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Modelling at the edge: habitat types driving the occurrence of common forest bird species at the altitudinal margin of their range

Mattia Brambilla* & Paolo Pedrini

*M. Brambilla, P. Pedrini, Trento Science Museum, Vertebrate Zoology Section, Corso della Scienza e del Lavoro 3, I-38123 Trento, Italy. * Corresponding author's e-mail: brambilla.mattia@gmail.com*

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We investigated habitat drivers of occurrence of five common forest bird species (*Erithacus rubecula*, *Phylloscopus collybita*, *Sylvia atricapilla*, *Periparus ater*, *Fringilla coelebs*) at the upper margin of their range in the Alps. Our work aimed to i) identify methods to analyse species-habitat relationships at the margin of species distribution, ii) provide recommendations for conservation and management in this changing environment. We recorded species occurrence at 149 points in Trento province (Italy; 1,365–2,200 m a.s.l.), and related occurrence to elevation and cover of habitats in a 100-m radius. We estimated factors affecting occurrence by single-species and multi-response MARS models. We also evaluated factors driving the overall species richness at point counts by means of a glmmPQL approach. Multi-response models performed well (in general they performed better than single-species models) and suggested important effects of elevation (negative), conifer forest (not significant for *P. collybita*, positive up to a threshold for other species) and wood pasture (not significant for *S. atricapilla*, positive for other species). Conifer forest, wood pastures, shrubland and elevation affected the number of species at point counts (positive effect for all variables except for elevation). Multi-response models may help elucidate ecological relationships for 'rare' species, including common species at the margin of their range. Wood pasture promoted the occurrence of common forest species and the number of species, even if scarcely represented, and thus could deserve more consideration in conservation and management planning, given that several species are of high conservation concern.

1. Introduction

Modelling species' distributions at the edge of their range can be challenging for several reasons. Generally widespread and common species may be rarer at range margins and the low prevalence and occurrence rates may complicate the understanding of species-habitat relationships, which could also be different at the edge of the range than towards the centre of the species' range (Fuller *et al.* 2007).

Researchers have often explored species' ecology at geographical margin of their range (Sexton *et al.* 2009); here, we investigate the habitat preferences of some common forest species at the altitudinal margin of their distribution in Europe, in the Italian Alps.

Alpine ecosystems are rapidly changing: land-use and climate change are strongly modifying landscape structure in alpine mountains which requires dedicated conservation strategies to address (Chamberlain *et al.* 2013). In fact, the major habitat changes currently ongoing in the Alps are probably forest recovery and upward tree line shift, which are due both to the abandonment of traditionally grazed habitats (pastures and wood pastures), and to the upward shift of many tree species favoured by an increase in temperature (MacDonald *et al.* 2000, Dullinger *et al.* 2003, Gehrig-Fasel *et al.* 2007, Harsch *et al.* 2009). Forest recovery is often anticipated by shrub encroachment (Brambilla *et al.* 2010). Without human disturbance, at the upper tree limit on mountainsides, shrubland (with scattered trees) generally occurs at forest edge and gradually turns into alpine grasslands. Management for grazing pastures historically has increased grassland habitats at the expense of forest and shrubland habitat: the resulting habitat mosaic often includes open woodlands grazed by livestock (also known as wood pastures) among the transition habitats between forest and grasslands.

Grasslands often occur at lower altitudes than the natural limit of forests, whereas shrublands are confined to marginal portions or slopes topographically unsuitable for grazing. However, the above mentioned abandonment of rural mountain areas, coupled with climate warming, have decreased the extent of open and semi-open habitats, which have been progressively covered by shrubs and trees, ultimately leading to forest recovery over once grazed and open habitats (Didier 2001, Gehrig-Fasel *et al.* 2007, Tattoni *et al.* 2010).

Although it is obvious that open habitat species are threatened by this process, whereas forest birds are generally favoured, specific patterns of habitat association have been poorly investigated, with a few notable exceptions (see, e.g., Chamberlain *et al.* 2013); furthermore, the status and trends of alpine bird populations are often poorly known (EEA 2010), largely because of the logistical constraints due to the challenging environment (Chamberlain *et al.* 2013). An understanding of the link between the availability of the habitats occurring in mountains and the occurrence of bird species is crucial in evaluating the possible impact of landscape change, and to plan conservation strategies.

