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ORIGINAL ARTICLE

The contribution of broadscale and finescale habitat structure to the distribution and diversity of birds in an Alpine forest-shrub ecotone

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Abstract

In a mountain context, the forest-shrub ecotone is an area of high biodiversity. Relatively little is known about the habitat requirements of birds in this habitat, yet it is facing potential threats from changes in grazing practices and climate change. Moreover, it is not clear at which scale habitat associations should be assessed in Alpine birds. Further information on key habitat components affecting bird communities of the ecotone is needed in order to inform management strategies to counteract potential habitat loss, and to better inform predictions of how bird communities may be affected by future environmental change. Data on bird occurrence and broadscale (land cover) and finescale (vegetation structure and shrub species composition) habitat variables were collected in an Alpine forest-shrub ecotone in Val Troncea (northwestern Italian Alps) in order to address two objectives: to identify the key habitat variables associated with the occurrence of individual species and with the diversity of the bird community; and, to assess which scale of habitat measurement (broadscale, finescale or both combined) is needed to model bird occurrence. Broadscale variables, or combinations of broadscale and finescale variables, tended to have the best performing models. When combined models performed best, shrub species identity was included in many cases. Shrubs also played an important role in explaining variations in species diversity and richness. Vegetation structure was of relatively little importance, either for individual bird species or for species richness and diversity. These findings suggest that management should strive to maintain a mosaic of habitats whilst minimizing forest encroachment, which could be achieved through targeted grazing. Broadscale habitat data and data on shrub species composition should provide a sufficient basis for identifying relevant species-specific habitat parameters in a mountain environment in order to model future scenarios of effects of habitat change on the bird community of the alpine forest-shrub ecotone.

Keywords Habitat management · Grazing · Mountains · Vegetation structure · Species distribution models · Habitat mosaic

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Zusammenfassung

Die Rolle von groß- und kleinräumigen Habitateigenschaften für Verbreitung und Diversität von Vögeln des Waldgrenz-Ökotons der Alpen

Das Waldgrenz-Ökoton der Alpen ist ein Gebiet, welches durch eine hohe Biodiversität gekennzeichnet ist. Obwohl aktuelle Bedrohungen durch Klimawandel und Veränderungen in der Beweidungspraxis omnipräsent in diesem Areal sind, sind die Habitatansprüche, welche für die Vögel in diesem Bereich gelten, bislang kaum erforscht. In welchem Maßstab diese Habitatanforderungen für Alpenvögel erfasst werden sollten, ist ebenfalls nicht bekannt. Es ist daher erforderlich, jene Habitatelemente zu identifizieren, die eine Schlüsselrolle für die Vogelgemeinschaften im Waldgrenz-Ökoton der Alpen spielen. Mit Hilfe dieser Informationen wird es in Zukunft möglich sein, potentiellem Habitatverlust entgegenzuwirken und Vorhersagen zu treffen, wie Vogelgemeinschaften des Ökotons auf zukünftige Umweltveränderungen reagieren könnten. Durch die Aufnahme von Daten über das Vogelvorkommen sowie groß- (Landbedeckungsdaten) und kleinräumigen (Daten zur Vegetationsstruktur und zur Straucharten-Zusammensetzung) Habitatdaten im Waldgrenz-Ökoton des Naturparks Val Troncea (NW Italien) wurden zwei Zielstellungen verfolgt: Die Identifikation von Habitatelementen, welche für das Vorkommen einzelner Arten sowie für die Vogeldiversität und den Vogelartenreichtum von wesentlicher Bedeutung sind und die Beurteilung des Maßstabs zur Habitatdatenaufnahme (großräumig, kleinräumig oder eine Kombination aus beidem), welcher erforderlich ist, um das Vorkommen einer Art modellieren zu können. Großräumige Habitatvariablen oder eine Kombination von groß-und kleinräumigen Habitatvariablen führte zu den besten Modellen. Wenn die besten Modelle durch eine Kombination von Habitatvariablen erzielt wurden, war die Identität der Strauchart eine oftmals beinhaltete Variable. Generell spielten Sträucher eine wichtige Rolle, um Variationen in der Vogeldiversität und dem Vogelartenreichtum zu erklären. Von geringer Relevanz für individuelle Vogelarten sowie Vogelartendiversität und -reichtum waren kleinräumige Habitatvariablen zur Vegetationsstruktur. Diese Ergebnisse zeigen, dass zukünftige Naturschutzmaßnahmen darauf abzielen sollten, das Habitatmosaik im Waldgrenz-Ökoton zu erhalten und einer Ausbreitung des Waldes entgegenzuwirken. Dies könnte durch gezielte Beweidung erreicht werden. Großräumige Habitatdaten sowie Daten zur Strauchartenzusammensetzung stellten zudem eine solide Basis dar, um relevante artspezifische Habitatansprüche für alpine Vogelarten zu identifizieren und potentielle Auswirkungen zukünftiger Habitatveränderungen auf die Vogelgemeinschaft des alpinen Waldgrenz-Ökotons modellieren zu können.

Introduction

Mountain biodiversity is under a range of environmental pressures, including land use change (Laiolo et al. 2004), increased human leisure activities (Rolando et al. 2007; Arlettaz et al. 2007), climate change (Sekercioglu et al. 2008; Dirnböck et al. 2011), and interactions between these factors (e.g. Brambilla et al. 2016). Climate change may be a particular problem given that the rate of warming in mountains is approximately double the global average, a trend that is expected to continue (Böhm et al. 2001). A consequence of climate change is that vegetation zones are likely to shift upwards—for example, the upper forest limit has shifted to higher elevations in many mountain regions in line with rising temperatures (Harsch et al. 2009). The loss of high-altitude open habitats as a consequence of such vegetation shifts has been identified as a potential future conservation problem (Sekercioglu et al. 2008; Chamberlain et al. 2013), especially as the proportion of species of conservation concern tends to increase with elevation (Viterbi et al. 2013). However, vegetation shifts in some areas have also been due to abandonment of grazing, which maintained the forest limit at a lower altitude than would be possible under only climatic constraints. This effect has had a greater effect than climate change on tree line shifts in the European Alps (Gehrig-Fasel et al. 2007).

