and percentage (e) area treated of both blocks combined.

5.1 ha (mean = 1.2, standard deviation = 1.1): 0.1–5.1 ha for mechanical cutting and 0.3–6.2 ha for prescribed burn.

2.3 | Vegetation and bird data collection

2.3.1 | Vegetation plots

To assess vegetation structural dynamics over time, 108 circular plots (surface area: 78.5 m², radius: 5 m) were established and monitored from 2017 to 2022. Plots were distributed across treated and reference areas, with each plot undergoing at least one pre-treatment and one post-treatment survey. However, not all plots were monitored in each year (Table S1). Sampling locations were georeferenced using

a Trimble Juno GPS with differential correction to achieve a spatial accuracy of less than 5 m. Plot centres were physically marked using numbered metal tags tied to the nearest heather stump. Within each plot, forest structural attributes were recorded, including species, diameter at the root collar and the height of all individual trees. For individuals of woody species, the number of seedlings and stump or root resprouts was recorded. Heather stump counts were also measured within each plot. Densities were upscaled by species to stems per hectare. Sampling also included estimates of percent cover of soil surface components (rocks and bare soil, deadwood, grass) and the canopy cover of trees exceeding 10 cm in height for each quadrant of the circular plot and then averaged at the plot scale. Two operators (always the same throughout the whole study) independently estimated the ground cover of each class for each quadrant. The values estimated by

TABLE 1 Overview of the four study blocks, including total block extent, designation as treatment or reference area, types of fuel reduction interventions applied, number of interventions conducted and total area treated.

Block name	Total extent (ha)	Extent of reference/treatment areas (ha)	Treatment	Number of interventions	Extent of treatment (ha)
Massanera	40	Reference (40)	None	-	-
Poggio della Regina	49	Reference (49)	None	-	-
Cocollo	68	Treatment (51), reference (17)	Mechanical cutting Prescribed burn Hand cut Hand cut+burn	11 5 1 1	13.0 7.7 3.0 1.1
Casacce	151	Treatment (151)	Mechanical cutting Prescribed burn	55 1	62.2 0.8

TABLE 2 Variables to describe vegetation structure and composition measured at each 5-m radius plot.

Variable name	Unit of measure	Variable description	PCA
Erica cover	%	Percentage cover of <i>Erica</i> spp.	Y
Tree canopy cover	%	Percentage cover of tree canopies spp.	Y
<i>Ulex</i> cover	%	Percentage cover of <i>Ulex europaeus</i>	Y
Grass cover	%	Percentage cover of grasses	Y
<i>Genista</i> cover	%	Percentage cover of <i>Genista</i>	Y
Fern cover	%	Percentage cover of ferns	Y
Coarse woody debris cover	%	Percentage cover of coarse woody debris	N
Soil and rock cover	%	Percentage cover of soil and rocks	Y
<i>Erica</i> height	m	Mean height of <i>Erica</i> spp.	Y
<i>Genista</i> height	m	Mean height of <i>Genista</i>	N
Tree height	m	Mean height of tree spp.	Y
<i>Prunus spinosa</i> height	m	Mean height of <i>Prunus spinosa</i>	N
Density of <i>Erica</i> sprouts	sprouts/ha	Density of <i>Erica</i> spp. shoots	N
Density of tree sprouts	sprouts/ha	Density of tree spp. shoots	Y
Density of <i>Prunus spinosa</i> sprouts	sprouts/ha	Density of <i>Prunus spinosa</i> shoots	N
DBH	cm	Average diameter of trees at the root collar	Y
Slope	%	Plot slope	N
Aspect	°N	Plot aspect	N
Elevation	m a.s.l.	Elevation above sea level	N

Note: The column named 'PCA' indicates the variables that were used in the principal component analysis (see Table S3).

the two observers were then averaged to the nearest percent for each quadrant and then averaged at the plot scale. Heather (shrub) height was measured at five fixed points per plot. Data were processed to derive vegetation structure parameters, including species composition, average plant height and diameter, basal area and tree density (Table 2). The topographic variables, slope, aspect and elevation were derived from spatial layers in a GIS.

2.3.2 | Bird surveys

We surveyed birds along 26 fixed transects (7 in reference blocks, 19 in treatment blocks, total transect length=34.9 km) each year during the study period (2017–2022). Transect routes were selected a priori using

desktop GIS to ensure uniform coverage of the heathland study area. Paths, tracks and wild pig trails were targeted to facilitate movement through the terrain. Transects were surveyed three times per year during the breeding season (March to June), with surveys conducted within 5 h of sunrise under fair weather conditions. Surveys were carried out by three surveyors (T.C., G.L., S.C.). Where possible, repeat surveys of transects were conducted by each observer, that is no transect was surveyed only by a single observer. Additionally, we standardized the collection method among observers prior to monitoring by conducting multiple surveys prior to the breeding season. During each survey of open habitat birds, the location of the point of first detection of each individual was recorded on detailed maps (scale 1:1200, with orthophoto base). Detections were categorized as either 'singing', 'calling' or 'visual detection'. Transects were first surveyed in 2017/2018 breeding

season, during the pre-treatment phase (interventions began after the summer of 2018): in 2017 we surveyed 80 sampling units, in 2018 another 33. No transects were surveyed in both 2017 and 2018. No surveys were conducted during 2020 because of COVID-19 restrictions. Note: no permits were required to undertake the field work.

