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Skylark conservation in alpine habitats should focus on areas where conspecifics are already present

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Farmland bird diversity has declined precipitously for decades because of the incessant intensification of agricultural practices in semi-natural landscapes in Europe. Consequently, formerly common and widespread ground-nesting species, such as the Eurasian Skylark *Alauda arvensis*, have shown severe declines on intensive grasslands and arable areas in western mainland Europe. In the Swiss Alps, populations are more stable, suggesting that high-elevation areas could act as refugia for Skylarks. We studied the habitat preferences of Skylarks in subalpine and alpine habitats across Switzerland. Using 3 years of territory mapping across a wide range of habitat types, land-use management and topographical characteristics, we aimed to elucidate the limiting factors for these populations to better inform conservation management. Skylarks occurred more frequently at lower elevation (1400 m versus 2600 m), with gentler, south-facing slopes and areas with higher land-management diversity. Skylark occurrence was lower closer to tall structures and higher in the presence of conspecifics. Skylark densities in these alpine areas are also much lower than in remaining intact lowland populations in Switzerland and their reproductive output is lower because of a shorter breeding season, questioning the role of alpine areas as refugia. The areas with high Skylark occurrence are also those most at risk of development for agricultural intensification or infrastructure projects. At the same time, the abandonment by farmers of extensively used agricultural areas – exacerbated by a longer vegetative growing season due to climate change – results in shrub encroachment in higher-elevation areas thereby further limiting the potential of alpine areas as a refuge for Skylarks. Management should limit the intensification of agricultural areas, but also prevent further abandonment of extensively used meadows and pastures to maintain open landscapes. Our results also indicate that establishing new populations in areas unoccupied by Skylarks could be far more difficult than maintaining or expanding existing populations. We therefore stress the importance of protection of those grasslands that currently host Skylark populations.

Keywords: agri-environment, *Alauda arvensis*, alpine refugia, farmland birds, grassland management, habitat selection, social attraction.

Farmland bird diversity has been declining precipitously for decades in response to the incessant intensification of agricultural practices in semi-natural landscapes (Donald *et al.* 2006, Inger *et al.* 2015). This has been well documented across Europe and although measures have been proposed to halt the collapse of farmland biodiversity, these agri-environment schemes have, by-and-large, had limited impact in averting this decline for birds (Pe'er *et al.* 2014, Daskalova *et al.* 2019, Elmiger *et al.* 2023). Structural improvement programmes, increased fertilization and irrigation facilitated earlier and more frequent mowing and led to a large-scale intensification of grasslands (Buckingham *et al.* 2015). More frequent mowing results in the destruction of nests and direct mortality of ground-nesting birds, such as Corn Buntings *Emberiza calandra*, Whinchats *Saxicola rubetra* and

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Eurasian Skylarks *Alauda arvensis* (Donald *et al.* 2002, Grüebler *et al.* 2008). Concurrently, more intensive management leads to larger parcels with fewer edges and therefore lower landscape-level habitat heterogeneity and a reduction in associated biodiversity (Benton *et al.* 2003, Šálek *et al.* 2018). This not only results in fewer, larger farms that are more intensively managed, but also in more farmland being abandoned or converted to other land uses (Graf *et al.* 2014). This quantitative and qualitative habitat loss due to landscape homogenization and management intensification has had far-reaching implications for ground-nesting bird populations across Europe (Donald *et al.* 2001a, 2001b, Rigal *et al.* 2023).

In the Swiss alpine region, grassland specialist bird species have largely disappeared from the valley bottom and now occur mostly at higher elevations where management remains less intensive (Maggini *et al.* 2011, Hallman *et al.* 2022). For example, Eurasian Skylarks (henceforth, 'Skylarks') are found in alpine habitats at elevations up to 2500 m, but at lower densities than the populations in lowland arable land in northern and western Switzerland, where intact populations are present to this day (Knaus *et al.* 2018). Similarly, Whinchats now occur mostly at higher elevations in upland areas in Switzerland (Knaus *et al.* 2018), the UK (Calladine & Bray 2012) and France (Archaux 2007), and in lower densities in more intensively used areas in the Alps (Assandri *et al.* 2019a). However, constrained by topography and environmental restrictions at higher elevations (e.g. cooler temperatures and shorter growing season), breeding Whinchat densities in the UK are also much lower, indicating poorer habitat suitability at higher elevations (Calladine & Bray 2012). Corncrakes *Crex crex* have also shown a progressive shift towards higher elevations and have now nearly disappeared from the valley floors in the Italian Alps, where the species was once common (Brambilla *et al.* 2021). Corncrakes too are at lower densities at higher elevations because they also prefer the environmental conditions of lowland valleys over those of subalpine meadows (Brambilla *et al.* 2021). The environmentally constrained, shorter breeding season in alpine habitats means that grassland birds such as Skylarks often produce only one brood per season at high elevations (maximum two broods per year, Guyot *et al.* 2018) which, when combined with an already low success rate per nest and high fledgling mortality at low-altitude habitats (Delius 1965, Donald *et al.* 2002), could mean that these populations are not self-sustaining. With the increasing intensification of agriculture at higher elevations (Korner *et al.* 2018), exacerbated by longer vegetative growing seasons due to the effects of climate change, these populations are now threatened too (Brambilla *et al.* 2021). It therefore remains unclear if alpine meadows can be considered a refuge for farmland birds (Archaux 2007).

The Skylark is a flagship passerine, characteristic of traditionally farmed landscapes. However, this once common and widespread ground-nesting species has declined severely in grasslands and arable areas in Europe (Rigal *et al.* 2023). In Switzerland, 85% of the breeding population currently occur in arable areas of western and northern Switzerland below 1500 m above sea level, and only a small proportion inhabit subalpine and alpine grasslands (Knaus *et al.* 2018). The Swiss population has been declining for decades (Knaus *et al.* 2018), and Skylarks are now listed as vulnerable (VU) in Switzerland (Knaus *et al.* 2021). The decline of the Skylark is thought to be mainly the result of insufficient breeding success (Wilson *et al.* 1997, Chamberlain & Crick 1999). In intensively managed grassland areas where mowing occurs up to eight times per season (Weber *et al.* 2023), sufficient breeding success is not possible because the time between two cuttings is too short (Jenny 1990). Moreover, vegetation growth is very dense, making it difficult for the larks to forage and nest, as they prefer short and sparse vegetation (Wilson *et al.* 1997, Donald *et al.* 2001a, 2001b, Toepfer & Stubbe 2001). Furthermore, like many other ground-nesting birds, Skylarks require open, unobstructed habitats and avoid proximity to hedges (Wilson *et al.* 1997, Ludwig *et al.* 2012), trees (Graf *et al.* 2014, Mayer 2023), buildings (Golawski *et al.* 2023) and other infrastructure (Püttmanns *et al.* 2021). Skylarks are also territorial and will defend their territory against conspecifics with song flights and confrontations (Briefer *et al.* 2008). Although territory density is mainly determined by habitat type and vegetation height (e.g. Toepfer & Stubbe 2001), territory size is also density dependent, with larger territories being maintained when conspecific densities are low (Delius 1965, Wilson *et al.* 1997). Despite this territorial behaviour, Skylark territories tend to be aggregated (Delius 1965), which might indicate the importance of social attraction when establishing territories.