The ecotone between the forest and the alpine grassland zone is characterized by a high structural diversity, typically being a mix of open grassland areas, pioneer forest and shrub species. It is therefore often an area of high biodiversity (Dirnböck et al. 2011). Whilst abandonment of grazing and vegetation shifts due to climate change may, at least initially, have the capacity to create new habitats, in particular through colonization by shrub species (Laiolo et al. 2004), there are also threats to this habitat. First, it seems plausible to consider that structural diversity is a key factor driving the relatively high biodiversity of the ecotone (e.g. MacArthur and MacArthur 1961), and grazing is likely to maintain a habitat mosaic that underpins the structural diversity, hence further abandonment of grazing may be detrimental. Second, many mountainous areas do not reach altitudes that are high enough to maintain the ecotone habitat given the likely magnitude of vegetation shifts (Dirnböck et al. 2011)—such areas are likely to be mostly forest in the future. Third, it cannot be assumed that all components of the vegetation community will respond simultaneously to climate change (Theurillat and Guisan 2001). For example, there is evidence that vegetation zones respond differentially to warming

temperatures in the Alps (Cannone et al. 2007) , and that trees and shrubs may respond differentially to reduced snow cover resulting from climate change. Snow has insulating properties that benefit some shrub species from frost damage (Neuner 2014), and lower snow cover or earlier snow melt could potentially lead to a net loss of ecotone habitat.

Within the gradient of alpine habitats from mountain forest to the highest altitude nival zone (Kapos et al. 2000; Körner and Ohsawa 2006), the highest biodiversity is typically found in the forest-shrub ecotone, yet it has been little studied in an avian context. Whilst common species such as Dunnock *Prunella modularis*, Linnet *Carduelis cannabina*, Lesser Whitethroat *Sylvia curruca* and Wren *Troglodytes troglodytes* have been studied in lowland habitats (usually at higher latitudes), the few studies that have assessed habitat associations in these species in mountain habitats have considered only broadscale, usually remote-sensed, habitat data and have not considered more detailed measures of habitat complexity (Chamberlain et al. 2013, 2016). With a few exceptions, notably Black Grouse *Tetrao tetrix* (e.g. Patthey et al. 2012; Braunisch et al. 2016) and Ring Ouzel *Turdus torquatus* (von dem Bussche et al. 2008), there is as yet insufficient information to determine at which scale species-habitat associations should be assessed in order to plan conservation actions for the majority of common Alpine ecotone species in the context of environmental changes. Furthermore, such studies would also allow improvement of our ability to forecast potential effects of future environmental change for ecotone species. Species distribution models for typical ecotone species such as Dunnock, Wren and Tree Pipit *Anthus trivialis* show generally less good model performance, and greater inconsistency in model outcomes between different scenarios of change, compared with forest and grassland species (Chamberlain et al. 2013, 2016). This may be because these species are more dependent on finescale habitat characteristics, such as vegetation structure, and hence are not well-described by land cover and topographic variables that typically underpin many species distribution models.

Heterogeneity plays an important role in bird species diversity in a range of different habitats, including farmland (Benton et al. 2003), rainforests (Guerta and Cintra 2014), temperate forests (Freemark and Merriam 1986) and grasslands (Hovick et al. 2014). However, the role of heterogeneity in the forest-shrub ecotone is still not well understood. We would expect that, based on the influence of habitat diversity and structural vegetation diversity, species richness in the ecotone would be positively associated with measures of habitat heterogeneity. A recent study on Black Grouse in the Swiss Alps showed that horizontal and vertical structural heterogeneity was the best predictor of the occurrence of the species (Patthey et al. 2012). We similarly expect that ecotone species will in general be positively associated with habitat complexity. In this study, we consider complexity in terms of the diversity of vegetation structure, the heterogeneity in vegetation height, and also in terms of the habitat mosaic formed by shrubs, grassland and forest. We focus in particular on non-linear relationships between the bird community and shrub cover as a measure of the habitat mosaic, the expectation being that bird diversity and individual species occurrences will peak at intermediate values of shrub cover.

The specific objectives of this study are: (1) to assess key habitat attributes that influence bird diversity and individual species occurrence in an Alpine forest-shrub ecotone; and (2) to determine whether habitat cover and altitude are adequate to model species distributions in the ecotone, or if more detailed information on vertical vegetation structure and shrub species composition is needed.

Methods

Study area and point selection

The study was carried out in Val Troncea Natural Park (44°57′28″N, 6°56′28″E) in the western Italian Alps. At lower altitudes the area is dominated by larch *Larix decidua*. The natural tree line is typically found at around 2200 m a.s.l., but varies depending on local conditions. Typical shrub species are *Juniperus nana* (henceforth 'juniper') and *Rhododendron ferrugineum* (henceforth 'rhododendron'), which rapidly encroach upon wide areas of grasslands after the decline of agro-pastoral activities. Grasslands were mainly dominated by *Festuca curvula*, *Carex sempervirens*, and *Trifolium alpinum*. Scree and rocky areas occur predominantly at higher altitudes, above approximately 2700 m a.s.l.

Point counts were carried out in the forest-shrub ecotone, which we defined as the transition zone between forest and alpine grasslands. We included both natural ecotones where the tree line is limited by climatic conditions, and areas where open grassland has been maintained at lower altitudes, mostly due to grazing by domestic livestock, but also due to avalanches in some locations. Point count locations coincided with the centroids of a pre-existing grid at a scale of approximately 150 × 150 m [there was some variation, e.g. due to access constraints (Probo et al. 2014)] along the western-facing slope of the valley. Points were selected that had a minimum shrub cover of 5% and a maximum tree cover of 70% (i.e. representing the forest-shrub ecotone) within a 100-m radius according to vegetation surveys (see below). All points were spaced a minimum of 200 m apart.