2.4 | Statistical analysis

2.4.1 | Vegetation structure and composition

An exploratory pairwise correlation analysis (Kendall's Rank Coefficient) on pre-treatment data revealed collinearity within and between heathland and tree variables. We used principal component analysis (PCA) to reduce collinear variables into new derived components that summarized the original tree and heathland variables (Quinn & Keough, 2002). The PCA was based on a correlation matrix that included both tree and heathland variables measured across 437 observations, representing the monitored plots (treated and reference) in the years from 2017 to 2022. PCA scores of the first and second components were extracted for each treatment and year combination. These two independent components were then used as response variables in subsequent ANOVA analyses to test treatment differences at each time step (Objective 1). Assumptions of ANOVA were tested for the unbalanced experimental design following Quinn and Keough (2002), and when ANOVA indicated significant effects, planned contrasts were performed.

2.4.2 | Open habitat birds

To assess initial responses of open habitat bird species to mosaics of cutting and burning, we used non-linear mixed-effects models to assess changes in species' relative abundance (1) over time in both treatment and reference areas and (2) across the treatment areas only in response to measures of treatment mosaics.

Sampling units

To standardize sampling units for bird analyses, first a buffer area around the transects was calculated based on the minimum convex polygon that contains 95% of all location data for the target species combined. The buffer delineates the extent of the area sampled for birds and was determined in QGIS. This sampled area was then divided into 3-ha sampling units (31 reference and 62 treated units) by overlaying a random 3-ha grid. Shapes of the sampling units were not uniform to ensure that as much of the sampled area as possible was included. These sampling units served as the replicates for the bird analyses—that is explanatory and response variables were calculated for each sampling unit.

Explanatory variables

For each sampling unit, we generated a range of variables to represent mosaics of treatments, topography, variability in productivity and

land-use (Table 3). To represent the spatial and temporal influence of heathland treatments on birds, specifically, we calculated three treatment variables for each sampling unit and year: the extent (% of sampling unit) of vegetation treated <1 year (ET_recent in Table 2), 1 year (ET_1year) and >1 year (ET_2year) prior to the bird survey. To calculate these variables, maps of treated areas were generated for each study year by manually delineating treated vegetation from aerial imagery. Maps were ground-truthed and then adjusted to ensure treated areas were accurately delineated. Using these vector layers, the area treated within each sampling unit was calculated for each year. The type of treatment could not be assessed due to insufficient replication—that is the vast majority of treated vegetation was by mechanical cutting (Figure 1d,e). Additionally, PCA revealed no strong differences in vegetation structure following each type of treatment.

Land-use maps were generated by using aerial imagery with 20cm resolution (Regione Toscana, 2020) from 2016 and manually delineating the following land-use classes: shrubland (including with scattered trees or exposed rock), grassland (including with scattered trees or exposed rock), forest/woodland and bare rock. This vector layer was used to calculate the extent of each land-use type for each study year by subtracting the cumulative area treated within each land-use class from the pre-treatment land-use map. For instance, a sampling unit with 5ha of shrubland in 2021 that experienced 2ha of cutting in 2022 would be recorded as having 3ha of shrubland and 2ha classified as 'treated' in 2022.

Variability in productivity was calculated annually within each sampling unit as the standard deviation of the Normalized Difference Vegetation Index (NDVI) by using all available Sentinel-2 imagery from Google Earth Engine from June to August for each year.

The mean elevation, slope, aspect and topographic position index (TPI) of each sampling unit were derived from a Digital Elevation Model (DEM) with 10m resolution (Regione Toscana, 1998). Topographic variables were generated by using the 'terra' package in R (Hijmans, 2025).

Response variables

Response variables for all bird models were the relative abundance of singing individuals of all species combined and of each individual species of open habitat bird. Relative abundance for each species was calculated as the maximum number of detected individuals over the three survey rounds within each sampling unit per year. Four species did not occur in the two reference blocks (Table S1). For these species, analyses were conducted using only data from the two treatment blocks. Models were built for individual species that occurred in >15% of sampling units each year ($n=7$ species).

Models

We assessed the responses of open habitat birds to treatment mosaics in four ways. First, we used redundancy analysis (RDA) in the 'vegan' package in R (Oksanen et al., 2025) to explore the relationships among covariates and response variables to show how

TABLE 3 Explanatory variables calculated for each sampling unit.

Variable	Unit of measure	Variable description	Temporal status
ET_recent	%	Extent of vegetation treated less than 1 year prior to the bird survey	Dynamic
ET_1year	%	Extent of vegetation treated during the year that preceded the bird survey. That is for 2022 bird surveys, this was the extent of vegetation treated during 2021	Dynamic
ET_2year	%	Extent of vegetation treated at least 2 years prior to the bird survey. Includes vegetation with 2, 3 and 4 years' treatment age	Dynamic
Forest	%	Extent of forest (broadleaf or conifer) vegetation minus the cumulative area of forest treated	Dynamic
Shrubs	%	Extent of combined shrubland categories (shrubs, shrub_trees, shrubs_rocks) minus the cumulative area of shrubland treated	Dynamic
NDVI_SD	Decimal number	Standard deviation of NDVI across the sampling unit	Dynamic
Year	Integer	Survey year: 2018, 2019, 2021, 2022	Dynamic
Hab.Div	Index	Spatial diversity of vegetation types calculated for each year	Dynamic
Rocks	%	Extent of bare rock or sparsely vegetated rock	Static
Elevation	m	Average elevation across the spatial unit	Static
Slope	%	Average slope across the spatial unit	Static
TPI	Index	Average Topographic Position Index. TPI > 0 when the location is higher than its surroundings (i.e. ridges, hilltops). TPI ≈ 0 when the location is similar to its surroundings (i.e. flat areas, mid-slopes). TPI < 0 when the location is lower than its surroundings (i.e. valleys, depressions)	Static
Treatment	Category	Treated or reference areas	Static
Site_ID	Category	Unique site ID (1–93)	Static
Block	Category	Massanera, Poggio della Regina, Cocollo, Casacce	Static
Transect_length	m	Length (m) of transect within each sampling unit	Static