We studied the habitat preferences of Skylarks in subalpine and alpine regions across Switzerland. Using 3 years of territory mapping across a wide range of habitat types, land-use management and topographical characteristics, we aim to understand the limiting habitat factors for these alpine populations to better inform conservation management. We predicted that proximity to tall structures such as trees, buildings and other infrastructure would have the largest negative effect on the probability of Skylark occurrence, and intensive land management – especially the mowing regimen – would have an additional negative effect. We also expected that vegetation height (predicted from a separate model) would have an important effect on Skylark occurrence. Lastly, we predicted Skylark occurrence to increase with increased density of conspecifics.

METHODS

Study area

We studied 51 sites across the Swiss Alps between 2011 and 2018 (Fig. 1a). In the northern Alps, we focused on the westernmost areas, as almost no large subalpine–alpine Skylark populations are known east of Simmental. We selected study sites known to have (at least until recently) Skylarks present, and which varied considerably in elevation (range: 1372–2707 m), slope (0–52 degrees) and aspect (between 90 and 286 degrees, i.e. east, south or west facing). Although most study sites (n = 39) had a set area of 100 ha (1 × 1 km square), others ranged in size from 54 to 239 ha (104 ± 23 ha, 53 km^2 in total). Detailed information on the study sites can be found in Sutter *et al.* (2020).

Gridpoints

To analyse habitat suitability for Skylarks in the study area, we used a gridpoint approach (Fig. 1c), with spatial covariates and Skylark occurrence assessed for each gridpoint. Gridpoints were placed on a regular grid 100 m apart and were excluded if they overlapped with forest, scree or rocks (Fig. 1b,c). This grid size was chosen to optimize computational speed (i.e. larger scale) and provide sufficient representation of all categorical variables. A total of 4559 gridpoints were considered in the analysis; on average, there were 89 gridpoints per study site (n = 51).

Skylark territory mapping

Territory mapping was carried out with three visits per study site on predefined transects from May to

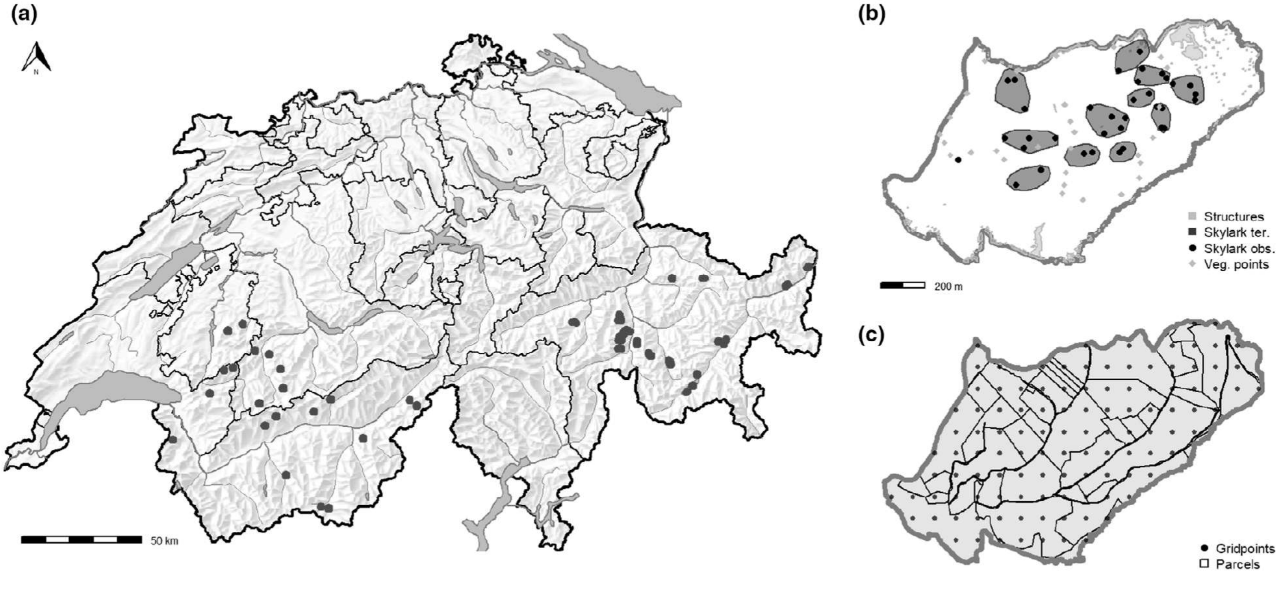

Figure 1. Map showing (a) the 51 study sites across the Swiss Alps, (b) example study site no. 47 showing mapped Skylark observations (black), derived Skylark territories (green), structures from swissTLM3D data (grey) and vegetation measurement points (yellow), and (c) gridpoints (black dots) and individual parcel locations (black lines).

mid-July (breeding season; 75% of data collected between 23 May and 26 June) according to the Swiss Breeding Bird Atlas scheme (Knaus *et al.* 2018). Transects were on average 3.9 ± 1.5 km long (one transect per study site, c.200 km in total). Skylarks needed to be present during at least two visits in a transect section of potential territory size (c.1–3 ha) along the transects to be designated as a territory. The transects were laid out in such a way that they covered as wide an elevation range as possible while including as much agricultural land as possible (meadows, year-round and summer pastures) and ran along roads, footpaths, plot boundaries or rivers. We do not expect the location of the transects to have created bias as these structures are not avoided by Skylarks; in fact, territories can sometimes integrate unpaved paths and field boundaries (Fischer *et al.* 2009).

Skylark occurrence

Skylark territory polygons were drawn around presence locations of Skylarks displaying territorial behaviour, such that assigned territories did not overlap. Skylarks were then considered present if gridpoints overlapped with these Skylark territories (Fig. 1b,c). Although some study areas were visited in several years – yielding up to three Skylark presence records per gridpoint – only one was retained: if Skylarks were present in any year, this gridpoint was considered suitable and recorded as 'Skylark present' in the analysis. Overall, 17% of all gridpoints overlapped with a Skylark territory.