Here, we focus on a set of common bird species, with different ecological traits but generally tied to forest habitat, in order to evaluate whether natural and semi-natural habitats commonly occurring on mountainsides in the Alps may contribute to their occurrence. We considered the effects of different types of forest and shrubland, wood pastures (open, grazed woodlands with tree cover lower than 20%), grassland, rocky areas and built-up habitats on species occurrence. Forest is obviously expected to have a positive effect on forest species, and is promoted by ongoing habitat changes; shrubland may be preferred or avoided by species according to specific needs, and is generally temporarily favoured by climate change and abandonment, although over the long term it is largely replaced by forest (depending on elevation and topography). Grassland is contracting because of both abandonment and climate warming (Cannone *et al.* 2007, Harsch *et al.* 2009, Laiolo *et al.* 2004). Wood pasture (a broad category characteristically referring to habitats with trees scattered through an open area, generally grassland; Hartel *et al.* 2013) is currently declining, basically for the same reasons as those causing grassland decline. The association between this habitat and forest birds in the Alps is largely unknown, with the notable exception of some conservation-priority or charismatic species (e.g., Capercaillie *Tetrao urogallus*, Borgo *et al.* 2001). Recently, Hartel *et al.* (2014) showed how wood-pastures may host rich and unique bird communities, more diverse than the combination of the respective communities of forest and pastures.

Therefore, we are particularly interested in the potential use of wood pasture by forest species, since it represents a habitat used by some conservation priority species among birds (Gustin *et al.* 2009), harbours rich avian communities (Hartel *et al.* 2014), has high landscape and cultural values (Plieninger *et al.* 2015) and is an economically valuable environment, being used for livestock grazing and recreational activities, and providing timber and forage (Garbarino *et al.* 2011). Despite its value, wood pasture is currently declining at a fast rate (Garbarino *et al.* 2013), because current agricultural policies promote a segregation of land uses, leading to a loss of wooded pastures (Chételat *et al.* 2013).

We investigated species-habitat relationships by means of species-specific and multi-response models, respectively. Multi-response models have been shown to better perform with limited sample size (Elith & Leathwick 2007, Heinanen & von Numers 2009), which is typically the case of (at least locally) rare species (e.g., Brambilla & Gobbi 2014). In general, multi-response models may be useful for conservation aims as they can highlight the habitat factors likely affecting the largest number of species. Given that multi-response models have been seldom adopted to model bird distribution or occurrence, we believe that a comparison of the results offered by single-species and multi-species approaches would offer useful insights into their potential contribution to understanding factors affecting the occurrence of rare species, including elsewhere common species at the edge of their range.

In addition to species-specific analyses, we also evaluated the effect of the same environmental traits on the species richness at point counts in order to assess habitat associations on the whole bird community.

2. Material and method

2.1. Study species

In the current study, to evaluate species-habitat relationships for forest species we selected those occurring in at least 30 (out of 149) point counts. Therefore, we considered the following five common forest species (in parentheses: *n* – number of occurrence sites, and maximum elevation recorded at occurrence sites in this study): Robin (*Erithacus rubecula*; *n* = 30; 2,189 m a.s.l.), Blackcap (*Sylvia atricapilla*; *n* = 31; 1,997 m a.s.l.), Chiffchaff (*Phylloscopus collybita*; *n* = 39; 2,221 m a.s.l.), Coal tit (*Periparus ater*; *n* = 39; 2,221 m a.s.l.) and Chaffinch (*Fringilla coelebs*; *n* = 37; 2,189 m a.s.l.). These are all common species in mountain forests of the southern eastern Alps (Pedrini *et al.* 2005, Gustin *et al.* 2010), showing different food habits and habitat preferences. Robin is insectivorous, feeding mostly on the ground, and can occur in several types of woodland, irrespective of their composition, but prefers fresh and wet sites (Cramp 1998). Blackcap is insectivorous, feeding mostly on the foliage, and can tolerate different habitats with adequate cover of trees and/or high shrubs (Cramp 1998). Chiffchaff is an insectivorous species, which feeds largely in foliage and predominantly occupies open woodland with shrub elements (Cramp 1998). Coal tit is also insectivorous, feeding mostly on conifer canopy and being strictly tied to conifer trees, preferring Spruces *Picea abies* in that part of its range (Gustin *et al.* 2010). Lastly, Chaffinch is granivorous, but feeds chicks with insects, and can occupy a broad range of different habitats, provided that a minimum tree cover is available (Cramp 1998).

All those species except Chiffchaff have a favourable conservation status in Italy (Gustin *et al.* 2010). Chiffchaff is considered to be in ‘inadequate’ conservation status (see Brambilla *et al.* 2013a) because of population declines and range contraction in some parts of its range, and especially in Northern Italy (Gustin *et al.* 2010). Although most conservation research and efforts are targeted at ‘rare’ species, common ones also deserve attention, because they contribute enormously to ecosystem structure and functioning, and depletion of common species may have broad implications (Gaston & Fuller 2008).

To evaluate the effect of habitat traits on species richness, we considered the total number of species counted at each point count, thus including also rarer species and species not tied to forest habitats.