Note: The 'temporal status' indicates whether the variable was either calculated each year (dynamic) or remained constant cross years (static).

the composition of the bird communities is related to environmental gradients (Objective 2). The variables included in RDA are listed in Table 2. To explore temporal dynamics in these relationships, we conducted four separate analyses—two each for both the reference and treatment areas, one using data from 2018 (i.e. the first survey round, pre-treatment) and another using data from 2022 (i.e. the last survey round). Bird survey data from 2017 and 2018 were combined as 2018, signifying the first survey year because each sampling unit was surveyed in only 1 year (80/93 were surveyed in 2017, 13/93 were surveyed in 2018).

Second, to test for changes in relative abundance within sampling units over the study period (Objective 2), we built a Generalized Additive Model (GAM) for each response variable as a function of year (2018, 2019, 2021, 2022) and treatment (a categorical variable with two levels: reference, treatment), with an interaction between the two specified. Degrees of freedom of the smooth term (k) was set to four to limit overfitting. Data from all study years were included in the model (including years in which the species was not detected). A categorical variable, 'site_ID' was included as a random spline to account for repeated measures at sites. 'Block' (Massanera, Poggio della Regina, Cocollo, Casacce) was included as a categorical variable to account for spatial clustering of sites. To account for the potential influence of variable transect lengths within each sampling unit, transect length (\log_{10})

was included as an offset. We also included covariates (Table 3) to account for the influence of terrain and topographic gradients (i.e. TPI, elevation, rock cover). To select covariates for inclusion in models, first, we built a 'global' model with all candidate variables (Table 3). We then removed all non-significant variables (except year) and re-ran the model.

Model 1: Response ~ year × treatment + TPI + elevation + rocks
+ block + (site_ID), offset = transect length

Third, to assess the influence of spatio-temporal mosaics of treatments on open habitat bird species within the treatment area only (Objective 3), we built a GAM for each response variable as a function of three main treatment variables: extent of vegetation treated <1 year, 1 year and >1 year prior to the bird survey. To account for variability in forests and shrub cover among sampling units irrespective of treatment, the percentage cover of forest and shrubland was both included in each model and transect length (\log_{10}) was included as an offset. We also included covariates (Table 3) to account for the influence of topographic gradients, productivity and spatial clustering (block). Site_ID was included as a random spline and k was set automatically during model fitting. We aimed to test the influence of all three treatment variables; so, to select variables to include, we built a model with all candidate variables and then removed all non-significant variables and re-ran the final model.

Model 2: Response ~ ET_recent + ET_1year + ET_2year + forest
+ shrubs + topography + block + (site_ID), offset = transect length

All statistical analyses were conducted in the R statistical environment (R Core Team, 2022). For all models, we used a Poisson error distribution. Explanatory variables were assessed for collinearity prior to analyses using Pearson's correlation coefficient and the 'PerformanceAnalytics' package (Peterson & Carl, 2024). All GAMs were built using the 'mgcv' package (Bates et al., 2015; Wood, 2017). Unless otherwise stated, all spatial analyses were conducted in QGIS.

3 | RESULTS

3.1 | Effects of treatments on vegetation characteristics

The PCA identified two components that, together, explained 63.6% of the total variance (Table S2). Variables representing heathland structure were highly correlated (Kendall's correlation >0.77) with the first eigenvector—the cover of shrubs, and the height and cover of *Erica* species were positively correlated, while grass cover was negatively correlated. These variables contributed only minimally to the second component (Table S3; Figure S1). Tree-related variables (tree canopy cover, average tree diameter, cumulative height of tree individuals [tree_ind]) contributed significantly to the second eigenvector (Kendall's correlation=0.67). As a result, the first component was interpreted as a gradient primarily related to heathland regeneration

success (PC-heath), while the second component reflected increasing tree encroachment (PC-tree).

The temporal trend in mean component scores differed depending on the treatment (Figure 2). ANOVA revealed no significant differences in pre-treatment (time=0) mean values among treatment groups for either the first [$F(4, 175)=6.87, p=0.24$] or the second component ($p=0.09$). The first year following treatment highlighted a reduction in the tree component, indicative of treatment effectiveness in reducing tree competition in the short-term (Figure S2). However, 4 years after treatment application, strong resprouting from roots and stumps restored the tree canopy cover (not the height), and there were no significant differences in the tree component [PC-tree, $F(4, 71)=39.07, p=0.521$] between the treatments and the reference. Also, the heathland component regenerated markedly after treatment application but significant differences with the reference (PC-heath, $p<0.01$) were still present 4 years after treatment, indicating that the pre-level treatment was not yet restored (Figure 2; Figure S2). Prescribed burning displayed a heathland recovery rate slightly greater than other treatments (Figure 2), resulting in significantly higher scores 4 years after treatment when compared to cutting treatments.