Skylark density

We calculated Skylark territory density per gridpoint as the number of territories within a circular buffer of 300 and 500 m around each gridpoint, excluding the territory overlapping with the gridpoint, if any, to obtain a measure of territory density independent of our response variable. We considered these buffer sizes to be appropriate as the resulting area could include several neighbouring territories (territories were often around 100–200 m long, Fig. 1) and at the same time exclude territories that would be too far away to affect territorial behaviour (Loretto *et al.* 2019). This yielded territory densities of up to 12 territories per 10 ha (mean ± standard deviation (sd) across study area 1.2 ± 1.7 territories per 10 ha), comparable with previous studies (Wilson *et al.* 1997, Toepfer & Stubbe 2001). In seven study sites, 3 years of data were collected (2016, 2017, 2018), while in five study sites, 2 years of data were collected (2017, 2018); the other sites had only 1 year of data. Where multiple years of Skylark territory mapping were carried out, we calculated the average territory density per gridpoint across years for each buffer.

Habitat mapping

Habitat types were mapped in the field once at each gridpoint (10 m^2 area) using the '*Alauda alpina*' habitat classification key (Graf *et al.* 2014; self-developed, simplified key based on the Swiss national ALL-EMA key; agroscope.ch). This original key uses the habitat typology of Delarze *et al.* (2008). If points were inaccessible or in an unsuitable habitat for Skylarks (e.g. settlements, scree slopes, rocks, forest), they were not visited in the field and were not used for the analysis.

We recognized 26 habitat types across all study sites. Some of these only occurred sporadically and were merged with more common habitat types that had similar characteristics, yielding 14 categories that were considered in the vegetation height analysis (Fig. S2).

Vegetation measurements

As vegetation height is crucial for Skylark habitat selection but is difficult to estimate using remote-sensing data, we performed field measurements of vegetation height in at least 30 locations in 37 study sites (not all sites were included due to time and resource constraints). Vegetation sampling points (1 m^2) were located along the Skylark survey transects and were chosen so that (1) all different habitats of the study sites were represented, and (2) the vegetation structure at the location was homogeneous. Vegetation height was measured using the 'direct measurement method' (Stewart *et al.* 2001) in the centre of the sampling points. Vegetation height is defined as the height of the dominant vegetation stage (dwarf shrubs or grass) when 80% of the vegetation touches a flat, horizontal plane. Measurements recorded before snow melt and after mowing events were excluded from the analysis (Data S1). Three to 12 measurements per point were recorded in either 2017 ($n = 60$) or 2018 ($n = 902$), between May and August. On average, the first and last vegetation height measurements per point were 42.4 days (sd = ±15.8 days) apart, with a minimum of 15 days apart.

Spatial covariates

We used the swissTLM3D 2.2 spatial data to select polygons or point data on structures within our study sites (Fig. 1b; Swisstopo 2021). We selected the following structures relevant for Skylark settlement within a 1-km buffer around each study site: buildings, single trees, tall infrastructure and forest. For each gridpoint, we calculated the distance to the nearest structure (any category) and to the nearest specific structure. For those gridpoints that were further than 1 km away from the nearest structure, we truncated this distance to 1 km. We further calculated the density of structures (any category) within a 50-m and 100-m buffer around each gridpoint. Density was recorded as percentage of buffer area covered by structures (0–100%). Single trees, recorded as point data, were assumed to have a radius of 3 m (or an area of 28 m^2).

Land-use intensity

We used data produced by Weber *et al.* (2023) on the timing of the first grassland mowing event and the number of annual mowing events as a proxy for land-use intensity. This product is derived from remotely sensed data that were extensively ground-truthed, and covered grasslands and pastures across Switzerland between 2018 and 2021. However, Weber *et al.* (2023) note that while their modelled grazing/mowing events corresponded well with observed events (>78%), the algorithm did not detect a substantial proportion of grazing events, especially on high-elevation pastures, and so underestimated land-use intensity in those areas. These so-called 'summer pastures' are managed during the alpine summer season only, are communally used and are located above the treeline, setting them apart from year-round pastures (Bundesamt für Landwirtschaft 2021). We accounted for this discrepancy by adding a covariate distinguishing between summer pastures and other grasslands. Summer pasture areas comprised 45% of our gridpoints. Lastly, as our data were collected (2011–2018) before the study period of Weber *et al.* (2023) (i.e. 2018) and there was considerable and unpredictable between-year variation in mowing frequency and timing, we opted to average these yearly data and then calculated an average mowing and grazing event frequency and timing within a 50-m buffer around each of our gridpoints. We chose a buffer of 50 m to maximize the variation in land-use intensity variables and to allow for potential small-scale variation in land management. Mowing and grazing frequency within 50-m and 100-m scale buffers had a Pearson's correlation coefficient of 0.94.

Land-management diversity

Different landowners manage their land differently: timing of mowing or cattle grazing, rotation choices, removal of hedges and inclusion of biodiversity initiatives can all vary between different parcels (Šálek *et al.* 2018). Additionally, boundaries of land ownership often have hedges, trees or other habitat structures that diversify the landscape (Benton *et al.* 2003). We used publicly available data on land ownership across our study area (Swiss cantons of Vaud, Valais, Fribourg, Bern and Graubünden) to calculate the number of unique land-ownership parcels within the Swiss cadaster as a proxy for land-management diversity. This was calculated as the number of individually recognized parcels per 100-m circular buffer (standardized unit) for both a 50-m and 100-m buffer for each gridpoint.

Statistical analyses

Vegetation height model

To be able to use vegetation height as a predictor for all sites and at the same time of year, we constructed a predictive model for seasonal change in vegetation height based on topographic variables (i.e. elevation (in m), aspect (in degrees from due north) and slope (in degrees)) and habitat type (12 levels; Fig. 2) from which we then could extrapolate to sites without vegetation height measurement data. We performed a K-fold cross-validation (Davison & Hinkley 1997) on all possible variable combinations and their interactions (models = 167) and selected the model with the smallest prediction error. Using this model, we predicted vegetation height for each gridpoint