2.2. Study area

Our work was carried out in Trento province, Northern Italy. The landscape in the valleys surveyed for this study is characterized by intensively cultivated and urbanized valley floors, with mountainsides covered by woodlands interspersed with secondary (anthropogenic) grasslands at middle elevations (1,000–2,000 m), and alpine grasslands, rocks and snow-covered ground dominating at higher elevations (above 2,000 m). Rainfall ranges from 700 mm / year to 1,500 mm / year (and locally higher). Human density is lower than in

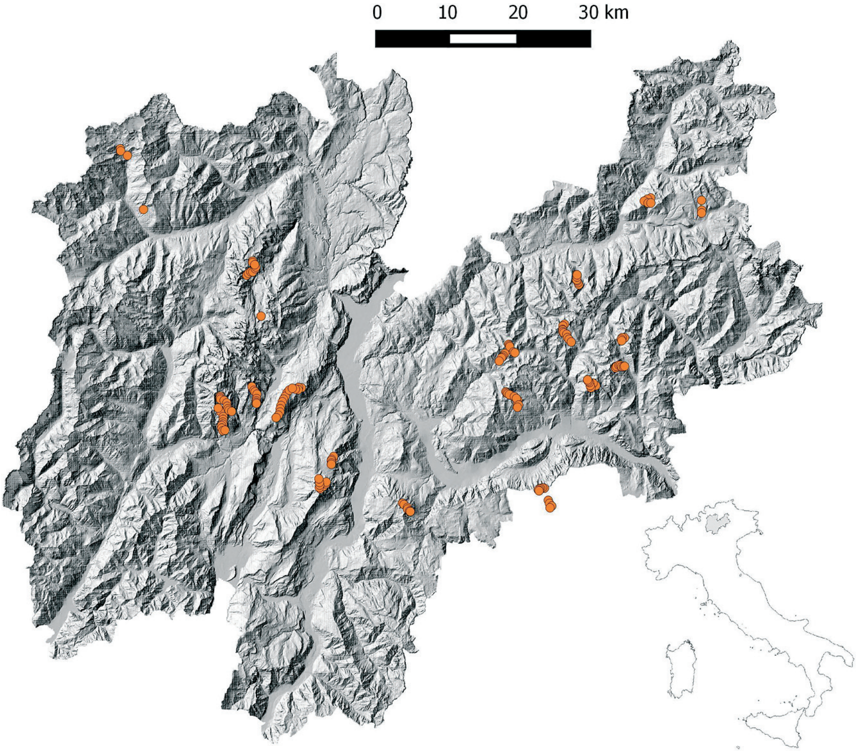

Fig. 1. Study area with point counts located along altitudinal gradients/transects. The inset shows the position of Trento province within Italy.

most Italian regions, being equal to c. 85 inhabitants / km^2 (Servizio Statistica Provincia Autonoma di Trento 2013).

Censuses were carried out at 149 point counts located in the main mountain areas of the province (a few were actually in Veneto, close to the province boundary), and distributed along altitudinal gradients, from 1,365 to 2,200 m (Fig. 1); some additional sites located above 2,200 m were discarded. The dominant land cover types at sampled points were pastures and grassland, followed by coniferous forests, high shrublands and bare rocks (Table 1). The cover of conifer forest peaked between 1,600 and 2,000 m, but small patches occurred up to 2,200 m. Broadleaved woodlands were much rarer and mostly confined to below 1,600 m. Pastures and grasslands occurred at all elevations, but their cover peaked at sites above 1,800 m. High shrubland occurred only above 1,600 m, with relative cover peaking at elevations between 1,700 and 2,100 m. Bare rocks occurred mainly above 1,900 m. Wood pastures occurred between 1,700 and 1,950 m. There were no clear latitudinal or longitudinal gradients in habitat occurrence in the study area.

2.3. Fieldwork and habitat variables

Birds were recorded by means of 10-minutes point counts, within a 100-m radius from the point. Contacts farther than this distance were discarded prior to analyses. Each point was surveyed once in early morning, with clear weather and no wind, between 27th June and 15th July 2011.

At each point, we measured the cover of the main habitat types found in our study system, using a detailed map (scale 1:10,000) of land-cover types in the province (as defined according to the database – Provincia Autonoma di Trento 2005), and recorded elevation on a 10-m resolution Digital Terrain Model. The 12 habitat variables used for this study are listed in Tab. 1. Habitat cover refers to a 100-m radius around the point. We chose this radius because i) it matched the area surveyed for birds, ii) it was associated with an ecologically

Table 1. List of habitat variables considered in the analyses. Cover values refer to the 100-m radius around the point (values calculated by using raster cells, leading to an approximated maximum extent of 3.16 ha instead of 3.14 ha).