Bird surveys

Point counts ($n = 79$) were carried out from mid-May to mid-July over a period of 2 years (46 in 2015 and 33 in 2016) following the methods of Bibby et al. (2000), using a 10-min count period. At each point count location, all individual birds seen or heard were recorded within a 100-m radius (estimated with the aid of a laser range finder). Point counts commenced 1–1.5 h after sunrise and continued until 1200 hours. Surveys did not take place in excessively wet or windy conditions. Each point count location was visited once.

Broadscale and finescale habitat

Habitat data were classified into two categories representing 'broadscale' habitat data (land cover, altitude and other variables estimated at a resolution of the whole point count location), and 'finescale' habitat data (vegetation structure and shrub species composition estimated from plots at a finer scale of resolution within the point count location). Broadscale habitat comprised visual estimation of the percentage cover of canopy (i.e. vegetation above head height), shrubs (woody vegetation below head height), open grassland and bare rock (including scree and unvegetated areas) within a 100-m radius of the point's centre. The number of mature trees (greater than ca. 20 cm in diameter at breast height) within a 50-m radius of a point count location was also counted. These estimates have been shown to correlate well with estimates of land cover derived from remote sensing and have been used as the basis of predictive models for several species considered here (Chamberlain et al. 2013, 2016).

Finescale habitat data on vegetation structure and composition were collected at the centre of the point count location and along two 100-m-long transects, each divided into five plots spaced 20 m apart originating at the point's centre (thus there were 11 plots sampled per point count location including the central point). The compass bearing of each transect from the centre of the point to its perimeter was selected at random, the only constraint being that there had to be an angle greater than 90° between two transects at the same point. Following Bibby et al. (2000), on each plot, vegetation density was measured at three different heights (0 m, 0.5 m, 1 m) using a chequered board (50 × 30 cm), divided into 10 × 10-cm square subdivisions, placed vertically in the vegetation, the bottom of the board coinciding with the appropriate height class. To produce an index of vegetation density, an estimate was made of the number of squares of the board that were obscured by vegetation observed from a distance of 5 m. A square was considered obscured by vegetation when < 50% of it was visible. The diversity of vegetation density over all 11 plots was then calculated with the Shannon diversity index $(H') = -\sum p_i \ln p_i$, where p_i is the proportion of squares obscured at the ith plot. Data were also collected on grass and shrub height (if present), and the SD of height calculated across the 11 plots was used as a measure of vegetation height heterogeneity for each point. The dominant shrub species at each plot within a 1-m radius was recorded and classified into four groups: rhododendron, juniper, bilberry (*Vaccinium myrtillus* and *Vaccinium gaultherioides)* and other (e.g. green alder *Alnus*

Table 1 Variables considered in the analysis, abbreviations used in the text, and the scale at which they were measured

Parameter	Category	Description
Canopy	Broadscale	Percentage cover of canopy (above head height) within a radius of 100 m of the point count centre
Shrubs	Broadscale	Percentage cover of shrubs within a radius of 100 m of the point count centre
Trees	Broadscale	Number of mature (greater than ca. 20 cm in diameter) trees within a radius of 50 m of the point count centre
Rocks	Broadscale	Percentage cover of rocks within a radius of 100 m of the point count centre
HCOV	Broadscale	Shannon index of broadscale habitat diversity ($H' = -\sum p_i \ln p_i$, where p_i is the percentage cover of the different habitat types)
Alt	Broadscale	Altitude of the point count location in metres a.s.l. estimated from a global positioning system
H1	Finescale	Shannon Index of vegetation density diversity at 1 m above the ground
H05	Finescale	Shannon Index of vegetation density diversity at 0.5 m
SDShrub	Finescale	Shrub height heterogeneity measured as the SD of the average shrub height at the point count location
Canfreq	Finescale	Frequency of vegetation sampling points for a point count location where canopy was present
Shrubfreq	Finescale	Frequency of vegetation sampling points for a point count location where shrubs were present
Rodfreq	Finescale	Proportion of vegetation sampling points for a point count location where rhododendron was the dominant shrub species
Junfreq	Finescale	Frequency of vegetation sampling points for a point count location where juniper was the dominant shrub species
Bilfreq	Finescale	Frequency of vegetation sampling points for a point count location where bilberry was the dominant shrub species

The broadscale category was measured at the whole point count location scale and the finescale category was measured at the plot level ($n = 11$ for each point)

viridis, willow *Salix* spp., and also young trees less than 2 m in height, mostly European larch *Larix decidua*). The frequency of plots in which a given group was present was calculated for each point (i.e. the maximum frequency was 11). All habitat variables used in the analysis are listed in Table 1 [a complete list of variables measured in the field, but not included in the models due to collinearity, are given in Electronic Supplementary Material (ESM) Table S1].

Data analysis

Birds detected within a 100-m radius of a point count location were used to analyse species richness (simply the number of species detected on each point count), species diversity (expressed using H') and species distribution (presence/absence of individual species) with regard to habitat composition and structure within the forest-shrub ecotone.

Data were analysed using an information theoretic approach with the MuMIn package in R [R version 3.3.2 (R Development Core Team 2016; Bartoń 2013)]. This entailed first deriving full models at each scale and for each dependent variable (richness, diversity or species presence) using a mixed modelling approach in the R package lme4 (Bates et al. 2015). Model-averaged parameter estimates were derived for all combinations of variables in each full model in order to identify variables that were most closely associated with bird distribution and diversity. *p*-values derived from the model-averaged parameter estimates and their SEs were considered to represent significant effects when $p < 0.05$. In addition, the Akaike information criterion corrected for small sample size (AICc) was determined for each individual model and was used to assess model performance at different scales (see below).

