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Altitudinal Shift of *Tetrao urogallus* in an Alpine Natura 2000 Site: Implications for Habitat Restoration

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Received: 10 August 2018; Accepted: 12 March 2019; Published: 19 March 2019

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Featured Application: Observed shifts in the altitudinal distribution of capercaillie confirms the relevance of habitat restoration actions.

Abstract: Capercaillie (*Tetrao urogallus* L.), a territorial galliform species, is known to prefer mature conifer stands with canopy gaps and a vigorous understory of ericaceous species. Capercaillie is a useful umbrella species that has recently shown declining population trends and distribution changes in its southern geographic range. We aim to identify and assess the possible changes in summer capercaillie habitat selection between 2001 and 2011 in the Scanuppia Natura 2000 site (south-eastern Alps). The area is dominated by spruce (*Picea abies* (L.) Karsten) forests, followed by mixed forests, scrub, and open habitats. In both years, summer presence–absence of capercaillie was verified through the detection of droppings over 10 m radius circular plots located along contour lines (1500–1800 m). A set of environmental and habitat features was also surveyed. While overall population numbers remain unchanged over the surveyed period, results have shown an altitudinal shift in capercaillie distribution. Habitat variables had a stronger effect on the presence of capercaillie in 2001 than in 2011. Land cover and climate change are likely among the drivers of the shift in altitudinal distribution. This confirms the relevance of habitat restoration actions and to monitor changes in factors explaining capercaillie habitat selection.

Keywords: landscape management; habitat change; species distribution; climate change; alpine vegetation; wildlife conservation; capercaillie

1. Introduction

In mountain regions, global changes linked to climate and human impacts are serious threats to animal species. This issue is particularly relevant for those species with limited dispersal ability during part of or all their life stages [1]. Besides impacts on habitat quality due to climate change, land use and cover changes are usually considered to have important impacts on biodiversity [2]. Upper shifts of the Alpine timberline were reported to be more due to land cover changes than climate change, with a probable interaction between the two [3]. Indeed, sensitive species in mountain environments are more likely to be threatened by land cover changes, which are usually associated with direct human impact. At high altitudes, since physical space is already a limitation [4], the encroachment by shrubs and trees might result in the complete loss of habitat suitable for specialized residents of relatively open forest stands [5], including species of conservation concern [6].

One important example is the capercaillie (*Tetrao urogallus* L.), a species of conservation interest according to the Birds Directive (2009/147/EC) of the European Union. This species is found in boreal and temperate forests of Europe (including Russia) and its geographical range stretches from the Alps, Pyrenees, and Balkans to northern Norway. Capercaillie is thought to be an umbrella species for other mountain birds [7], making any change in its habitat distribution a good predictor of changes affecting sympatric bird species. The average home range size of capercaillie in the Alps is around 550 ha [8]. Despite this relatively large home range, the species shows narrow habitat preferences [9,10]. Habitat suitability models have been developed at the stand and the landscape scale. Using presence–absence data, Graf et al. [11] found that the best single large scale to build habitat suitability models corresponds to a small annual home range, about 250 ha. Ideally, data collected at large scale should be combined with those collected at the stand scale to efficiently develop management guidelines for capercaillie conservation [12].

At the stand scale, capercaillie prefers mature, structurally diverse forests characterized by canopy gaps and rich undergrowth with the presence of *Vaccinium* species [13]; branches of trees are used as shelters and roosts [12] and conifer needles form most of the capercaillie winter diet [14]. At the stand mosaic scale, ecotonal zones are important for nesting and brood rearing [13], as well as the proportion of forests, particularly coniferous [11]. At the landscape scale, habitat patches are mostly occupied when their size is 800–1100 ha (minimum: ca. 50 ha) and their distance from the nearest occupied patch is less than 10 km [15]. The uppermost slopes at the tree line are outside capercaillie altitudinal range because they offer little habitat, such as bilberry and trees [16]. Therefore, land cover and climate change together with human pressures, such as tourism, have all been highlighted as impacting on this species [17–20].