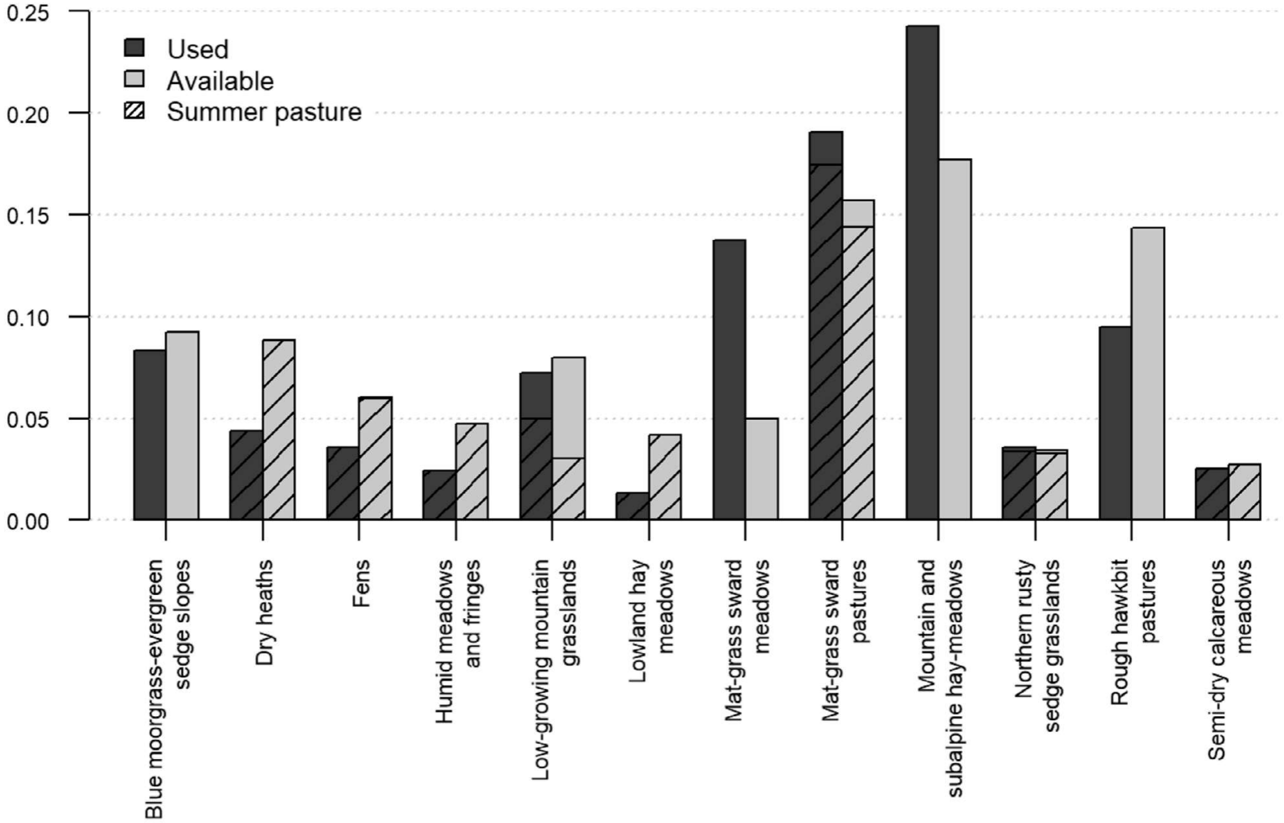

Figure 2. Proportion of gridpoints available and used (i.e. gridpoints overlapping with territories) within each habitat category. Categories are defined according to Delarze *et al.* (2008). Dashed area indicates the proportion of this habitat that was in summer pastures (as opposed to areas in use year-round). We dropped two habitat types ('dry grasslands and fringes' and 'mesophile pastures') as these represented only 1% and 0.3% of the data, respectively.

given its topographical characteristics (i.e. elevation and slope) and habitat category at a particular day of the year. However, as date of snowmelt drastically differs across the elevational range of our study area and this determines the start of vegetation growth, we additionally predicted vegetation height on an approximate date of snowmelt (in day-of-year; Vorkauf *et al.* 2021). We assumed a linear relationship between elevation and date of snowmelt, which yielded an estimated date of snowmelt of 1 April at 1300 m and 1 August at 2700 m (Vorkauf *et al.* 2021). At this date at these elevations, no mowing or grazing would have taken place to affect our vegetation height prediction. We opted to use the predicted vegetation height estimates from the model for all gridpoints for consistency, and because measurements were recorded on different dates and could not be directly compared. More detailed information is available in Data S1.

Skylark occurrence model

We modelled Skylark occurrence using a hypothesis-based overall model structure but undertook model selection to select the best-fitting spatial scale for covariates that were measured at different buffer sizes. We compared two different buffer sizes for density of tall structures (50 and 100 m), territory density (300 and 500 m) and density of land parcels (50 and 100 m). This resulted in eight models, of which we compared the Akaike Information Criterion for small sample sizes (AICc) to select the best-fitting combination of buffer sizes (Anderson & Burnham 2002). The model with the smallest AICc was selected as the best-fitting model for our data – a method extensively explored by Andreatta *et al.* (2025). The selected model included a 100-m buffer for both density of tall structures and parcel density, and a 300-m buffer for territory density; the second smallest ΔAICc value was 6.5.

Having selected buffer sizes for the relevant covariates, we fitted a model which included 11 independent variables (Figs 3–6). We included an interaction between density of structures and distance to structures as well as between land-use type and mowing/grazing event frequency. We included a quadratic effect date of first grass cut and predicted vegetation height and included a smoothing function on territory density as we expected a non-linear relationship. Habitat type was not included in the model as the marginal effect after accounting for all other parameters would be difficult to interpret for this variable; rather, we show the relationship between Skylark density and habitat types in the raw data (Fig. 2).

We fitted a binomial mixed effects regression model in a Bayesian framework (R package *brms*; Bürkner 2017) on 4559 observations. We used *brms* default priors and initialization settings. We included study site ($n = 51$) as a random intercept effect. No spatial autocorrelation was found (Moran's *I*, $P = 0.321$; R Package *DHARMa*; Hartig 2024). Model residuals were checked and did not show any problems. Correlation between covariates was checked and showed no issues (all correlation coefficients were below 0.59), and variation inflation factors were all less than 3.14, well within acceptable limits (Zuur *et al.* 2010).

RESULTS

Skylark observations

Skylark territories were observed in 44 of the 51 study areas. In those with territories, there were on average 1.2 territories per 10 ha. Some grid-points ($n = 44$, or 1%) had a notably higher territory density (c.2–4 territories/10 ha). They were