Variable	Description	Range	Mean ± SD
Elevation	Elevation in meters above sea level	1,365–2,189	1,891 ± 188
Buildings	Cover of buildings (m^2)	0–1,900	20 ± 168
Broadleaved forest	Cover of broadleaved woodlands (m^2)	0–27,600	481 ± 2,932
Coniferous forest	Cover of coniferous forests (m^2)	0–31,600	6,199 ± 10,378
Pastures and grasslands	Cover of grazed pastures and alpine grasslands (m^2)	0–31,600	15,294 ± 11,699
Moorland and other low shrubland	Cover of alpine moorland and low shrubs (e.g., *Genista* spp., *Rubus* spp., *Calluna* spp.) (m^2)	0–10,100	105 ± 868
Shrubland	Cover of high shrubs (e.g., *Alnus viridis*) and Mountain Pine (m^2)	0–31,200	3,843 ± 7,553
Wood pasture	Cover of wood pastures (grazed areas with trees; tree cover < 20%) (m^2)	0–27,100	493 ± 2,831
Bare rocks	Cover of bare rocks and bare soil (m^2)	0–31,600	3,479 ± 7,228
Wooded cliffs	Cover of steep, rocky terrain with trees and/or other vegetation (m^2)	0–18,200	1,160 ± 3,108
Watercourses	Cover of rivers and streams (m^2)	0–2,200	93 ± 375
Lakes	Cover of lakes (m^2)	0–7,500	68 ± 530

meaningful extent for the target species we considered, which usually defend small territories (Cramp 1998). All GIS layers were produced and made available by the provincial authorities.

2.4. Statistical analyses

Prior to analyses, we checked variable correlations; no pair of variables was highly intercorrelated ($|r| < 0.51$ for all possible pairs of variables). We also checked for the potential occurrence of spatial autocorrelation in species occurrence, by calculating Moran's I for the occurrence of all species, and testing significance using 199 permutations in the program SAM (Rangel *et al.* 2010). For all species, the occurrence pattern was not spatially autocorrelated (all $P \geq 0.06$).

For the description of the species-habitat relationships, we adopted a two-step approach. Firstly, we built habitat-species models for each single species; then, we built a multi-response model, which aims at identifying the habitat factors more likely to be important across all species.

In both cases, we estimated factors affecting species' probability of presence by means of multivariate adaptive regression splines (MARS). MARS is a non-parametric, machine-learning technique (Friedman 1991, Hastie *et al.* 2009), now increasingly used in ecology (Leathwick *et al.* 2005, Mac Nally *et al.* 2008, Heinanen & von Numers 2009, Brambilla & Gobbi 2014) thanks to its flexibility and ability to properly model non-linear relationships (Elith & Leathwick 2007). We used the earth package version 3.2-1 (http://cran.r-project.org/web/packages/earth/index.html) in R 3.1.2 (R Development Core Team 2013) to build the MARS models with a binomial distribution of the response variable (Milborrow 2011a). We used the following settings for model selection: threshold = 0.01, penalty = 2, degree of interactions = 1 (no interaction allowed among variables), and evaluated variable importance by means of the evimp command (Milborrow 2011a, Brambilla *et al.* 2013b, Jedlikowski *et al.* 2014). The latter estimates variable importance in MARS models on the basis of: (i) the number of model subsets generated by the pruning pass, which include a given variable; (ii) the decrease in the residual sum-of-squares (RSS) for each subset relative to the previous subset (scaled to 100); (iii) the generalized cross validation (GCV) of the model, calculated using the penalty argument, which considers the