In the present study, we repeated twice over a decade the investigation of the relationships of capercaillie with habitat structure, at a single stand scale over a 400 ha study area. Our study case is located in a mountainous area on the southern edge of the Alps, which has undergone open land loss and forest expansion in recent decades [21]. At this southern edge of distribution, capercaillie population numbers do not show tendency to cycle [22] and have recently been declining [23]. Two surveys of capercaillie presence–absence, one in 2001 and the other in 2011, were compared to detect any change in the stand-level species-habitat relationships. The results will permit on the one hand to assess the consistency of capercaillie habitat suitability models across time, on the other hand to provide guidelines for managing and conserving habitats for this and other sympatric species living in the studied area.

2. Materials and Methods

2.1. Study Area

This study was conducted in the IT3120018 “Scanuppia” Natura 2000 site, an area (529 ha) protected under the Directive 92/43/CEE [24] in Trento Province, south-eastern Alps (45°57′ N 11°09′ E) (Figure 1). The forest is dominated by Norway spruce (*Picea abies* (L.) Karsten) with some areas covered with silver fir (*Abies alba* Miller), European larch (*Larix decidua* Miller), and European beech (*Fagus sylvatica* L.). Mixed stands as well as small pastures are also found in the area.

The forest management plan [25] highlights a decreasing pressure on natural resources. Half of the forests in the protected area are grazed, although numbers of grazing animals decreased from more than 130 cows and 900 sheep in 1839, to 75 cows in 2007. At the beginning of the 20th century, timber yield was higher than 700 m^3/y and firewood production more than 20,000 kg/y [25]. Since the 1950s timber harvests have been reduced to zero and the site has been integrally protected since 1990. The reduction in the intensity of logging and grazing has led to rewild the area with the gradual spread of shrubs and vertical stratification of the canopy structure. The existence of this trend is supported both by aerial photos observation (Figure 2) and by the expansion of trees and shrubs on former open lands which has been quantified (0.1% forest cover annual growth rate) in the region by comparing remote sensed data from different time periods [5,26].

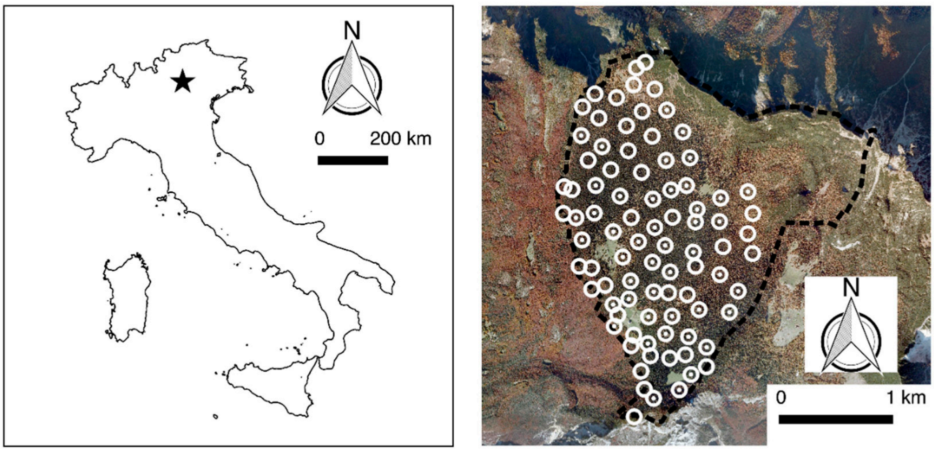

Figure 1. (**a**) The black star indicates the study area in northern Italy. (**b**) Distribution of the capercaillie sampling plots (circle = summer presence–absence surveyed in 2001 and 2011, empty circle = habitat surveyed in 2001, filled circles = habitat surveyed in 2001 and 2011) in the Scanuppia Natura 2000 site (black dashed line) is reported (background: 2008 aerial photo).