3.2 | Bird responses to treatment mosaics

A total of 3983 detections of singing individuals of 12 open habitat bird species were made during the bird surveys. One species listed as 'Near Threatened' on the IUCN Red List, the Dartford warbler (*Curruca undata*), was recorded and seven of the 12 species are described as having 'decreasing' trends across Europe (BirdLife International, 2021;

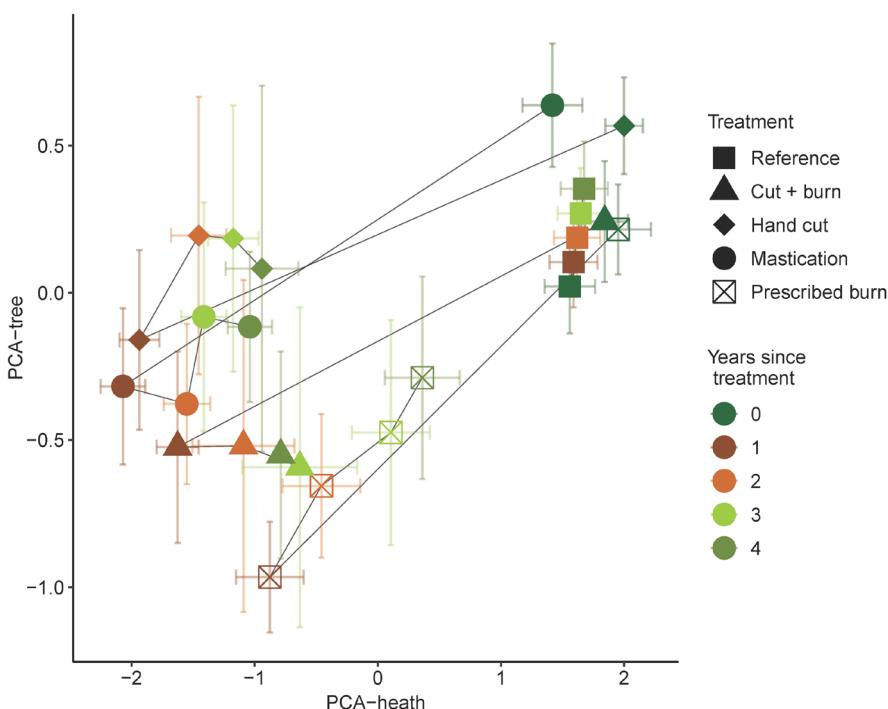


FIGURE 2 Mean eigenvalues (\pm SE) for PCA 1 (heathland) and PCA 2 (trees) for each heathland treatment (represented by shapes) and year since treatment (0–4, represented by colours). Grey lines indicate temporal trajectories of each treatment type.

Table S4). The most widespread species recorded were the Moltoni's warbler (*Curruca subalpina*), recorded within 99% of sample units in 2018, 98% in 2019, 96% in 2021 and 96% in 2022, the Dartford warbler, recorded within 60% of sample units in 2018 and 47% in 2022; and the Sardinian warbler (*Curruca melanocephala*), recorded within 52% of sample units in 2018, 48% in 2021 and 46% in 2022 (Table S4).

Two rare species, the red-backed shrike (*Lanius collurio*) and Eurasian skylark (*Alauda arvensis*) were recorded for the first time in 2019 and the Eurasian skylark was recorded again in 2021 and 2022.

In both the reference and treatment blocks, negative associations between open habitat species and forest cover were observed in 2018 and 2022 (Figure 3). Some species showed