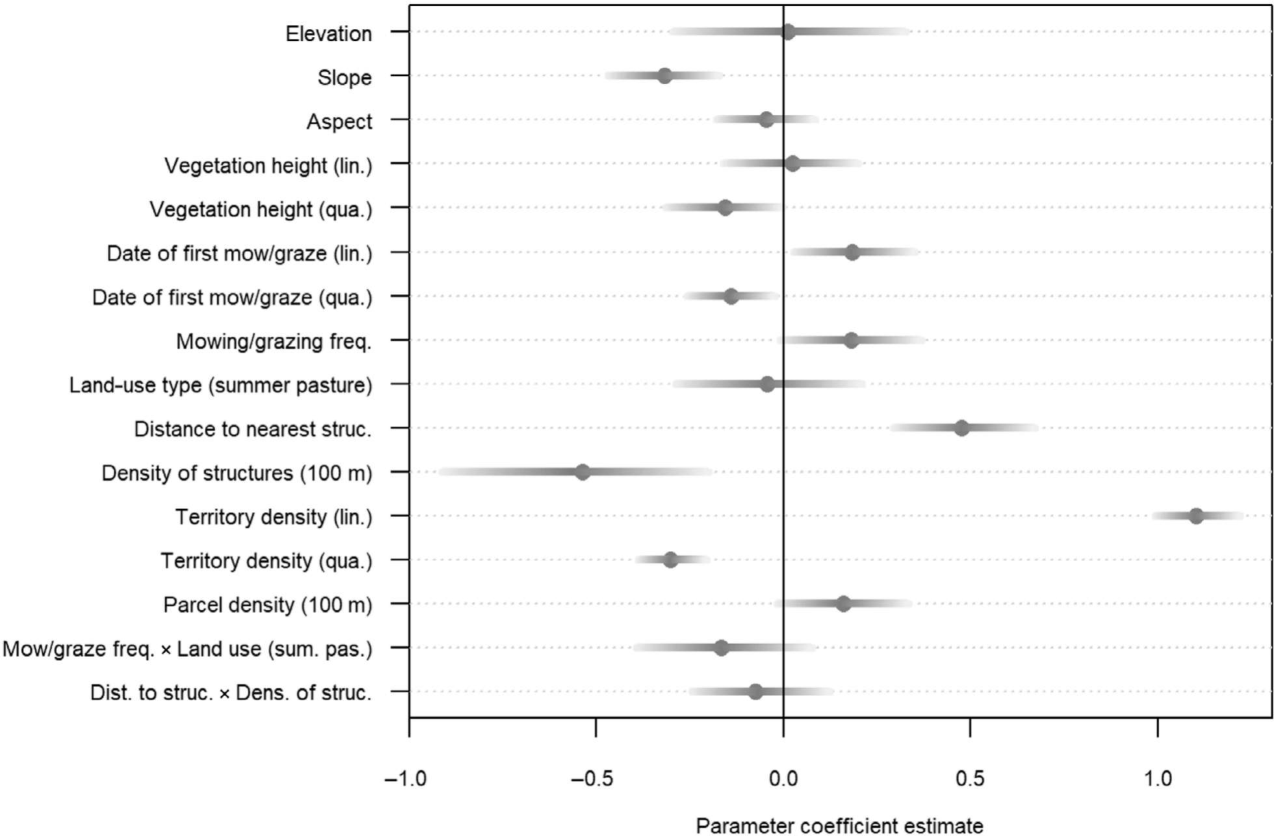

Figure 3. Standardized coefficients of each predictor variable (with 95% credible interval) in the logistic regression model explaining Skylark occurrence, showing the relative importance of each predictor. These estimates are from the model including a linear-quadratic function of territory density, allowing comparison of parameter estimates. The final model (and effect plots) includes a smoothing parameter of territory density instead. For factors, the reference level is given in parentheses.

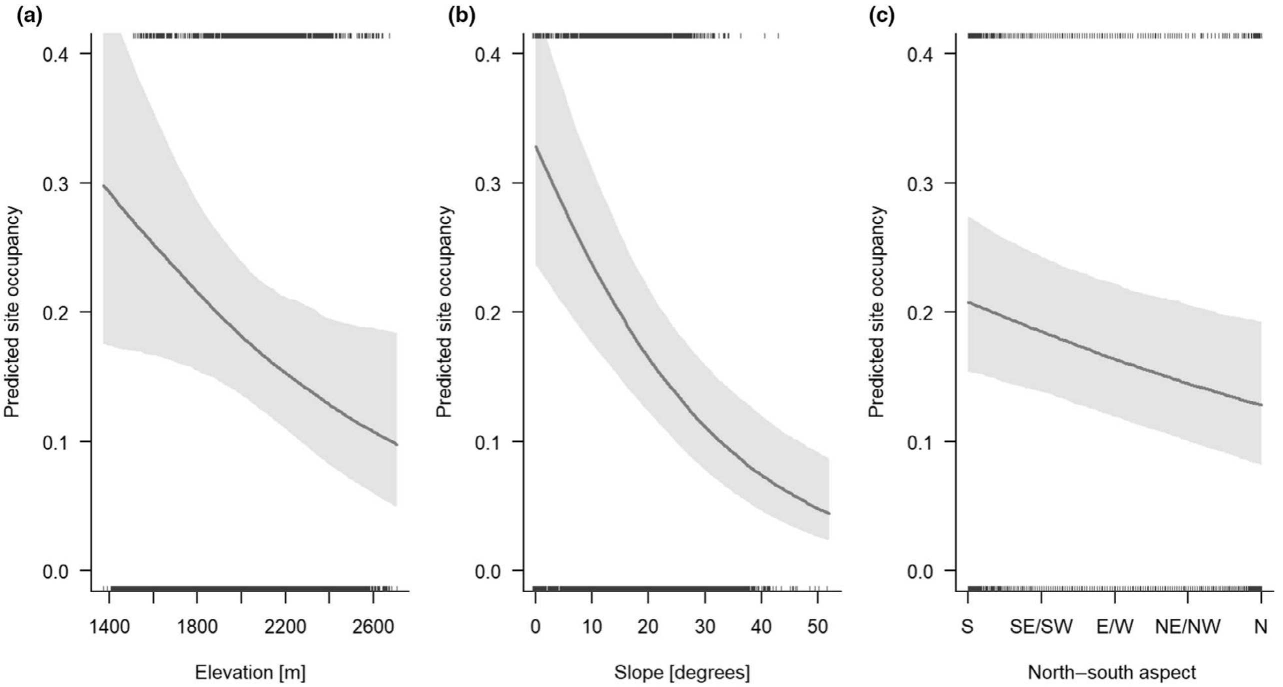

Figure 4. Logistic regression model effect plots showing the relationships between (a) elevation, (b) slope and (c) north–south aspect and predicted Skylark occurrence. Rugs show the distribution of occupied (1) and unoccupied (0) gridpoints. Lines and shaded polygons show predicted mean values and 95% credible interval, respectively.

all located within a specific area in southeast Switzerland called *Muntogna da Schons*, which is known for its high density of Skylarks. In total, 961 territories were mapped (n = 263 in 2016, n = 268 in 2017, n = 430 in 2018) with a median territory size of 0.83 ha (sd = ±0.81 ha).

Vegetation height model

The vegetation height model fit the data well, explaining 83% (Bayes R^2) of the variation in vegetation height measurements. Vegetation height was mainly affected by habitat, with vegetation height being highest in the 'lowland hay meadows' (Delarze *et al.* 2008) and lowest in low-growing mountain grasslands. It should be noted that in our data, the 'lowland hay meadows' habitat category occurs between 1372 and 2080 m above sea level and is therefore not considered to be Swiss lowlands.