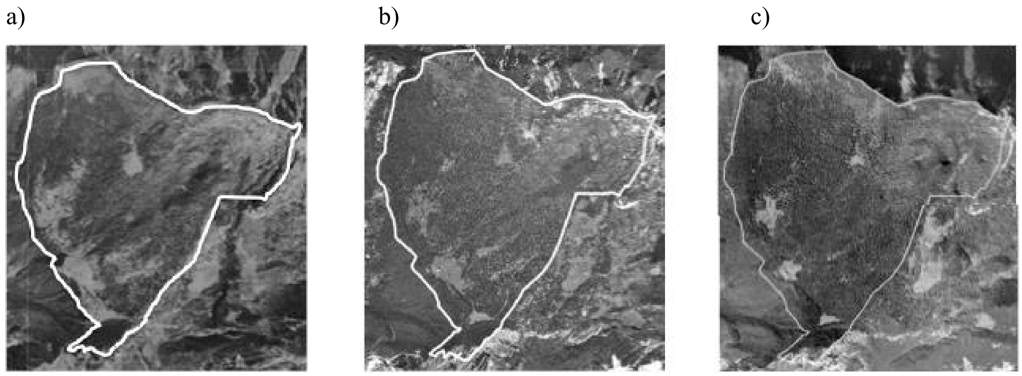

Figure 2. Historical aerial photos comparison which show the reduction of open lands from (**a**) 1954; to (**b**) 1973; and (**c**) 2006, in the Scanuppia Natura 2000 site.

The altitude of the Natura 2000 site ranges between 1450 m and 2130 m a.s.l. (highest summit located at its north-eastern vertex) and has western facing slopes. To understand recent climate changes, data series from 1989 to 2010 available from three nearby (12 km NW of the study area) weather stations on Mt. Bondone can be used as they are at a similar altitude (1490–1552 m a.s.l.) and latitude to our study site. Mean annual rainfall and temperature of this period are 1407 mm and 5.7 °C, respectively. Using a linear time trend model, the averaged surface air temperature has increased by 1.3 °C in April (mean = 3.6 °C, std = 1.2), 2.5 °C in May (mean = 8.8 °C, std = 1.3), and 2.7 °C in June (mean = 12 °C, std = 1.5). Similar trends have been observed in maximum temperatures. These changes may affect capercaillie hatching time and number of brood rearing females, and hence breeding success [18].

Following a request to the Autonomous Province of Trento, which performs them annually, we obtained historical data derived from local censuses of capercaillie presence. The annual estimated number of individuals is available for a period between 1991 and 2011 and, for the latest years, capercaillie population ranged between 20 and 30 individuals with an estimated annual breeding success that varied from 0.7 to 3.5 chicks per female (mean = 2.5). In general, for this period of analysis, no marked decreasing or increasing population trend was observed.

2.2. Data Collection

Data on capercaillie presence–absence and environmental variables were collected in 2001 and 2011. A systematic sampling design formed by a set of 86 plots distributed at regular distances of 250 m was set along contour lines between 1500 and 1800 m a.s.l. (i.e., altitude interval of 50 m). Surveys were conducted in 10-m radius circular plots (314 m^2) (Figure 1b). In 2011 a random subset of 45 plots was fully re-surveyed with the same protocol applied in 2001. We also collected presence–absence data and identified the habitat type for those plots of 2001 not fully re-surveyed in 2011.

Presence–absence of capercaillie was recorded in the plots through the detection of droppings with a 15-min search. In both years, the survey was done during the post-reproductive season in summer (July–August). Droppings are a valid indicator of this species presence [27] and summer droppings can be distinguished from winter ones as they are partially coated with uric acid [28], with consequent parts of lighter color, and being less curved and solid. This approach addresses typical detectability issues for direct observation of elusive species that, for capercaillie, are usually dependent on sex and habitat type [29,30].