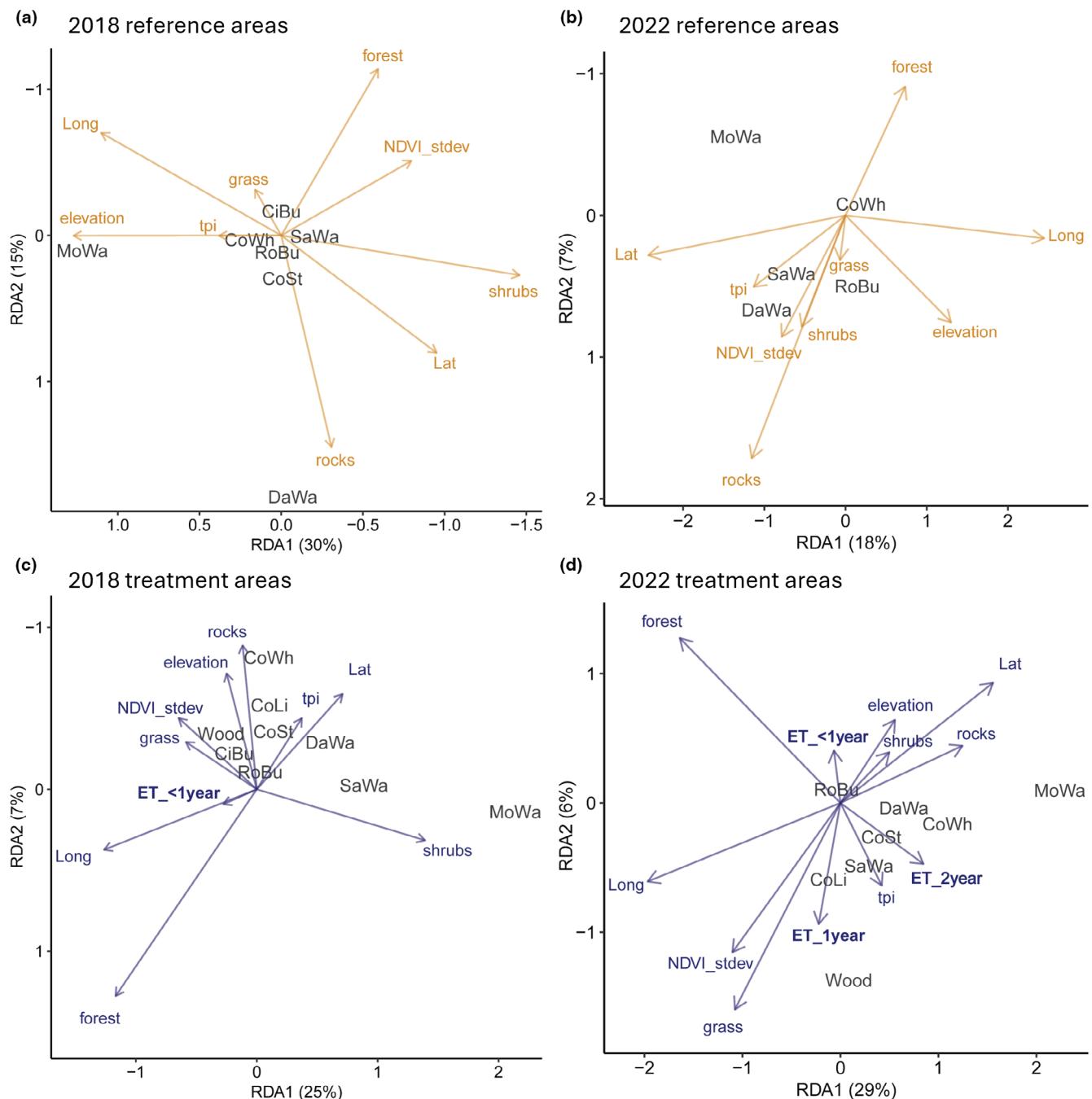


FIGURE 3 Redundancy analysis of the open habitat bird communities within reference (a, b) and treatment areas (c, d) in 2018 (a, c) and 2022 (b, d). Arrows are environmental variable vectors. Arrow length indicates the strength of the relationship. Grey text indicates species codes. Position of species relative to environmental vectors indicates the level of association—direction indicates correlation, distance indicates strength of association. Environmental vectors were generated by extracting the 'scores' from the RDA analysis. Species codes: CiBu, cirl bunting; CoWh, common whitethroat; CoLi, common linnet; CoSt, common stonechat; DaWa, Dartford warbler; MoWa, Moltoni's warbler; RoBu, rock bunting; SaWa, Sardinian warbler; Wood, woodlark.

associations with specific habitat attributes such as shrubland cover (Sardinian warbler in 2018 treatment areas) or rocks (common whitethroat in 2018 treatment areas). Warblers (Curruca species, for example Dartford warbler, Sardinian warbler) were generally associated with shrub-dominated sites, while the woodlark was typically associated with more open vegetation with bare rock, grass and treated areas.

The relative abundances of seven species with sufficient data fluctuated over the study period in both the reference and treatment areas (Figure 4); however, compared to the reference areas, populations in the treatment areas showed more positive responses, steeper recoveries or greater stability over the study period. Abundance of all species combined declined in both the reference and treatment areas over 2 years but showed a steeper recovery in the treatment areas (Figure 4a). The woodlark showed an increasing trend over time in the treatment areas but did not occur in the reference areas (Figure 4b). The Dartford warbler declined significantly in the reference areas before a steep recovery in the last 2 years, but remained more stable in the treatment areas (Figure 4c). The common stonechat showed an increasing trend in treatment areas and a declining trend in reference areas (Figure 4d). Moltoni's warbler

showed a non-significant decline and recovery in the treatment areas, where abundance was greater than in reference areas (Figure 4e). Relative abundance of the Sardinian warbler (Figure 4f) and common whitethroat (Figure 4g) did not fluctuate significantly over the study period. The cirl bunting declined steeply approaching local extirpation by 2022 in the reference areas, but abundance remained higher in treatment areas despite an initial slight decline (Figure 4h). Detailed model outputs can be found in Table S5.

Total species' abundance (Figure 5a) and that of the Dartford warbler (Figure 5c), common stonechat (Figure 5d) and Moltoni's warbler (Figure 5e) declined significantly in response to the extent of vegetation <1 year since treatment. The Sardinian warbler showed a declining trend that approached significance ($p < 0.01$) (Figure 5f). The woodlark showed an increasing trend in relation to the extent of treated vegetation >1 year since treatment (Figure 5b). The common whitethroat (Figure 5g) and cirl bunting (Figure 5h) did not respond significantly to any measure of treatment extent. However, the woodlark and cirl bunting showed non-significant positive trends to the extent of vegetation >1 year and <1 year since treatment, respectively. Detailed model outputs can be found in Table S6.