Prior to modelling, all variables within each set (i.e. broadscale or finescale) were scaled and centred. Variance inflation factors (VIFs) were calculated using the corvif function [package AED (Zuur et al. 2009)] to assess collinearity between continuous explanatory variables. All variables with a VIF > 3 were sequentially removed from the variable set until all VIFs were < 3. Inter correlations between remaining variables were then checked, and for those with Spearman correlation coefficients > 0.50, one of the pair was subsequently omitted (variables with a large proportion of zeroes were preferentially omitted, otherwise the choice was random). As a final check, variables that had been removed in the procedure to minimise collinearity were substituted for closely correlated variables (in particular between overall shrub cover or frequency, and the frequency of individual shrub species). Cases where the model with the substituted variable had a lower AICc were used in the final full model. As we were particularly interested in how the shrub-grassland habitat mosaic affected the bird community, we included a quadratic effect of variables representing shrub cover (including the frequency of individual shrub species) in all models. For other variables, non-linear effects were included in the models following visual assessment of scatter plots (following Zuur et al. 2009). Year was specified as random effect in every model to account for possible inter-annual effects.

Species richness and species diversity were analysed using generalised linear mixed models in relation to habitat variables, specifying a Poisson and a normal error distribution, respectively. The occurrence probability of the commonest species [present on 15% of points—Chamberlain et al. (2013) found that models performed persistently poorly below this threshold] in relation to habitat was analysed using binomial logistic regression, each species being recorded as either present or absent per point. At each scale, the residuals for all full models were extracted and tested for spatial autocorrelation using Moran's *I* (Moran 1950). There was no strong evidence of spatial autocorrelation across species or scales (see details in ESM Table S6 and S7), therefore this was not considered further.

At the end of the above process, for species richness and diversity and for each individual species, candidate models with model-averaged parameter estimates were derived for each combination of variables based on the full model for broadscale and finescale habitat variables separately. The next step was then to derive combined models based on the most important variables from both broadscale and finescale models, defined as those variables which were either significant ($p \leq 0.05$) or which approached significance ($p \leq 0.1$) from the broadscale and finescale model sets. In the few cases where no variables had $p < 0.10$, those with a high Akaike weight (> 0.50) in each scale-specific model were used in the combined model. The new data set was again subjected to variable set reduction according to VIFs and correlation coefficients, and subsequently combined models were derived, which were again subjected to model averaging.

The extent to which broadscale or finescale habitat structure, or a combination of the two, was necessary to model species diversity and distributions was assessed using AICc. At each scale (finescale, broadscale and combined) and for each dependent variable, models were ordered according to the AICc, where lower values indicate better performing models. Change in AICc relative to the top ranked model was calculated as ΔAICc. Models with ΔAICc < 2 were considered equivalent. Models from all three scales were compared in order to assess whether high model performance was associated with either broadscale or finescale habitat variables, or a combination of both. The importance of each variable at each scale was assessed by calculating Akaike weights based on all combinations of models (Burnham and Anderson 2002), which are expressed as the likelihood contribution of each model as a proportion of the summed

likelihood contributions of all models. The weight for each variable is the sum of model weights for all models in which a given variable was present (Burnham and Anderson 2002).

Results

In total, 263 individuals of 29 species were recorded in 79 point counts over an altitudinal range of 1800–2600 m a.s.l. There were eight species that were recorded on at least 15% of the points: Tree Pipit, Water Pipit *Anthus spinoletta*, Dunnock, Northern Wheatear *Oenanthe oenanthe*, Lesser Whitethroat, Wren, Chaffinch *Fringilla coelebs*, Rock Bunting *Emberiza cia*. No significant model-averaged parameter estimates could be identified to predict Rock Bunting occurrence for broadscale or finescale models, therefore this species was not considered in further analyses.

Broadscale habitat structure

Details of model-averaged parameters of the model set for broadscale habitat structure are given in ESM Table S2. Bird species richness and diversity showed a positive relationship with the number of mature trees. Shrub cover showed a quadratic effect on bird diversity whereby diversity increased initially with the percentage of shrub cover, but declined after a shrub cover of approximately 55% was reached. Furthermore, diversity was negatively associated with altitude. Among individual species, Dunnocks showed a positive linear association with shrub cover, whereas both Lesser Whitethroat and Wren showed a quadratic association, where the probability of occurrence of Lesser Whitethroat and Wren peaked at ca. 45% and ca. 50% shrub cover, respectively. The number of mature trees showed a positive relationship with Chaffinch presence. There was also a negative effect of rock cover on Tree Pipit occurrence. Altitude was the only variable within the full model that was not linked to vegetation cover, and had different effects on the occurrence probability of Chaffinch, Wren (negative) and Northern Wheatear and Water Pipit (positive).

Finescale habitat structure

Details of model-averaged parameters of the model set for finescale habitat structure are given in the ESM Table S3. A number of dependent variables showed significant quadratic effects (e.g. probability of occurrence or diversity peaking at intermediate frequencies), either for all shrubs (Northern Wheatear), or for individual shrub species (Wren and juniper frequency, Dunnock and rhododendron frequency, species diversity and bilberry frequency). Shrub height heterogeneity was positively correlated with Wren and Tree Pipit presence. A positive relationship of canopy presence was found for bird species richness and diversity, as well as for Chaffinch presence. In contrast, it showed a negative association with Northern Wheatear presence. Structural vegetation diversity was not selected in any model set (see ESM Table S3).

Combination of broadscale and finescale habitat structure

Details of significant model-averaged parameters of the final combined model sets are given in Table 2 (for a full list of parameters see ESM Table S4). In line with our expectation on effects of habitat mosaics on ecotone species, we here focus on shrub cover, but graphs of all significant variables in combined models are presented in ESM, Fig. S1. Shrub cover, as a broadscale variable, occurred in the combined model set for bird species diversity (Fig. 1) and Lesser Whitethroat (ESM Fig. S1). In a number of cases, individual bird species occurrences were closely associated either with shrub species identity or with shrub frequency (Table 2). Quadratic relationships between shrub species and bird species occurrence were found for Dunnock (rhododendron), Wren (juniper) and bird species diversity (bilberry; see Fig. 2). Tree Pipit occurrence declined with increasing rhododendron frequency (Fig. 2). Shrub height heterogeneity was closely related to Tree Pipit and Wren occurrences.

The frequency of canopy or the number of mature trees was retained in the combined models for bird species diversity, bird species richness and Chaffinch occurrence (positive associations) as well as for Dunnock occurrence (negative association). Altitude showed a negative relationship with the occurrence of Wren and Chaffinch, while it was positively associated with Northern Wheatear presence.