We assessed habitat type (canopy dominance) and structure (stand development stage) (Table 1). Vegetation was divided into four categories: tree (height $\geq$ 5 m), shrub (woody plants with height < 5 m), dwarf shrubs (i.e., *Vaccinium* spp., *Polygala chamaebuxus*, *Erica carnea*, *Orthilia secunda*, *Paederota bonarota* and *Thymus praecox*) and herbaceous layer. Mean height of each layer was also measured. We also recorded several habitat variables that could have been important for capercaillie: aspect, slope, altitude, and percentage cover of litter and of tree, shrub, dwarf shrub, and herbaceous layers. Deadwood was recorded as either fine woody debris, i.e., estimated percentage cover of pieces with diameter < 10 cm, or coarse woody debris, i.e., length of pieces with diameter $\geq$ 10 cm. Topographic position was assigned according to four classes: high slope, middle slope, valley, and ridge. Finally, signs of recent silvo-pastoral activities were recorded, such as: stumps of recently felled trees, plant species indicating grazing pressure, proximity to mountain huts, evidence of livestock trampling, and livestock feces.

Table 1. Habitat type and structure categories.

Variable Description	Classes and Abbreviations
Habitat type (canopy composition) (VEG)	(1) silver fir (aa); (2) beech (fs); (3) larch (ld); (4) spruce and fir (paA); (5) spruce and beech (paF); (6) spruce on moist soil (paM); (7) spruce on dry soil (paX); (8) pasture (pas); (9) mountain pine (pm); (10) tree plantation (rim)
Habitat structure (development stage) (STR)	(1) two-layered stand (bp); (2) adult stand (fad); (3) late pole stand (fgi); (4) irregular stand (fir); (5) mature stand (fma); (6) over-mature stand (fri); (7) multi-layered stand (mt); (8) young pole stand (pe); (9) wooded pasture (pra); (10) thicket stand (sp); (11) gap (vu)

2.3. Data Analysis

To understand the relationship between capercaillie and the studied environment we related response and predictor variables through boosted regression tree (BRT) modelling as it enables complex species-habitat relationships to be detected and explained [31]. This statistical framework has been successfully adopted for shedding light on the importance of single environmental features on the occurrence of bird species [32,33]. It combines regression trees and boosting to improve predictive power. Regression trees relate a response to predictors by recursive binary splits, producing a decision tree. Boosting is a machine-learning iterative procedure to obtain better predictive performance through multiple learning algorithms. This method enabled a set of variables different in type (both categorical and continuous) to be incorporated and non-linear relationships to be detected between the response variable and predictors [34].

The literature has highlighted the importance of both the canopy composition and the stand structure on capercaillie habitat selection; two factors that can be shaped through human interventions such as silvicultural operations [19,20,35]. We therefore first analyzed the relative importance of habitat type and structure (Table 1) [36]. The second analysis was conducted with the quantitative environmental and habitat variables (Table 2). When independent variables resulted correlated (correlation < ∣0.6∣), only one was included in the analysis [37].

Table 2. Variables used to explain changes in capercaillie presence–absence.

Variable Description	Abbreviation	Unit
Altitude	Alt	m a.s.l.
Aspect	Asp	cardinal orientations
Topographic position	Top	high slope, middle slope, valley, and ridge
Slope	Slo	%
Cover of beech	CBe	
Cover of common juniper	CJu	
Cover of mountain pine	CDp	
Cover of silver fir	CFi	
Cover of herbaceous layer	CHe	
Cover of larch	CLa	
Cover of litter	CLi	%
Cover of *Rhododendron ferrugineum*	CRf	
Cover of spruce	CSp	
Cover of dwarf shrubs	CSu	
Cover of *Vaccinium myrtillus*	CVm	
Cover of *Vaccinium vitis-idea*	CVv	
Cover of fine deadwood	CFD	
Height of trees	HTr	
Height of shrubs	HSh	
Height of herbaceous layer	HHe	
Height of fir	HFi	m
Height of larch	HLa	
Height of spruce	HSp	
Height of dwarf shrubs	HSu	
Presence of broadleaf species	PBr	
Evidence of silvicultural interventions	SIn	Presence–absence
Signs of grazing	SGr	