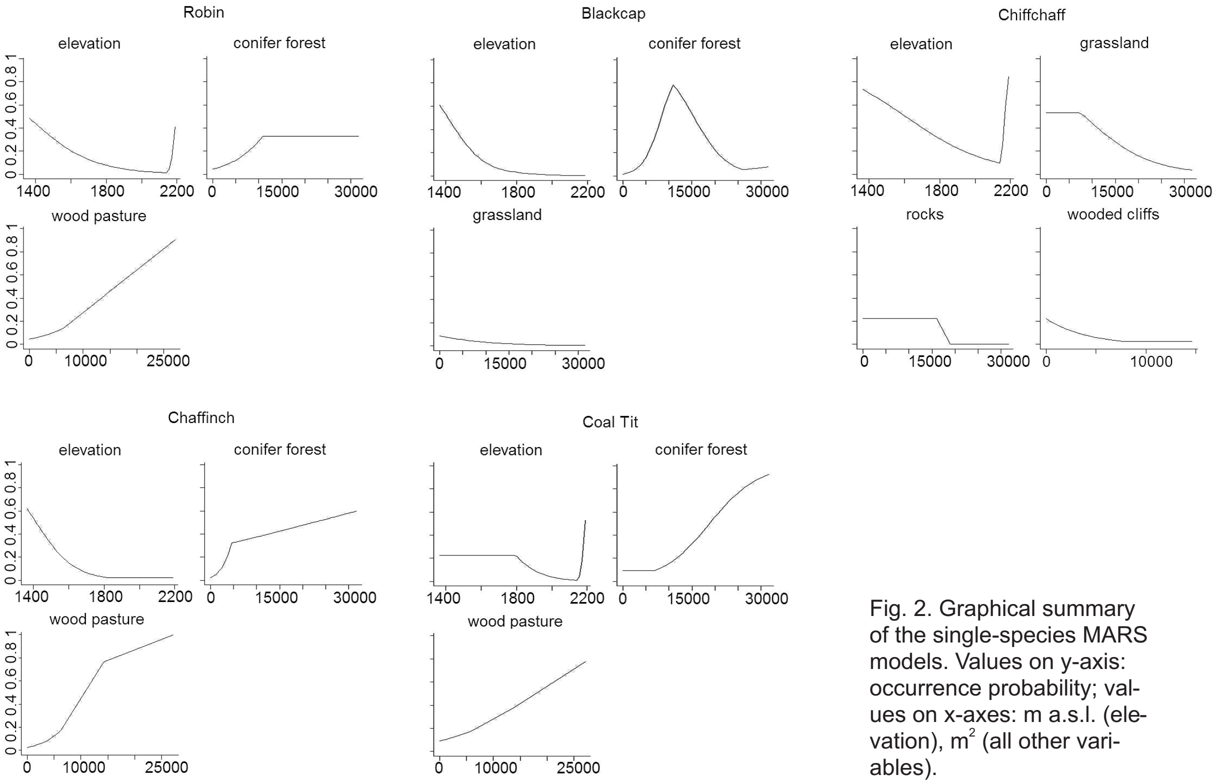

Fig. 2. Graphical summary of the single-species MARS models. Values on y-axis: occurrence probability; values on x-axes: m a.s.l. (elevation), m^2 (all other variables).

increase or decrease in the GCV associated with a variable being added to the model (scaled to 100) (Milborrow 2011a). The plotmo package version 1.3-1 (http://cran.r-project.org/web/packages/plotmo/index.html) was used to plot the fitted functions (Milborrow 2011b).

To confirm the importance of the land cover variables (describing the main vegetation at point counts) on species occurrence irrespective of elevation, we repeated the multi-species analysis after removing elevation from the potential predictors.

To investigate the potential effect of the environmental traits here considered on species richness at point counts, we modelled the effect of habitat variables on the number of species (a Poisson variable) counted at each point by means of spatial Generalized Linear Mixed Models via Penalized Quasi-Likelihood (glmmPQL), assuming a Poisson error distribution. glmmPQL enables the building of spatial models with dependent data not normally distributed, and is among the best techniques for this kind of data (Dormann et al. 2007). We adopted a Gaussian spatial correlation structure, but tests with spherical and exponential structures led to the same results. The package MASS was used to fit glmmPQL models (Venables & Ripley 2002). Prior to model fitting, we checked for collinearity among predictors (a potentially serious issue with parametric methods) by means of the variance inflation factor (VIF). We removed the dominant land cover variable (pastures and grasslands), and the remaning predictors showed low VIF values (all < 2). A progressive removal of non-significant terms ($P > 0.1$) was then used to obtain a model including only significant (or nearly significant) variables.

3. Results

3.1. Species-habitat relationships

Species-habitat relationships depicted by the single-species and the multi-response models are shown in Figs. 2 and 3, respectively. Variable importance and model performance are summarised in Tables 2 and 3, respectively.