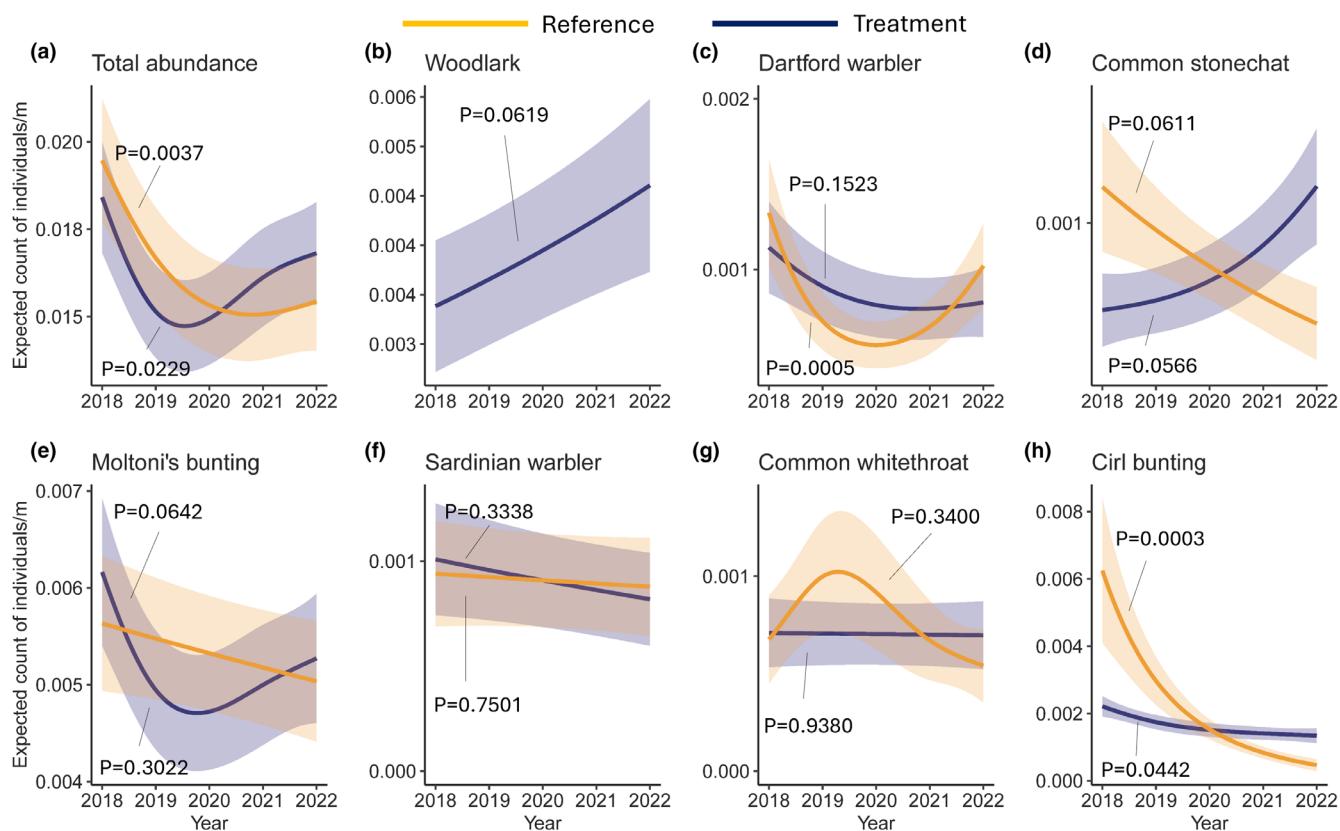


FIGURE 4 Bird responses to mosaic burning and cutting over time. Plots show changes in the relative abundance per sampling unit over time for all species considered together (a) and seven individual species (b-h). Blue lines represent trends in treatment areas; orange lines represent trends in reference areas. Lines are fitted Generalized Additive Models (GAMs). Shaded areas indicate standard errors. p -Values are displayed adjacent to the corresponding model. All models included transect length (\log_{10}) as an offset.