In both analyses, the response variable was the presence-absence (1-0) of capercaillie during summer 2001 and 2011. Following Elith et al. [34] indications, tree complexity, learning rate, and bag-fraction parameters were defined for the final models comparing predictive performance and fitting with 1000 trees, through the Bernoulli distribution of errors. The building procedure and cross-validation of BRT helped to control for overfitting [38]. Indeed, this method has been successfully applied with small sample sizes [33]). Model performance was evaluated with a 10-fold cross-validation, a commonly adopted approach that enables either a portion or all data at a certain stage to be used to test and fit the model. Furthermore, when not informative, variables were dropped as model simplification is more useful with small sample sizes.

The relative contribution of each predictor was estimated in the model and based on the number of times that the predictor was selected in each recursive binary split node, weighted by the squared improvement to the model as a result of each split, and averaged over all trees. The contribution of each variable is scaled so that the sum adds up to 100, with higher numbers indicating stronger influence on the response.

The overall statistical model was performed following specific guidelines [34] and using the 'gbm' package 2.1.5 [39] for R statistical software [40].

We report the results of the BRT model in two ways. First, we present a histogram showing the relative influence of variables produced from the 'summary.gmb' function of the R software package 'gbm'. Then, only for the variables with relative importance ≥ 10%, we plot the fitted functions in the BRT model using partial dependence functions that show the effect of a variable or group of variables on capercaillie summer occurrence after accounting for the average effects of all other variables in the model. BRT can be used with a variety of response types. If the response variable is binary, then the package 'gbm' of R adopts the Bernoulli logistic regression. The fitted values are the logarithms of the odds $p/(1-p)$ where p is the probability of capercaillie occurrence for a given value of the predictor.

3. Results

The type of habitat played a stronger role than its structure in both years (Figure 3). Its relative importance increased in 2011 compared to 2001. The BRT model for 2001 had an explained deviance of 20%, a cross-validation correlation of 0.39 and standard error of 0.12. Instead, the model for 2011 had an explained deviance of 26%, a cross-validation correlation of 0.46 and standard error of 0.09.

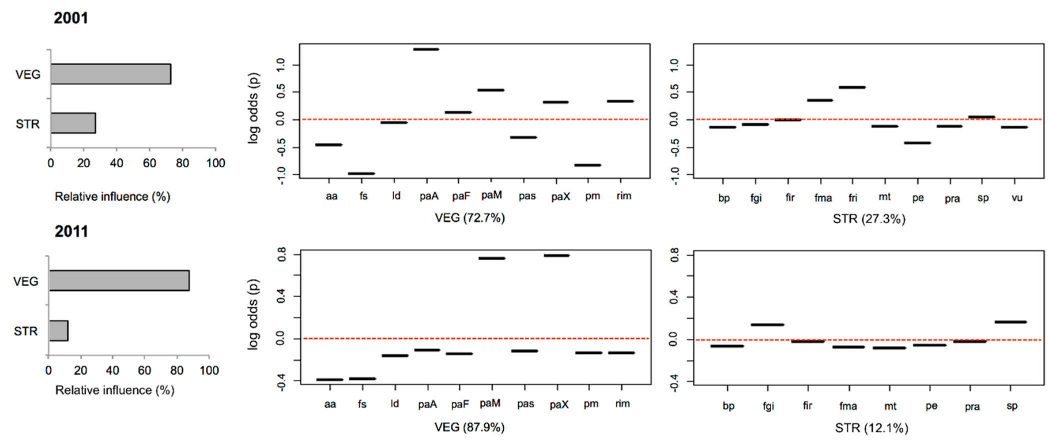

Figure 3. Relative influence of habitat canopy (VEG) and structure (STR) and relationship of each habitat category with capercaillie summer occurrence in 2001 and 2011 in a generalized boosted regression model obtained by integrating out all the other categories. A logistic regression was used, and y-axes report the fitted values on log-odds scale. The red line corresponds to a probability of 0.5 (odds (p) = 1, log odds (p) = 0). Explanatory variables, with their codes, are reported in Table 1.