Model comparison

A summary of the ten highest ranked models for each species and each diversity measure across scales is shown in Fig. 3. The higher ranked models were mostly based on combined models (i.e. combinations of broadscale and finescale variables), or broadscale models alone. The best models (ΔAICc < 2) for Dunnock, Lesser Whitethroat, Northern Wheatear, Tree Pipit, Chaffinch, Wren and species diversity contained only combined models. Finescale models were in the best model set only for species richness, but combined and broadscale models performed equally well (i.e. ΔAICc < 2). Figure 3 also illustrates that, for many species, there was a high degree of model uncertainty in that there were often several models where ΔAICc < 2. In general, finescale habitat variables of high weight that were present in the combined (best) models were related to the presence of shrubs either overall (Northern Wheatear) or of specific shrub species (Dunnock, Lesser Whitethroat, Tree Pipit, Wren and bird species richness and diversity; Table 3).

Table 2 Final significant model-averaged parameters of the model set derived by combining significant model-averaged parameters of broadscale and finescale habitat structure model sets for bird diversity, richness and the commonest species in the study area

Dependent variable	Parameter	Scale	Estimate ± SE	*z*	*p*
Lesser Whitethroat	Shrubs	*B*	2.171 ± 0.729	2.930	0.003
	$Shrubs^2$	*B*	− 2.041 ± 0.823	2.439	0.015
Tree Pipit	Rock	*B*	− 1.416 ± 0.648	2.151	0.032
	SDshrub	*F*	1.438 ± 0.514	2.754	0.006
	Rodfreq	*F*	− 1.120 ± 0.480	2.296	0.022
Dunnock	Trees	*B*	− 0.939 ± 0.471	1.963	0.050
	Rodfreq	*F*	1.601 ± 0.672	2.351	0.019
	$Rodfreq^2$	*F*	− 1.363 ± 0.589	2.286	0.022
Northern Wheatear	Alt	*B*	2.872 ± 0.482	5.873	≤ 0.000
	Shrubfreq	*F*	− 2.325 ± 0.469	4.884	≤ 0.000
	$Shrubfreq^2$	*F*	− 0.618 ± 0.031	19.595	≤ 0.000
Wren	Alt	*B*	− 2.435 ± 0.875	2.747	0.006
	$Junfreq^2$	*F*	0.583 ± 0.291	1.974	0.048
	SDshrub	*F*	1.096 ± 0.549	1.969	0.049
Chaffinch	Alt	*B*	− 1.533 ± 0.409	3.687	≤ 0.000
	Canfreq	*F*	1.238 ± 0.404	3.016	0.003
Species richness	Canfreq	*F*	0.169 ± 0.059	2.838	0.005
Species diversity	Shrubs	*B*	0.221 ± 0.062	3.508	≤ 0.000
	Canfreq	*F*	0.131 ± 0.053	2.451	0.014
	Bilfreq	*F*	− 0.171 ± 0.056	2.990	0.003
	$Bilfreq^2$	*F*	− 0.063 ± 0.025	2.491	0.013

The scale [broadscale (*B*), finescale (*F*)], estimate, SE, test value (*z*) and *p*-value are given for each parameter. Full details for all species and parameters are given in Table S4

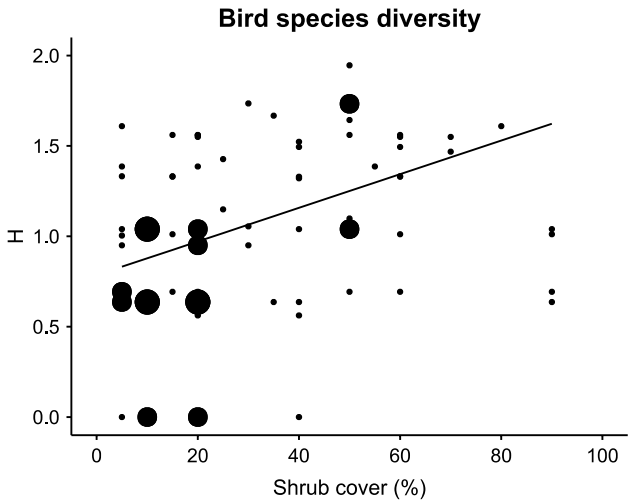


Fig. 1 Relationship between shrub cover (%) and bird species diversity based on the combined model. *Black circles* represent the Shannon diversity index (*H′*) value in relation to shrub cover for a given point count, where the *size* of the *circle* is proportional to the number of points for a given *H′* value at a particular level of shrub cover

Discussion

The aim of this study was to describe species-specific habitat requirements within a mountainous forest-shrub ecotone in order to assess the relationships between the diversity and distributions of birds and environmental variables measured at different scales, and hence to identify potential conservation priorities and to inform future modelling methods. Through the combination of broadscale and finescale habitat data in final models, we determined key habitat characteristics which shaped bird species richness and diversity. Furthermore, this enabled us to pinpoint habitat elements which are specifically required by common ecotone species. Our expectations of positive associations between bird community measures (diversity and individual species occurrence) and habitat complexity were partially met in terms of shrub cover and to a lesser extent by shrub height heterogeneity, but there was no evidence that the diversity of vegetation structure was important.

Comparison of model scales

To make management recommendations, the identification of key habitat characteristics (e.g. vegetation structure or plant species composition) supporting bird species diversity or target species is essential. The decision at which scale this objective will be addressed varies among studies representing a trade-off between broadscale [remote-sensing techniques (Braunisch et al. 2016)] and finescale data collection [detailed vegetation measurements in the field (Patthey et al.