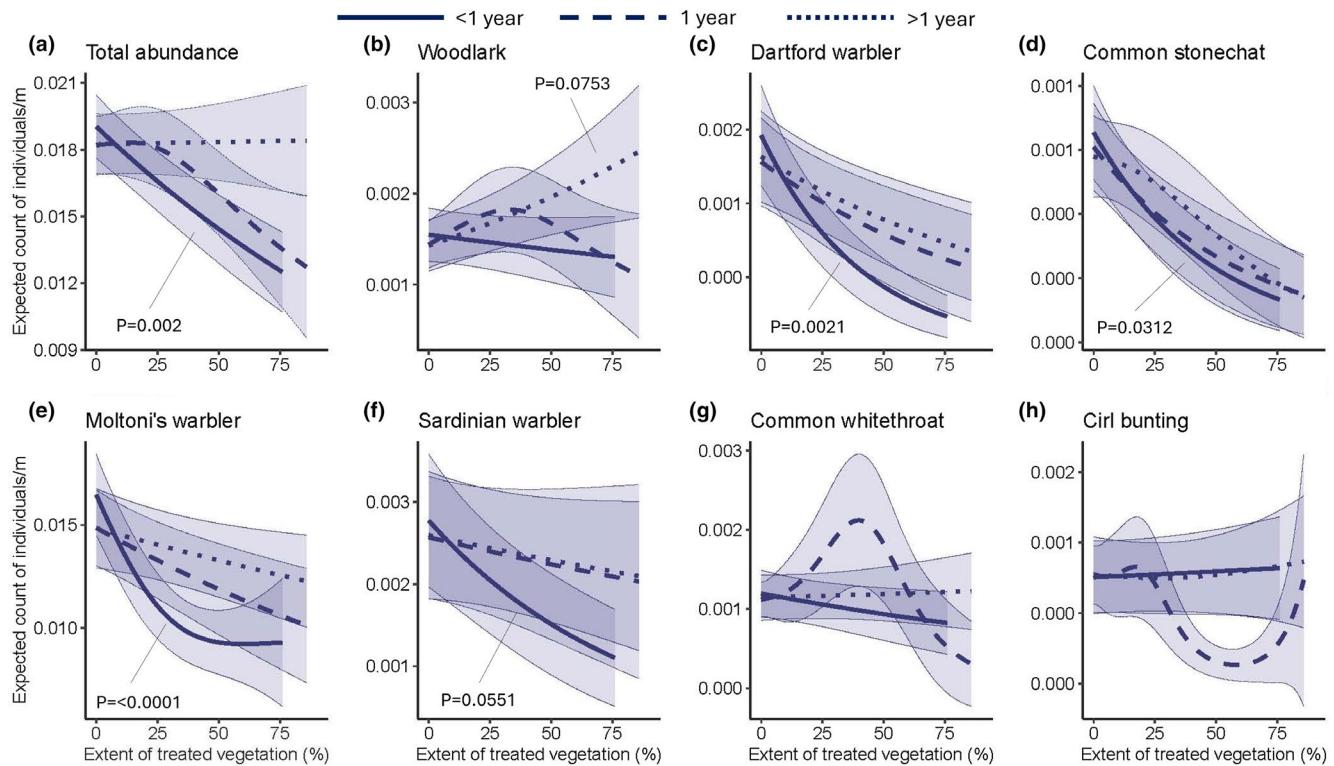


FIGURE 5 Influence of cutting and burning mosaics on the relative abundance of open habitat birds. Plots show expected counts of singing individuals per metre of transect as a function of the extent of heathland vegetation <1 year (solid lines), 1 year (dashed lines) and >1 year (dotted lines) since treatment for all species considered together (a) and seven individual species (b–h). X-axes are the percentage of sampling units treated within each time-since-treatment category. Lines are fitted Generalized Additive Models (GAM). Shaded areas indicate standard errors. *p*-Values are approximate significance of the smooth term of significant ($p < 0.05$) or approaching significant ($p < 0.1$) relationships only. All models included transect length (\log_{10}) as an offset.

4 | DISCUSSION

These findings suggest that treating vegetation in Mediterranean heathlands by cutting and burning can enhance conservation of declining open habitat bird species, but a mosaic approach is necessary to support diverse species within landscapes that are subject to treatment. Within 4 years of treatment, heathland vegetation was regenerating on a trajectory towards that of untreated vegetation, characterized by vigorous shrub growth and reduced tree height. Open habitat bird populations in the study area fluctuated over the study period; however, fluctuations in the treatment areas were positive or minimal for most species when compared to reference areas, indicating that the mosaic treatments allowed species to find suitable conditions at different times. The spatial pattern of treatment mosaics influenced the distribution of open habitat bird species within the treatment blocks. For four of these species, including the Dartford warbler (target species of the Natura 2000 SAC), the extent of recently treated vegetation reduced relative abundance, indicating an acute response to the initial disturbance. However, as the time since treatment increased, the influence on bird abundances dissipated, indicating that the mosaic of vegetation structures caused by staggering interventions over time helped maintain suitable habitat as regeneration continued throughout the period. The woodlark, another priority

species, by contrast, showed a non-significant positive association with the extent of vegetation treated >1 year, potentially indicating regeneration of preferred habitat for this species. Our findings highlight the necessity of applying vegetation treatments in a patchwork to sustain the open habitat bird community over time.

4.1 | Vegetation structural dynamics

Our results demonstrated that, after 4 years since treatment, vegetation plots, regardless of type of treatment, were following a trajectory towards that of untreated vegetation. Treatments reduced tree height in vegetation plots; however, some tree species (mainly *Prunus spinosa*) resprouted vigorously from roots following treatments, resulting in a high density of shoots that maintained values for tree canopy cover throughout the study period. Rapid resprouting of treated trees highlights the need for ongoing management to limit tree growth over time either through repeated treatments or combined with selective grazing on the tree component (Ascoli et al., 2013; Thompson et al., 2016). Immediately following treatment, plots were characterized by high levels of bare ground and litter. After 1 year, *Erica* spp. had begun to resprout. In the second year following treatment, vigorous shrub growth resulted in increased cover and reduced grass presence. These findings, in

accordance with previous studies, suggest that cutting, mastication and prescribed burning can be used alternately to temporarily reduce heathland biomass while stimulating regeneration (Fernández et al., 2015). The patterns of spatial and temporal dynamics of treated vegetation are similar to observations recorded previously in Mediterranean heathlands (Calvo et al., 2012) and define the dynamics in habitat structure, which ultimately drive bird responses to management mosaics.

4.2 | Bird responses to treatment mosaics

Habitat preferences of bird species help explain observed responses to management interventions (Rainsford et al., 2021). For example, the woodlark is known to prefer early-to-mid post-disturbance successional stages in other Mediterranean areas (Pons & Clavero, 2010; Puig-Gironès et al., 2022) as well as in the Pratomagno region (Campedelli et al., 2016). This species exploits mosaics of open habitats by foraging on the ground, avoiding areas of high tree and shrub cover. In contrast, the Dartford warbler, Moltoni's warbler, Sardinian warbler and common stonechat depend on a well-developed shrub layer (Chiante, 2014; Tellini Florenzano & Lapini, 1999), which takes several years to develop following disturbance in heathlands (Pons et al., 2012). Typically, the Dartford warbler abandons a severely disturbed shrubland and recolonizes after 2–4 years (Pons et al., 2012) once shrub cover at 0.25–1 m height has developed. Peaks in abundance at around 4–9 years have been recorded previously (Pons et al., 2012), although this process is influenced by the rate of vegetation regeneration and site climate (Pons & Clavero, 2010; Puig-Gironès et al., 2017). Finally, species that show more general habitat associations tended not to respond significantly to treatment mosaics. For example, the common whitethroat (Szymański & Antczak, 2013) and cirl bunting (Brambilla et al., 2008), which did not respond significantly to treatment mosaics, prefer structurally diverse habitats that include shrubs and grass. Knowledge of how species respond to post-disturbance habitat dynamics is critical for assessing how management interventions will shape ecological communities over time and space (Puig-Gironès et al., 2025). For open habitat bird species in heathland habitats, maintaining patches of heathland at various post-treatment ages will likely lead to the best conservation outcomes.