Skylark occurrence model

As expected, occurrence decreased with increasing elevation (Figs 3 and 4a), and flat areas were much preferred over steep slopes (Fig. 4b). Skylarks also showed a small preference for slopes with a southern aspect, compared with north-facing slopes (Fig. 4c).

Predicted vegetation height – estimated from the vegetation height model – had a small effect on Skylark occurrence (Fig. 3) but seemed to be optimal (i.e. peak Skylark occurrence) at 15 cm vegetation height (Fig. 5a).

Skylark occurrence increased as the mowing and grazing event frequency increased from 0 to 2 but only in areas with a year-round land use and not in summer pastures (Fig. 5b). Skylark occurrence was highest when grasslands were mown not before late August and lowest when grasslands were mown early (Fig. 5c). Lastly, Skylark occurrence increased with increasing parcel density (Fig. 5d).

Skylark occurrence was strongly correlated to the density of conspecifics, reaching peak occurrence at seven territories per 10 ha (Fig. 6a).

As expected, Skylark occurrence was strongly related to the proximity of tall structures (Figs 3 and 6b). Skylark occurrence increased strongly with increasing distance to the nearest tall structure, and this was especially the case in areas where structure density was low.

Overall, the model had good explanatory power (marginal R^2: 45.9%; R package *performance*; Lüdecke *et al.* 2021).

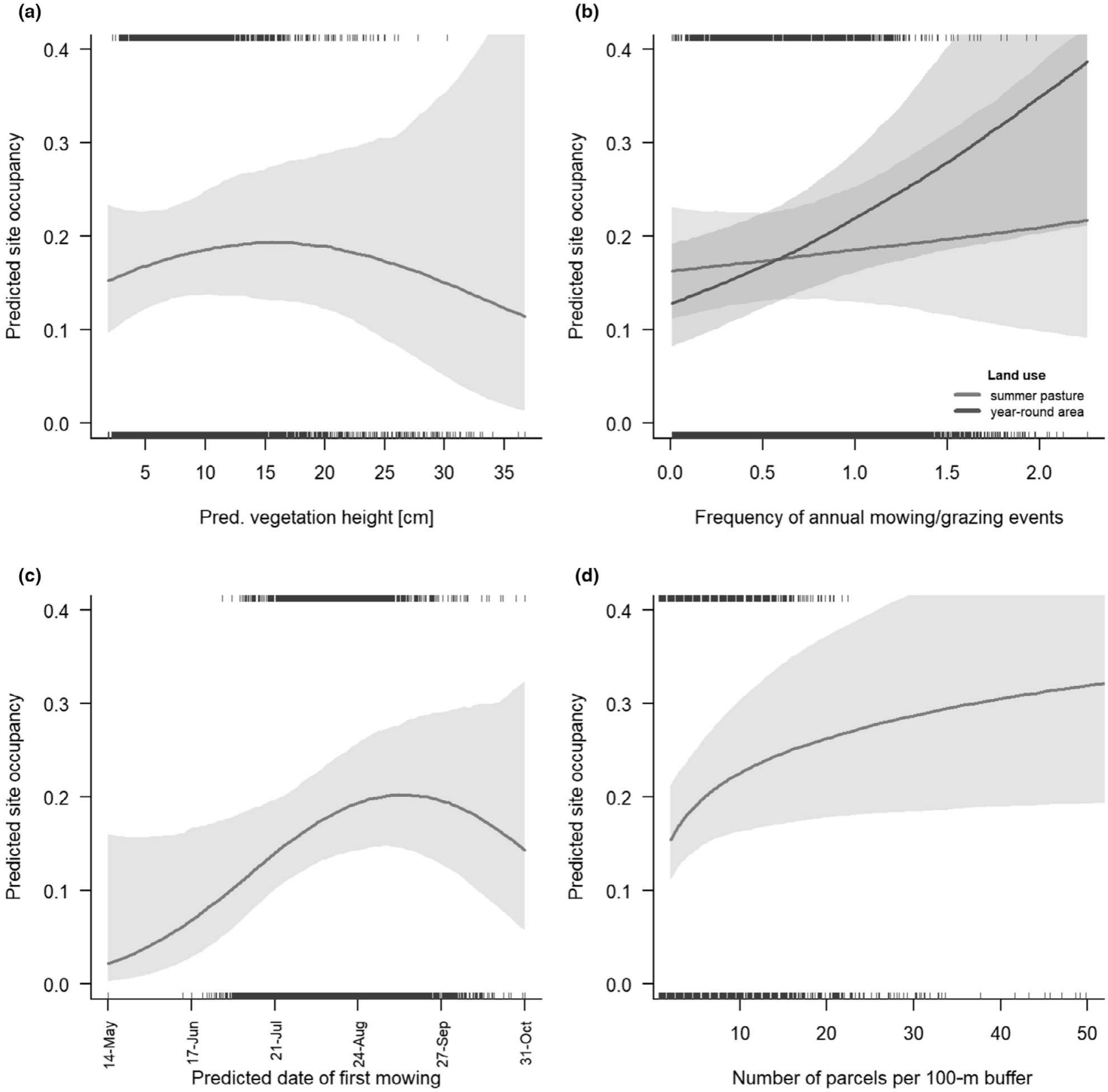

Figure 5. Logistic regression model effect plots showing the relationships between (a) predicted vegetation height, (b) annual mowing frequency in summer pastures (red) and year-round areas (blue), (c) date of first mowing and (d) density of land parcels (*x*-axis is constrained to 50, which omits four observations, maximum = 64) and predicted Skylark occurrence. Rugs show the distribution of occupied (1) and unoccupied (0) gridpoints. Lines and shaded polygons show predicted mean values and 95% credible interval, respectively.