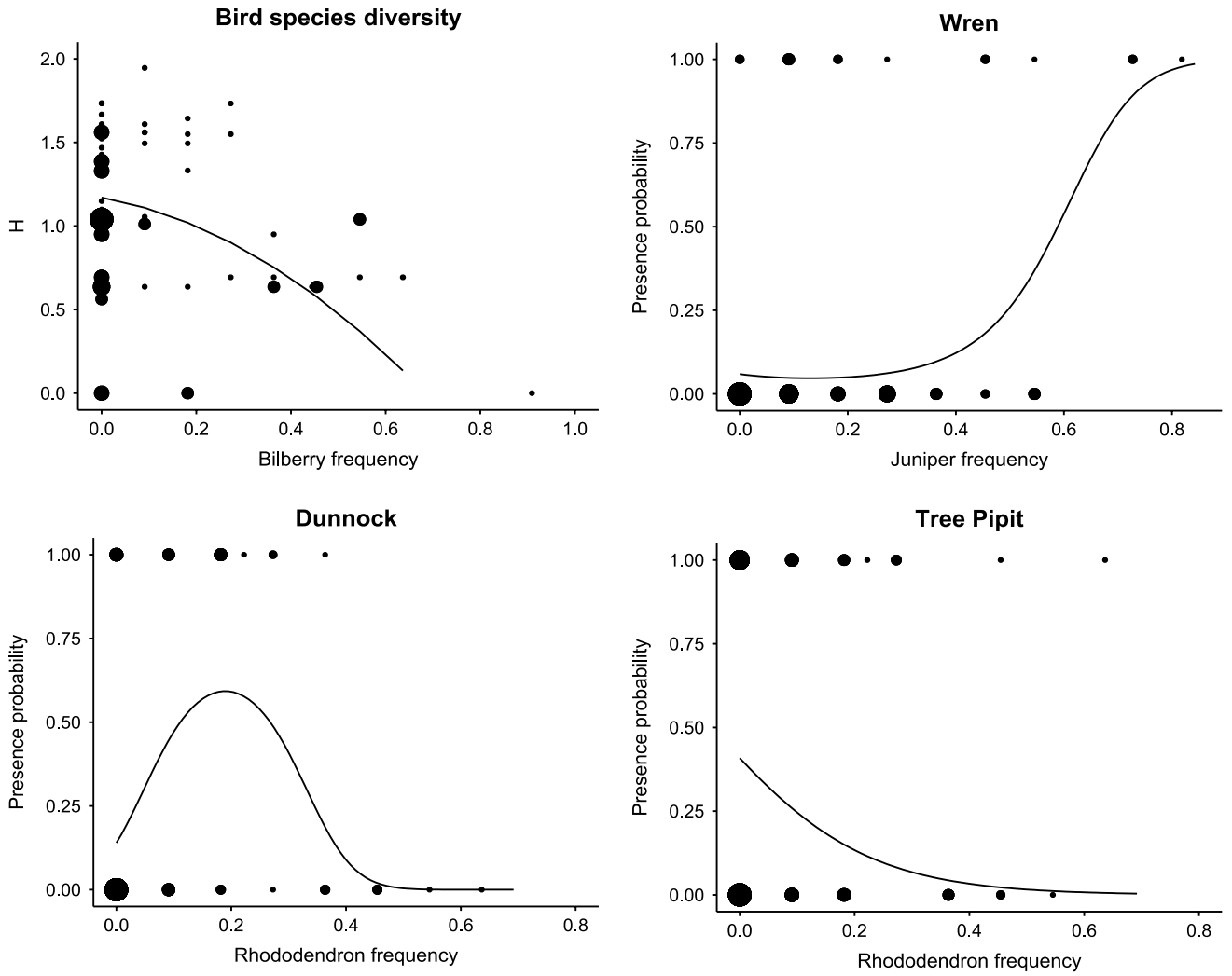


Fig. 2 Relationship between shrub species frequency (rhododendron, juniper, bilberry) and the probability of occurrence for individual bird species (Dunnock, Tree Pipit, Wren) and bird species diversity based on combined models. *Black circles* represent the point counts where a species was present/absent in relation to shrub species frequency, and the *size* of the *circle* is proportional to the number of points for a given category of presence/absence at a particular level of shrub frequency. For bird species diversity, *black circles* represent the H′ value in relation to bilberry frequency, where the *size* of the *circle* is again proportional to the number of points for a given *H′* value at a particular level of bilberry frequency

2012)]. Both techniques show advantages and disadvantages. Collecting broadscale data (for example, through remote-sensed data bases) allows large areas to be covered, but has the potential to miss relevant habitat features. Data collection in the field provides more detailed information, but is time-consuming and only applicable to smaller areas. Therefore choosing the appropriate scale is crucial as it directly determines the outcome of the study. The model scale comparison (broadscale, finescale or combined) applied to the same data allowed the assessment of the scale of data collection needed to identify habitat parameters determining bird species diversity or species-specific habitat requirements in the forest-shrub ecotone.

The comparison revealed that combined and/or broadscale models always performed better than finescale models for individual species. When combined models performed best, variables linked to shrub species identity (finescale variables) were included in several cases (Dunnock, Lesser Whitethroat, Tree Pipit, Wren and bird species richness and diversity). Other finescale variables were rarely included in the combined model set for individual bird species, or alternatively could be substituted by equivalent broadscale variables which had been excluded from the modelling process because of high collinearity between variables (e.g. Canfreq, a finescale variable which was highly correlated with canopy cover measured at the broadscale). Furthermore, finescale models were only included in the best model

set (i.e. ΔAICc < 2) for species richness, but combined and broadscale models performed equally well. Variables that described vegetation structural heterogeneity or diversity were only rarely included in the best model sets: SDshrubs was in the best model set for Wren, Tree Pipit and species diversity, although for the latter, the variable was not significant and was of low variable weight (ESM Tables S4 and S5).

These results therefore suggest that structural vegetation may be less important for the identification of factors determining species diversity and species distribution in the majority of cases. However, to further our understanding of individual species and bird species diversity, data collection in the field should focus on habitat data which considers horizontal vegetation cover collected at a broad scale, but which includes species-specific estimates of cover of relevant shrub species in the area in order to model distributions of birds in the shrub-forest ecotone. The assessment of horizontal habitat cover can be done quickly and easily by eye from a single location for the whole area of a point count, including cover of easily recognizable shrub species such as juniper and rhododendron, whereas detailed structural vegetation measurements (as undertaken here) require considerable effort and access to a much greater area of a given point. The results further suggest that land cover datasets analogous to the data collected here should also be adequate for species distribution modelling in the studied habitat if they are able to estimate the cover of the dominant shrub species. Thus, broadscale habitat data and data on shrub species composition should provide a sufficient basis for identifying relevant species-specific habitat parameters in a mountain environment. Future species distribution models should seek to incorporate species-specific estimates of shrub cover, especially as the dominant species in the area are likely to respond differently to future climate change (Theurillat and Guisan 2001; Neuner 2014).