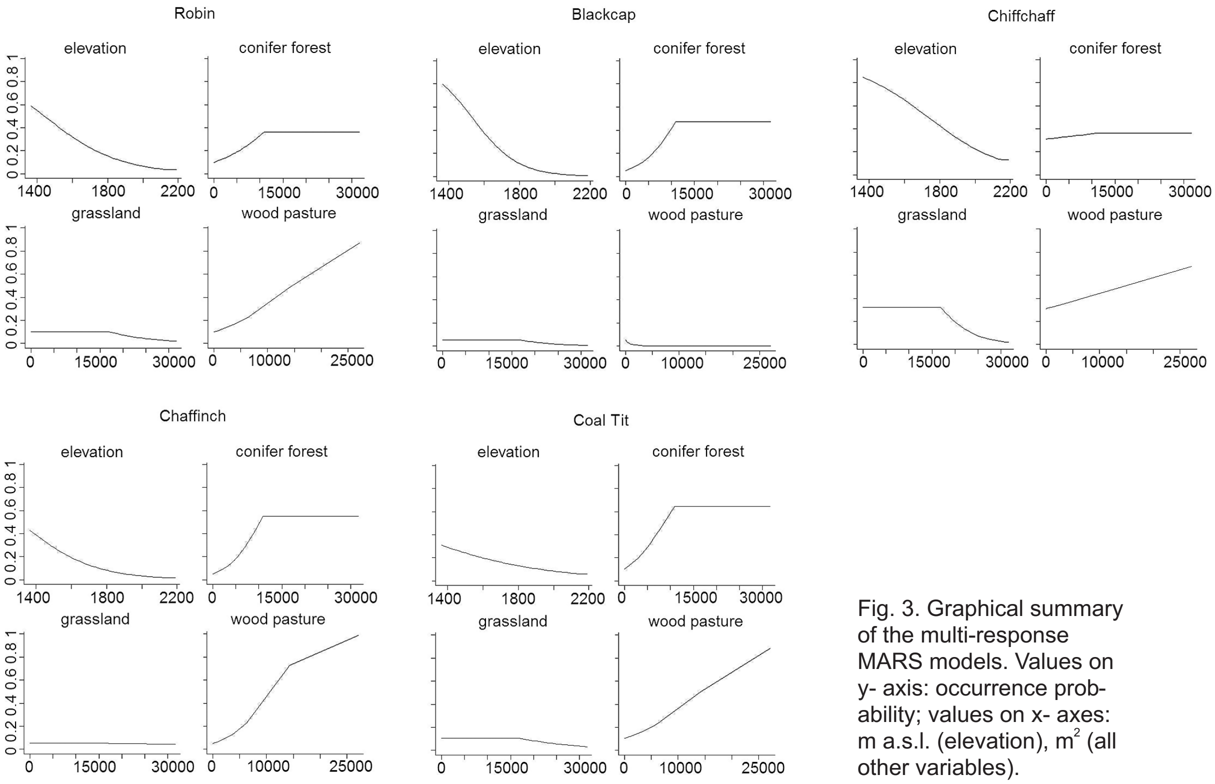

Fig. 3. Graphical summary of the multi-response MARS models. Values on y- axis: occurrence probability; values on x- axes: m a.s.l. (elevation), m^2 (all other variables).

Elevation, coniferous forests and wood pastures were the variables most often affecting species occurrence across the different models (Table 2 and Fig. 2), and were included, together with grassland, in the multi-response model (Table 2 and Fig. 3). In three out of five species there was a biologically unjustified increase in occurrence probability for the highest elevation (Fig. 2), which was due to some outliers; such a meaningless effect did not appear in the multi-response model.

The multi-response model showed that all species were negatively affected by elevation, and variably associated with cover of coniferous forest (Fig. 3). All species (except blackcap) were positively affected by the cover of wood pasture, whereas the effect of grassland was extremely weak and negative for all forest species (Fig. 3).

The multi-response models performed equally or better than the single-species models for all species, and were more stable (lower standard deviation for cross-validation R^2 and AUC than the single-species models) in all species (Table 3).

The multi-species analysis carried out to confirm the importance of the land cover variables describing the main vegetation at point counts irrespective of elevation led to results broadly consistent with the main analysis. The habitat factors driving species occurrence were the following, ranked according to relative importance as estimated by the 'evimp' command (in brackets: number of subset, GCV, RSS): conifer forest (4, 100, 100), wood pasture (3, 39.4, 53.3), shrubland (2, 29.4, 41.7) and broadleaved woodland (1, 20.1, 28.9). The effect of conifer forest and wood pasture was identical to the effect in the main analysis.

3.2. Factors affecting species richness

Species richness varied between 0 and 12 (mean 3.79) species counted at each point. The glmmPQL model suggested that species richness varied according to a negative effect of elevation ($\beta = -1.06 \times 10^{-3} \pm 2.74 \times 10^{-4}$, $P < 0.001$), and to positive effects of conifer forests ($\beta = 3.23 \times 10^{-5} \pm 4.30 \times 10^{-6}$, $P < 0.001$), shrubland ($\beta = 1.45 \times 10^{-5} \pm 6.50 \times 10^{-6}$, $P = 0.028$) and to a lesser extent

Table 2. Variable importance of MARS models. For complex hinge functions, the coefficient or the effect for the specified range of values is reported; see Fig. 2 for an explanation of the species–habitat relationships. Abbreviations: No. of subsets – number of model subsets generated by the pruning pass, which include a given variable; GCV – generalized cross-validation of the model; RSS – decrease in the residual sum of squares.

Species	Variable	No. of subsets	GCV	RSS
Robin	Elevation	3	57.0	65.9
	Conifer forest	4	100	100
	Wood pasture	2	32.0	45.4
Blackcap	Elevation	6	48.6	58.2
	Conifer forest	5	100	100
	Grassland	2	10.0	25.8
Chiffchaff	Elevation	5	100	100
	Grassland	4	73.7	78.1
	Rock	2	23.2	39.2
	Wooded cliffs	3	35.3	51.2
Coal tit	Elevation	2	28.1	37.0
	Conifer forest	4	100	100
	Wood pasture	2	19.5	31.8
Chaffinch	Elevation	2	38.2	43.3
	Conifer forest	4	100	100
	Wood pasture	3	53.3	58.4
Multi-response	Elevation	3	45.9	56.3
	Conifer forest	4	100	100
	Wood pasture	2	24.5	38.5
	Grassland	1	11.9	24.8

wood pasture ($\beta = 2.64 \times 10^{-5} \pm 1.54 \times 10^{-5}$, P = 0.087).