Further, spatial and temporal components of disturbance regimes are important to consider for management of birds and other fauna in disturbance-prone environments (Kelly et al., 2018; Rainsford et al., 2023), especially in areas where there is a history of vegetation management through disturbance (Fuhlendorf et al., 2012). Here, we show how mosaics of cutting and prescribed burning that resemble the historical disturbance regime can help maintain populations of open habitat species in the short term. A mosaic approach enables vegetation succession to be staggered across the landscape, maintaining suitable habitat for a range of species over space and time. Comparisons with previous studies highlight the benefits of mosaics for open habitat birds. For instance, the Dartford warbler

in Catalonia was observed to remain in an area after intervention as long as some shrub cover was retained (Pons, Henry, et al., 2003). This was supported by anecdotal observations during the current study of Dartford warbler individuals remaining in treated areas where there were shrubs. Research on tree removal in open habitats has also shown that retaining undisturbed habitat in the surrounding landscape during treatments can help reduce short-term displacement of wildlife in early phases of treatment (Thompson et al., 2016).

4.3 | Implications and limitations

Managing wildfire risk through vegetation treatments is a key goal of local land management agencies in southern Europe (Ascoli et al., 2023). However, altered fire regimes, exacerbated by climate change, are intensifying fire weather and extending fire seasons, making ecosystems increasingly vulnerable to wildfire impacts (Berchtold et al., 2025). In this context, the rapid recovery of vegetation structure after treatment means that fuel reductions are often short-lived, requiring frequent reapplications of treatments. These challenges call for adaptive and integrated strategies such as vegetation treatments that mimic historical disturbance regimes integrated with, for example, livestock grazing. By maintaining a heterogeneous landscape and implementing a temporal rotation of treatments, this approach can support the persistence of multiple species with contrasting habitat requirements while sustaining fire risk reduction efforts over the long term (Oliveras Menor et al., 2025).

Three key aspects must be considered when interpreting the findings. First, treatments were implemented by the local land management agency according to their management targets, goals and protocols. As such, the timing, extent and placement of treatments were at the discretion of the practitioners and under the influence of prevailing weather conditions. This meant that the study design was not completely balanced; that is, treatment and reference areas were not interspersed randomly but rather located as discrete blocks. However, not all vegetation within the treatment blocks was treated, and so, we could analyse the influence of treatments as spatio-temporal mosaics as the extent of vegetation treated at different points in time. Second, lack of data for some species of conservation concern (e.g. tawny pipit) prevented statistical analyses. For these species, we recommend continued monitoring. Third, imperfect detection of birds could have influenced the estimates of relative abundance as detection probability was not explicitly accounted for in the models. However, by using a buffer area to standardize sampling units, detection bias should be evenly distributed among treatments and we expect its influence on the main findings to be low.

5 | CONCLUSIONS

Mosaics of cutting and burning treatments in Mediterranean heathlands can regenerate habitats for a range of open habitat bird

species by reducing tree canopy cover and stimulating shrubland growth. Individual species responded differently to spatio-temporal measures of treatment intensity, highlighting the need for a mosaic approach to heathland management that maintains a variety of habitat structures across the landscape that can support diverse species. Ongoing management of heathlands is recommended to ensure tree encroachment is reduced over time and open habitats are maintained. New arrivals of rare species (e.g. the red-backed shrike, Eurasian skylark) are encouraging and warrant ongoing monitoring to determine the long-term benefits of management interventions. Initial responses of open habitat birds indicate short-term benefits, suggesting this approach to heathland management could benefit species in regions throughout the world and help to support habitat restoration, specifically in the Natura 2000 network.

AUTHOR CONTRIBUTIONS

Frederick W. Rainsford: Conceptualization; data curation and analysis; investigation; methodology; supervision; validation; visualization; writing—original draft; review and editing. Davide Ascoli: Conceptualization; funding acquisition; project administration; data curation and analysis; investigation; resources; supervision; validation; visualization; writing—original draft; review and editing. Tommaso Campedelli and Guglielmo Londi: Conceptualization; funding acquisition; project administration; data collection and curation; investigation; resources; supervision. Marcello Miozzo, Luca Tonarelli, Chiara Milanese and Nico Betti: Conceptualization; funding acquisition; project administration. Simonetta Cutini and Guido Tellini Florenzano: Conceptualization; data collection and curation; investigation; supervision. Pere Pons and Roger Puig-Gironès: Supervision; writing—original draft; writing—review and editing. Roberta Berretti: Conceptualization; data collection and curation; investigation; methodology; supervision; validation; writing—review and editing. Renzo Motta: Investigation; supervision; writing—review and editing. Luca Musio, Jose V. Moris, Gian Luca Spadoni, Cinzia Passamani: Data curation; investigation; methodology; writing—review and editing. Alessia Bono and Davide Vecchio: data curation; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository, <https://doi.org/10.5061/dryad.7h44j1085> (Rainsford et al., 2026).

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SUPPORTING INFORMATION

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

Table S1. Summary of vegetation monitoring plots including the treatment applied, the number of years it was surveyed, the number of plots that were surveyed each year and the total number of plots for each treatment.

Table S2. Output variables from principal component analysis (PCA), for each principal component score extracted.

Table S3. Variables used in plot-level vegetation analysis, as defined from the first three principal component scores obtained through principal component analysis (PCA).

Table S4. Open-habitat bird species recorded during surveys.

Table S5. Generalized Additive Models relating changes in the relative abundance of open-habitat species over time (year) to treatment and reference areas.

Table S6. Generalized Additive Models relating the relative abundance of open-habitat bird species to treatment mosaics.

Figure S1. Biplot from principal component analysis (PCA) showing the first two principal components.

Figure S2. Boxplots from analysis of variance (ANOVA) on the first principal component indicative of heathland dynamics (left column) and on the second component indicative of tree dynamics (right column).

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