Factors affecting bird diversity and distribution at different habitat scales

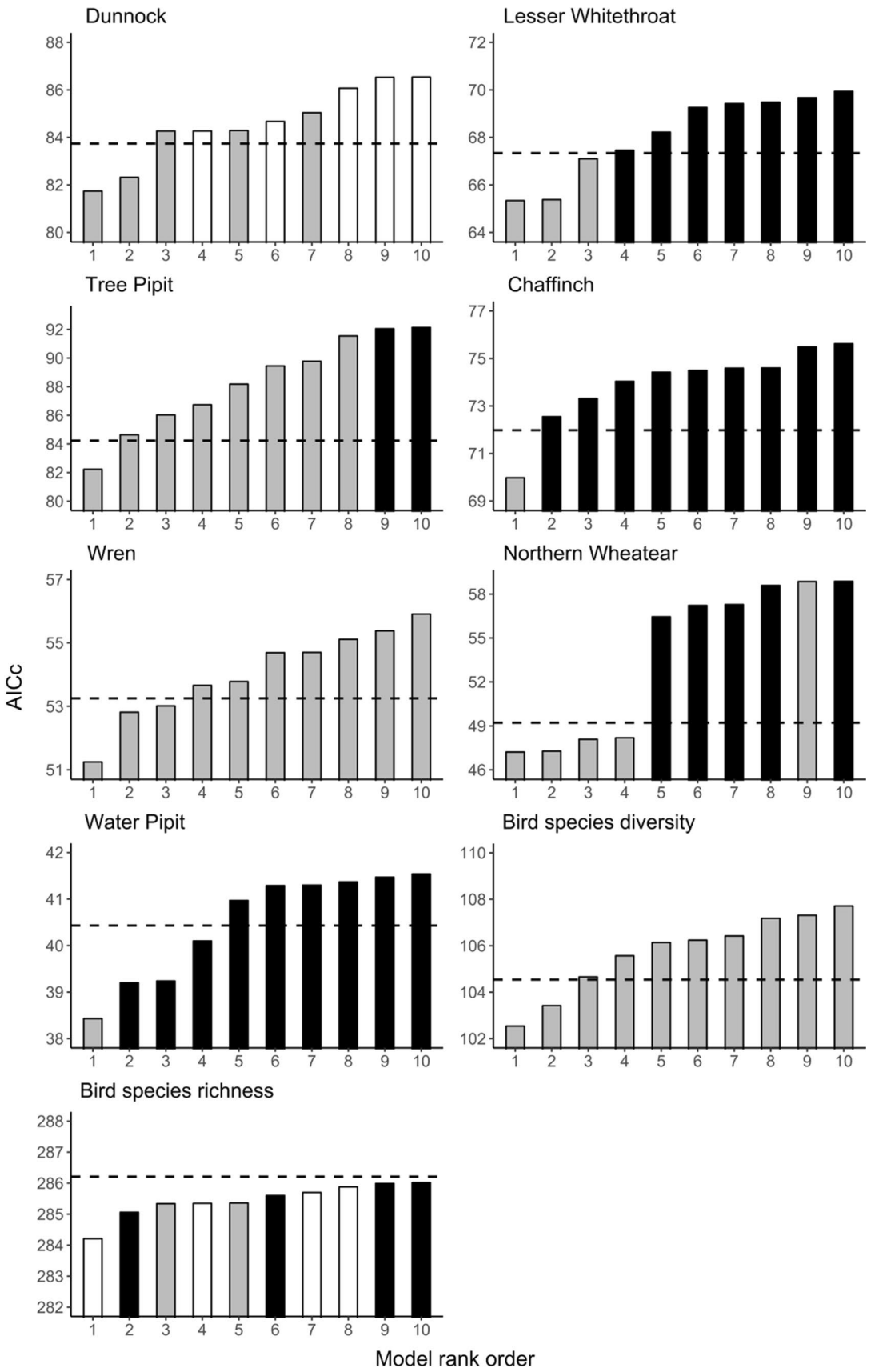
There was some support that a habitat mosaic was beneficial for some individual species in that Dunnock, Lesser Whitethroat and Wren showed significant non-linear associations with either shrub cover or shrub species frequency in at least one model. Furthermore, shrub cover and frequency occurred in two final models and were positively correlated with bird species diversity (shrub cover) as well as Northern Wheatear presence (shrub frequency). The general overall importance of shrubs can easily be understood as they provide nesting habitat for shrub-nesting species, provide shelter in harsh weather conditions and can shield birds from predators.

In addition to overall shrub cover, individual shrub species were also important for some bird species. Bilberry cover was negatively related to bird species diversity, presumably because, in contrast to the other shrub species present, this species does not provide dense cover that could be suitable for nesting. Only Wren was positively associated with juniper frequency. It was also negatively associated with altitude, which may suggest a link to the different growth characteristics of juniper along the altitudinal gradient (Hallinger et al. 2010). At high altitudes (> 2000 m), this shrub species typically grows fairly low to the ground [10–30 cm (Aeschimann et al. 2004)], which may make it unsuitable for nesting (due to predation risk for example). Suitable Wren nesting habitat may only be found at lower altitudes (1800–2000 m), where juniper tends to be taller, and possibly less dense.