4. Discussion

4.1. Single-species and multi-response models

Our results confirm how multi-response models can be particularly suited to analyse a set of species displaying rather low prevalence or number of occurrence rates (Leathwick *et al.* 2006, Heinanen & von Numers 2009, Brambilla & Gobbi 2014). Apart from a lower general performance, the single-species models seem much more prone to a potential overfitting of the species-habitat relationships, as suggested by the rather unreliable effect of elevation for most species (Fig. 2). Three out of five species-specific models showed a positive association with high elevation that was clearly a statistical artefact, without an ecological meaning. Such a flawed response likely arose because of outliers occurrence and overfitting/correlation problems, and was not found in the multi-response models. This suggests that common drivers of habitat association, i.e. factors identified as important by the multi-response models, may be particularly important for species ecology, and thus also highly relevant for management. Therefore, despite the lower R^2 than that of the species-specific models for Chiffchaff and Coal Tit (but AUC is equal or higher even for those two species), the multi-model approach seems to provide overall more reliable results; this kind of model may thus be useful also for modelling species-habitat relationships in common species at the margin of their distribution.

4.2. Factors affecting species occurrence and species richness and potential implications

Managing habitats for conservation in the transitional belt connecting forest and high-elevation grassland through shrubland, is a complex task that should take into account a large number of factors: in the Alps, those habitats are used for cattle grazing and timber production, are regarded as

Table 3. Performance of MARS models (over 10 replicates of the cross-validation process) for single-species models and for the multi-response model (R^2 – cross-validation R-squared; AUC – area under the curve of the receiver operating characteristic; SD cross-validation standard deviation, calculated across folds).

Species	Single-species		Multi-response	
	R^2 ± SD	AUC ± SD	R^2 ± SD	AUC ± SD
Blackcap	0.32 ± 0.16	0.87 ± 0.06	0.36 ± 0.25	0.89 ± 0.16
Coal tit	0.29 ± 0.31	0.82 ± 0.15	0.21 ± 0.42	0.86 ± 0.12
Chaffinch	0.33 ± 0.30	0.88 ± 0.11	0.37 ± 0.26	0.90 ± 0.07
Chiffchaff	0.15 ± 0.22	0.78 ± 0.13	0.07 ± 0.20	0.77 ± 0.12
Robin	0.11 ± 0.15	0.76 ± 0.12	0.19 ± 0.23	0.83 ± 0.01
All species	–	–	0.24 ± 0.12	0.85 ± 0.07

high-value landscapes, are exploited for recreational purposes and host many charismatic species of conservation concern (e.g., Borgo *et al.* 2001, Gustin *et al.* 2009). Forest habitats towards the tree limit are subjected to many pressures and are highly dynamic. After centuries of pushing towards lower elevation by clearing for grazing, now they are recovering, extending upwards (Dullinger *et al.* 2003, Gehrig-Fasel *et al.* 2007). Both forest cover and shrubland cover positively affected species richness in the study system we considered; this is likely due to the fact that in general there are more forest and ecotonal species than open-habitat ones in the study region (Pedrini *et al.* 2005). Moreover, we also found a marginally significant positive effect of wood pasture on species richness.

The positive effect of forest cover on species occurrence probability (according to the multi-species model) revealed an increase up to a threshold, followed by a constant occurrence probability for higher cover values (Fig. 3). The lack of increases in occurrence probability after a relatively low canopy cover suggests that the benefits of conifer cover accrue without continuous forest for these common species.