DISCUSSION

We found that Skylarks preferred areas at lower elevation (c.1400 m), with gentler and south-facing slopes (Figs 3 and 4). This corroborates other studies of Skylarks (Loretto *et al.* 2019, Tirozzi *et al.* 2024) and other farmland bird species, such as Corncrakes and Whinchats, which have been shown to occur at lower occupancy rates and lower densities at higher elevations (Calladine & Bray 2012, Brambilla *et al.* 2021). These results suggest that although alpine habitats might

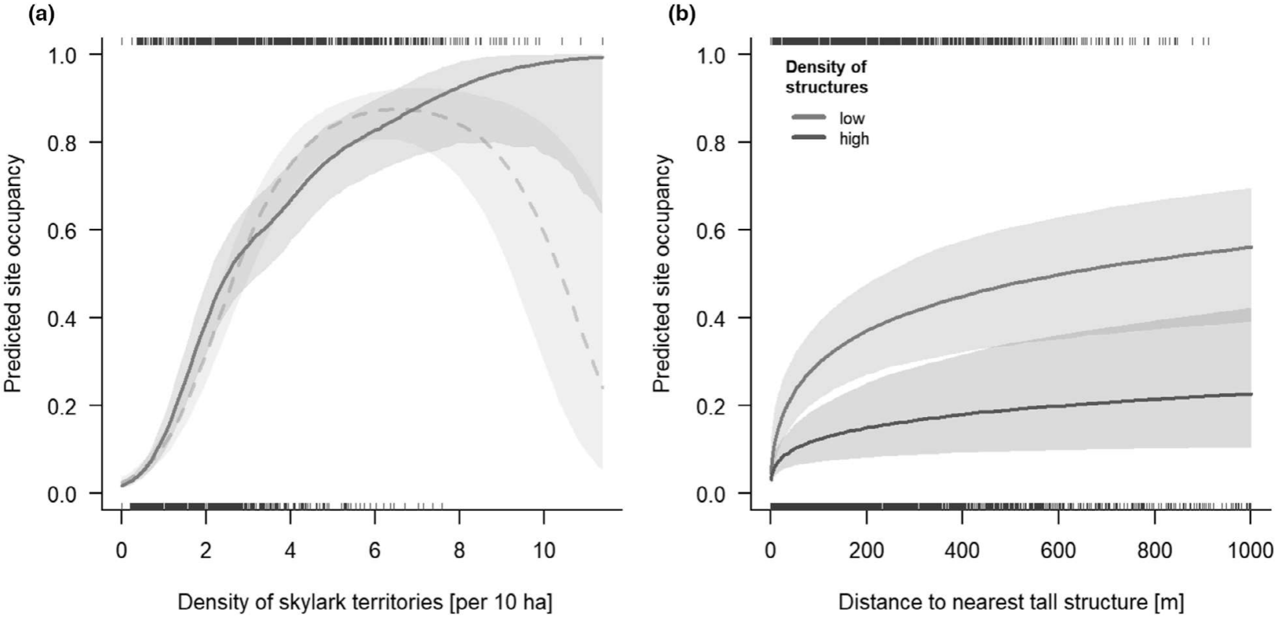

Figure 6. Logistic regression model effect plots showing the relationships between (a) Skylark territory density and (b) distance to nearest structure at low (c.0%; red) and high (c.10%, blue) density of structures (continuous variable, here presented as a categorical variable to ease visualization) and predicted Skylark occurrence. In (a), the grey dashed line represents the linear-quadratic predictor used to compare parameter estimates, and the red line represents the smoothing parameter, the latter showing a better and more realistic fit. Rugs show the distribution of occupied (1) and unoccupied (0) gridpoints. Lines and shaded polygons show predicted mean values and 95% credible interval, respectively.

be valuable secondary refugia for Skylarks, lower elevation areas are crucial for the conservation of Skylark populations. Additionally, as not all alpine areas seem suitable – Skylarks strongly preferred flat or gently sloping areas (Fig. 4b; Brambilla *et al.* 2020) – this limits the potential areas that Skylarks might occupy in the Swiss Alps. These areas are also preferred for more intensive agriculture and for development of infrastructure such as solar energy farms. Skylark populations in these areas are therefore likely to face similar challenges as populations in the lowlands.

Predicted vegetation height did not affect Skylark occurrence, contrary to our expectation (Fig. 3). Various studies have shown the importance of vegetation height and density for successful Skylark reproduction, especially when nests are in arable crops (Toepfer & Stubbe 2001, Hiron *et al.* 2012, Koleček *et al.* 2015). As ground-nesting birds, they rely on the cover of surrounding vegetation for the protection of their brood, but taller vegetation might hinder parental care and fledging (Eraud & Boutin 2002). However, at high elevations, as in our study, vegetation height at territory establishment might not be a limiting factor for Skylarks, as most vegetation did not exceed the suitable height range (between 15 and 60 cm; Toepfer & Stubbe 2001) within our data (90th centile = 32 cm; *n* = 3422). Indeed, Donald and colleagues (Donald *et al.* 2001a, 2001b) found no effect of vegetation height on territory density at the point of initial territory establishment in March on UK farmland. Our results therefore suggest that vegetation height (Donald *et al.* 2001a, 2001b, Schaub *et al.* 2010) currently does not limit Skylark occurrence in alpine areas.

Skylark occurrence increased with increasing mowing frequency in areas of year-round use, but much less so in summer pastures (Fig. 5b). We expected a higher mowing frequency to negatively affect Skylark occurrence, as frequent mowing results in the loss of nests and hatchlings for ground-nesting birds (Grüebler *et al.* 2008, Broyer 2011, Assandri *et al.* 2019b). Unlike agricultural areas at low elevation, where the growing season can last several months longer than in (sub-)alpine areas, allowing for up to eight mowing events per year (Weber *et al.* 2023), our study areas had a very low predicted mowing frequency, with most areas having less than one mowing event per year, on average. Mowing frequency might therefore not be a limiting factor in our study area and might in fact benefit Skylarks as it was shown that one or two mowing events per season can actually increase Skylark densities (Toepfer & Stubbe 2001). Bazzi *et al.* (2014) also found higher Skylark densities in areas with more frequent mowing events in the Italian pre-Alps at elevations of 1500 m, probably because it keeps areas open and prevents encroachment. However, in our study, Skylark occurrence increased considerably with a later date of first mowing, suggesting that even in areas with low agricultural productivity, and therefore low mowing frequency, delayed mowing is still beneficial for Skylarks (Fig. 5c). Delaying first mowing to mid- or end-August would also be essential to allow for replacement broods to be successful (Guyot *et al.* 2018). As subalpine areas become increasingly intensified, mowing frequencies have risen, with earlier first cuts leading to greater nest loss rates and adult mortality in Whinchats (Müller *et al.* 2005, Assandri *et al.* 2019b). This may also threaten local Skylark populations (Jenny 1990), particularly in lower-elevation areas.

Skylarks preferred mat-grass (*Nardus stricta*) sward meadows and mountain and subalpine hay meadows (Fig. 2, showing the raw data relationship). These meadow habitats occur between 1600 and 2500 m elevation and are often less intensively used (Bazzi *et al.* 2014, Korner *et al.* 2018). Humid habitats (e.g. fens and humid meadows), habitat with tall or dense vegetation (e.g. dry heaths), or intensively used habitat (e.g. lowland hay meadows and rough hawkbit pastures) were avoided, which is in line with other studies (Toepfer & Stubbe 2001, Koleček *et al.* 2015). Although these findings confirm previous knowledge of Skylark habitat preferences, here they are based on raw data and should be interpreted with caution.