In contrast to juniper, rhododendron can still grow to heights suitable for nesting [30–120 cm (Aeschimann et al. 2004)] in the upper fringe of the ecotone and could therefore be seen as an attractive alternative for shrub-nesting species. In the combined models, rhododendron showed a non-linear association with Dunnock presence, and seems to be preferred as a nesting habitat over other shrub species (personal observation). In the Alps, rhododendron can form very large and dense patches on north-, west- and northwest-facing slopes within the subalpine belt (Pornon and Bernard 1996). Its distribution is highly dependent on winter snow cover, which serves as a protective layer against excessive irradiation and frost (Neuner et al. 1999). However, due to climate change, snow cover is predicted to decrease by the end of the century (Beniston et al. 2003). Taking potential snow accumulation into account, Komac et al. (2016) showed that rhododendron could experience an important reduction in its realized niche, and that its future habitat could be confined to areas which are today scree and rocky hillside habitats. This outcome suggests that, even if current habitat is maintained, climatic conditions might become less favourable for the persistence of rhododendron and that suitable habitat for shrub-nesting species in the forest-shrub ecotone will disappear.

Conservation implications

The loss of open habitats due to abandonment of grazing (Gehrig-Fasel et al. 2007; Roura-Pascual et al. 2005; MacDonald et al. 2000) and climate change (Lenoir et al. 2008; Pauli et al. 2007) is likely to continue in the future to the extent that significant areas of more open habitats, including the shrub-grassland ecotone, will be replaced by forest. To maintain ecotone habitat, it may therefore be necessary to counteract shrub and indeed forest encroachment in targeted areas in order to keep a heterogeneous character of the forest-shrub ecotone. Possible methods to counteract shrub-encroached areas could be mechanical shrub clearance or the


Dunnock
Lesser Whitethroat
Tree Pipit
Chaffinch
Wren
Northern Wheatear
Water Pipit
Bird species diversity
Bird species richness
AICc
Model rank order

◂**Fig. 3** The ten best ranked models according to Akaike information criterion corrected for small sample size (*AICc*; where smaller AICc values indicate better performing models) for individual species, and for species richness and diversity. Each model is classified according to whether variables were finescale (*white bars*), broadscale (*black bars*) or a combination of the two (*grey bars*). The *dashed horizontal line* indicates ΔAICc = 2 (i.e. models *below the dotted line* are considered to be in the best model set)

re-establishment of grazing [e.g. rotational grazing systems with appropriate stocking level (Probo et al. 2014)]. However, mechanical shrub clearance can only be applied if the required equipment can be transported to the encroached areas, but accessibility by road is often limited in mountain areas. Moreover, encroached areas are frequently characterized by steep terrain, which influences the effectiveness of traditional grazing practices, as livestock tends to concentrate in flat areas and avoid steep slopes (Bailey et al. 1996; Mueggler 1965). Therefore, more specific pastoral practices involving targeted grazing are needed. The strategic placement of mineral mix supplements (MMS) would be one viable management option to be used in rugged shrub-encroached locations (Pittarello et al. 2015). The placement of MMS would lead to increased trampling in the surrounding 100 m of the MMS site, which would reduce shrub cover (Probo et al. 2013). A further more targeted option is the use of temporary night camps, where cows are fenced for up to 2 nights in shrub-encroached areas. Through intense trampling within the fenced area, shrubs get mechanically damaged and subsequently decrease in cover (Tocco et al. 2013; Pittarello et al. 2016; Probo et al. 2016). In the long-term, this pastoral technique has the additional advantage that it increases plant diversity (Pittarello et al. 2016), which in turn might positively influence invertebrate availability (Tocco et al. 2013) for birds. Any such initiatives would have to be managed carefully so as to open up encroached areas whilst maintaining a reasonable level of shrub cover. Similarly, grazing also has the potential to maintain open areas above the ecotone, which is important for Northern Wheatear and Water Pipit, both of which are open-habitat species at high altitudes. Although grazing could represent a viable management option in forest-ecotone areas, its potential direct or indirect effects on different bird species groups (e.g. grassland, ecotone, forest) are still unknown, and it is likely that some species might be more affected than others. Moreover, grazing management targeted in the wrong areas, or applied at intensive levels, could also be detrimental to biodiversity.

It should be noted that habitat requirements among the most common bird species within the forest-shrub ecotone can differ considerably. Chamberlain et al. (2013) argued that management for the maintenance of high-altitude grassland would be preferable to allowing forest expansion due to the high proportion of specialist species and species of conservation concern that could be negatively impacted.

Table 3 Variables with the highest importance (Akaike weight > 0.70) for combined models, derived from all combinations of models for each dependent variable, grouped according to whether they were broadscale or finescale

Variable	Broadscale	Finescale
Tree Pipit	Rock, Shrubs^2	SDShrub, Rodfreq
Water Pipit	Alt	Canfreq
Dunnock	Trees	Rodfreq, Rodfreq^2
Northern Wheatear	Alt	Shrubfreq
Lesser Whitethroat	Shrubs, Shrubs^2	–
Wren	Alt, Shrubs	SDShrub, Junfreq^2
Chaffinch	Alt	Canfreq
Species richness	–	Canfreq
Species diversity	Shrubs	–

Full details are given in Electronic Supplementary Material Table S5. *Dash* indicates Akaike weight < 0.70 for a given scale. Variable codes are given in Tables 1 and S1

However, our data showed that forested areas with high shrub cover had the highest bird diversity. Nevertheless, there are important bird species in the ecotone that were not well covered by our methods (von dem Bussche et al. 2008; Braunisch et al. 2016), and the ecotone also has a high biodiversity of other taxa (Dirnböck et al. 2011). In order to meet a range of species-specific habitat requirements, it might therefore be important to sustain a high level of heterogeneity and to maintain a habitat mosaic within the ecotone (Pathey et al. 2012). Management recommendations need to be adopted at appropriate scales for areas differing in altitude, topography, shrub species composition and the degree of shrub encroachment (Braunisch et al. 2016). Depending on the targeted area, it might therefore be necessary to apply a combination of different management techniques and to adjust the time period of application to promote heterogeneity. There is the possibility of managing for diverse landscapes that can incorporate a range of needs for different habitat types which facilitates species resilience and resistance to environmental change (e.g. Brambilla et al., in press), but further work is needed on the most appropriate scale of management through which this can be achieved.

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