Wood pasture is a peculiar habitat found in this highly dynamic zone, which in this area of the Alps occurs mostly between 1,500 m a.s.l. and 2,000 m a.s.l. Wood pastures are important both ecologically and culturally (Bergmeier *et al.* 2010, Plieninger *et al.* 2015), being among the oldest land-use types in Europe (Luick 2008). Wood pastures basically include habitats with trees scattered through an open area, generally grassland (Hartel *et al.* 2013); appropriate grazing regimes applied through centuries have been crucial for their formation and persistence (Hartel *et al.* 2013). Wood pasture is important for several species, including ones that are conservation-dependent (at least in the Alps). Species occupying wood pastures include Capercaillie (Borgo *et al.* 2001), Black Grouse (*Tetrao tetrix*; Laiolo & Rolando 2005), Pygmy Owl (*Glaucidium passerinum*; Stroem & Sonerud 2001, Pedrini *et al.* 2005), Grey-headed Woodpecker (*Picus canus*; Pedrini *et al.* 2005), Tree Pipit (*Anthus trivialis*; Pedrini *et al.* 2005), and Citril Finch (*Carduelis citrinella*; Förschler & Kalko 2006). Moreover, wood pastures harbour rich communities of passerine birds, hosting a larger number of species (and with a greater diversity of nesting requirements) than forest or open pastures (Hartel *et al.* 2014). Our results show a markedly positive effect of wood pastures, despite the relatively low cover, on the occurrence of four out of five common forest species, which were almost invariably detected at points with wood pastures as the dominant land-cover type. The positive effect of wood pastures is generally stronger than that of conifer forests (see Figs. 2 and 3). Therefore, wood pastures may be particularly suitable for many bird species in the Alps, fulfilling the requirements of both some conservation-dependent species, and of some of the commonest and widespread forest species. Further research is needed to evaluate in detail what type of fine-scaled habitat management may be better suited for bird conservation in changing mountains with wood pastures, including among others tree density and features of the herbaceous layer. In particular, the definition of wood pasture in the land-cover map we used was very simple (see Table 1), and does not provide enough information to evaluate the effect of canopy cover, shrub occurrence and structure of the grass layer. In reality there is a likely continuum from forest to wood pasture to scrub to grasslands, and further investigation is required to locate the optimum along this continuum for single species of conservation concern, and for community structure as well. Nevertheless, our results confirm the ecological importance of wood pasture (cf. Hartel *et al.* 2013, 2014, Plieninger *et al.* 2015).

This finding, coupled with its high aesthetic, recreational, cultural and economic (livestock grazing, forage and timber production) values (Garbarino *et al.* 2011), makes such a traditional habitat a particularly important environmental trait of the Alps. However, wood pasture, which in the Alps is usually dominated by larch (*Larix decidua*; Garbarino *et al.* 2013), is currently suffering a significant reduction due to land abandonment; being a traditional land use, it is threatened by current habitat changes, often developing into closed stands (Piussi 2000, Garbarino *et al.* 2011). In the Alps, in the light of expanding forest via upward shift of the treeline, wood pastures may be easier to maintain than other open or semi-open habitats, requiring less intensive management than, e.g., grassland, and thus in some areas they may be preferred in a management strategy that aims at contrasting forest expansion (due to abandonment and/or climate change) for conservation purposes.

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Yleisten metsälintulajien esiintyminen eri habitaateissa esiintymisalueidensa korkeusrajalla

Tässä tutkimuksessa tarkastelimme mitkä habitaattitekijät vaikuttivat viiden yleisen metsälintulajin esiintymiseen Alpeilla lajikohtaisten esiintymisalueiden korkeusrajoilla. Tutkittavat lajit olivat punarinta, tiltaltti, mustapääkerttu, kuusitiainen ja peippo. Tutkimuksen tarkoituksena oli määritellä lajikohtaisia habitaattisidonnaisuuksia näiden esiintymisalueiden korkeusrajoilla ja tuottaa hoitosuosituksia linnustonsuojelulle muuttuvissa elinympäristöissä.

Tutkimusalueemme sijaitsi Trentossa, Italiassa (1 365–2 200 mpy), jossa kirjasimme lajikohtaista esiintymistä 149 havaintopisteessä. Tutkimme miten esiintyminen oli yhteydessä korkeuteen merenpinnan yläpuolella sekä habitaattien pinta-alaan 100 metrin säteellä havaintopisteestä. Arvioimme esiintymisen todennäköisyyttä suhteessa kahteen edellä mainittuun ympäristömuuttujaan käyttäen epäparametrista monimuuttujaregressiomenetelmää (Multivariate Adaptive Spline Regression, MARS), sekä lajimäärään vaikuttavia tekijöitä käyttäen Poisson-regressiomenetelmää.

Monimuuttujaregression perusteella lajikohtaisen esiintymisen todennäköisyys laski korkeuden kasvaessa. Havumetsien pinta-alan kasvaessa useimpien lajien (tiltalttia lukuun ottamatta) esiintymisen todennäköisyys kasvoi tiettyyn lajikohtaiseen kynnysarvoon asti. Mustapääkerttua lukuun ottamatta kaikki lajit hyötyivät myös puoliavointen laidunmaiden pinta-alojen kasvusta. Lintujen lajimäärä kasvoi havumetsien, puoliavointen laidunmaiden sekä pensastomaiden pinta-alojen suurentuessa, mutta laski korkeuden kasvaessa. Tutkimuksemme perusteella ei-parametriset monimuuttujaregressiomenetelmät soveltuvat hyvin harvalukuisten lajien ekologisten suhteiden mallintamiseen. Luonnonhoitotoimenpiteitä tulisi kohdistaa enenevässä määrin puoliavoimiin laidunmaihin, koska näillä lintujen monimuotoisuus oli tutkimuksemme mukaan korkea, ja nämä ovat entuudestaan tunnettuja luontoarvoistaan.

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