Skylarks preferred areas with higher land-management diversity, here measured as the number of individual land parcels per 100 ha (Figs 3 and 5d). This finding corroborates previous research where smaller field sizes benefitted Skylarks (Eraud & Boutin 2002, Miguet *et al.* 2013). More individual parcels often result in a more structurally rich habitat, as different owners might employ different land-management strategies, for example by varying timing, mowing frequency or grazing intensity among fields (Denac & Kmecl 2021). Landscape heterogeneity commonly leads to a higher biodiversity and benefits many species (Benton *et al.* 2003, Vickery & Arlettaz 2012). On the other hand, consolidating individual fields into larger units is a common result of what in Switzerland are called 'amelioration projects' (i.e. development projects often leading to intensification of agricultural practices in an area; Koleček *et al.* 2015, Gayer *et al.* 2019, Denac & Kmecl 2021, Andreatta *et al.* 2025).

We found that increasing proximity of tall structures such as buildings, trees and electricity poles strongly reduced Skylark habitat occurrence, even when tall structures were at low density (Figs 3 and 6b). This result accords with previous studies showing that Skylarks are sensitive to the presence of a few or even a single tall structure in their vicinity and indicates their strong preference for open habitat (Donald *et al.* 2002). Our data suggest that forests and single trees are strongly avoided up to around 100 m, and buildings and high infrastructure (e.g. antennae, ski lift pylons and electricity lines) were avoided up to as much as 300 m distance (Fig. S3). The increasing abandonment of extensively managed meadows and pastures in the Alps has resulted in their encroachment by thickets and other tall vegetation (Graf *et al.* 2014), limiting the amount of suitable habitat for Skylarks. The encroachment effect due to abandonment is further exacerbated by climate change, which has been shown to result in a shorter permanence of snow cover, favouring shrub and forest growth (Gehrig-Fasel *et al.* 2007). At the same time, both agricultural and tourist infrastructure development projects, as well as Switzerland's push for new solar farms on alpine grasslands, will most likely result in many more tall infrastructures being built in alpine refugia, posing an additional threat to Skylarks (Loretto *et al.* 2019, Brambilla *et al.* 2020).

We found that Skylark occurrence probability increased sharply with increased density of conspecifics. Social attraction has been shown to be vital to many migratory songbirds (Szymkowiak 2013), sometimes even overriding typical habitat preferences (Betts *et al.* 2008). Skylarks, too, tend to aggregate until a certain territory density is reached (Delius 1965). Clustering can yield several benefits; for example, Powolny *et al.* (2012) found that increased Skylark local group size led to decreased time spent on individual vigilance and increased food intake. However, larger groups and higher conspecific density reduce habitat quality through, for example, modulating predation risk, and negatively affecting foraging efficiency (Powolny *et al.* 2012). Our data indicate that social attraction is the most important factor in determining territory occurrence (Fig. 6a); indeed, a model with only territory density explained 42% of the variation in Skylark occurrence, whereas a model without explained only 14% (marginal R^2). The effect of social attraction is probably not attributable to habitat quality, as our model already accounts for the most important aspects of habitat characteristics preferred by Skylarks (e.g. elevation, aspect, slope, land management, and structure density and proximity). Indeed, when playbacks were used to attract Whinchats into suitable habitat (which, admittedly, could in itself have affected territory settlement behaviour), Whinchats instead consistently preferred to settle in the neighbourhood of conspecifics, stressing the importance of social attraction and the importance of protecting existing populations (Vögeli *et al.* 2018, Shitikov *et al.* 2024). This suggests that 'suitable' habitat that lacks the attraction of other Skylarks might not be colonized by immigrants despite being good-quality habitat (Szymkowiak 2013). Indeed, because of reduced social signalling in small populations, these populations could experience reduced immigration from source populations, thus compromising population persistence (Laiolo & Tella 2008). We found very few studies that have examined social cues in Skylarks, yet clearly this should be explored more to better understand how to effectively protect the remaining Skylark populations.

In conclusion, we studied the habitat preferences of Skylark populations in the Swiss Alps. Skylark populations have been declining precipitously in alpine valleys, but much less so at higher elevations (Knaus *et al.* 2021), suggesting that these areas could represent refugia. However, we found that Skylark densities were much lower than populations in the western lowlands of Switzerland (Knaus *et al.* 2018). Additionally, because of the shorter vegetation growth period at high elevations, usually no more than one breeding attempt is made per season, limiting the degree to which these alpine areas can act effectively as refugia for Skylarks (Archaux 2007). Further research should investigate the reproductive success of these alpine Skylark populations and to what extent they are self-sustaining. Furthermore, we show that Skylarks occupy those areas that are most likely developed for agricultural intensification or for infrastructure and energy projects (because of their open aspects and flatness), while the abandonment of extensively used areas results in shrub encroachment (Graf *et al.* 2014), thereby further threatening alpine Skylark populations.

Our results delineate clear management recommendations to maintain and bolster Skylark populations in alpine areas. Apart from limiting the intensification of agricultural areas and preventing the abandonment of extensively used meadows and pastures (Korner *et al.* 2018, Brambilla *et al.* 2021), maintaining open meadows while mowing only once or twice late in the season would allow Skylarks to maximize their breeding success (Bazzi *et al.* 2014). Moreover, our results also show that Skylark occurrence is in a large part affected by the presence of conspecifics, indicating that establishing new populations in unoccupied areas could be far more difficult than maintaining or expanding existing populations (Delius 1965, Szymkowiak 2013). We encourage local and regional conservation projects to designate and protect suitable, low-intensity meadows and pastures that currently host Skylark populations, especially in areas hosting larger populations.

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AUTHOR CONTRIBUTIONS

Louis Hunninck: Writing – original draft; writing – review and editing; visualization; formal analysis. **Judith Zellweger-Fischer:** Conceptualization; methodology; writing – review and editing. **Pius Korner:** Formal analysis; writing – review and editing. **Claire Lischer:** Writing – review and editing; conceptualization; methodology; project administration.

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CONFLICT OF INTEREST

The authors have no conflicts of interest.

ETHICAL NOTE

This study was conducted using only non-invasive observational methods. No birds were handled or disturbed, and all observations were made at a safe distance to minimize any potential impact on bird behavior or habitat, in accordance with ethical guidelines for ornithological fieldwork.

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DATA AVAILABILITY STATEMENT

The data used in this study are available in the Data S2.

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SUPPORTING INFORMATION

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

Data S1: A detailed description of how vegetation height was modelled (S1), information on how various habitat categories were merged to be used in the final analysis (S2), additional figures showing the raw data of the proportion of used and available points in relation to the distance to various specific tall structures (S3), and a plot showing the pairwise Pearson's correlation coefficients between all predictors and response variable.

Data S2: data.