Moreover, in both years, spruce forests (paA, paF, paM, paX) showed a positive influence on capercaillie presence, while fir (aa) and beech (fs) forests were avoided. No important changes occurred between 2001 and 2011 (Figure 3). Habitat structure types (i.e., development stages) did not show a clear pattern considering both years. In 2001 there was an indicative positive relationship of the presence of capercaillie with mature (fma) and over-mature (fri) stands, while pole dense canopies (pe) had a negative impact.

The BRT models with quantitative environmental and habitat variables had an explained deviance of 29%, a cross-validation correlation of 0.36 and standard error of 0.14 in 2001, while in 2011 they were 26%, 0.42 and 0.17, respectively.

A remarkable outcome is the much higher influence of altitude (Alt) in 2011 than in 2001 (Figure 4). In 2001, in addition to altitude, the following variables had a relatively important influence on the capercaillie summer presence: cover of spruce in the tree layer (CSp) and the mean height of spruce trees (HSp), cover of berries (CVv, CVm) and dwarf shrubs (CSu). Instead in 2011, apart from altitude (Alt), only slope (Slo) and cover of spruce (CSp) in the tree layer had a relative influence higher than 3%.

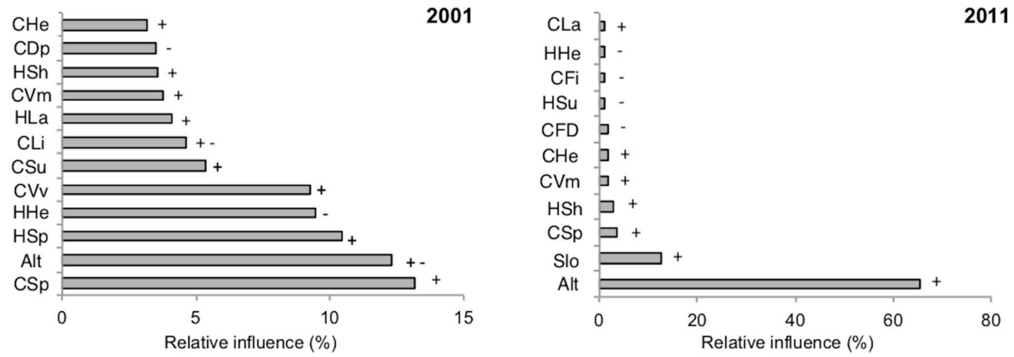

Figure 4. Relative influence of quantitative variables in a BRT model for capercaillie summer occurrence in 2001 and 2011. Signs indicate whether the relationship was negative (−) or positive (+) monotonic or non-monotonic (+ −). Explanatory variables, with their codes, are reported in Table 2.

Overall, only a limited number of explanatory variables had a relative influence ≥ 10% (Figure 5). Among these, for both years, altitude was a fundamental environmental factor. More specifically, in 2001, capercaillie was most commonly found at altitudes from 1570 to 1670 m a.s.l. with a decreasing trend at altitudes higher than 1670–1700 m a.s.l. On the contrary, the species had clearly moved to higher altitudes in 2011, ranging from 1620 to 1750 m a.s.l., with this factor being extremely important compared to other explanatory variables for the species (i.e., 65.3% of relative influence). Furthermore, there was no negative trend in presence of the species for higher altitudes.

Factors related to spruce were important for the presence of capercaillie. In 2001, capercaillie preferred forests where this tree species proportion exceeded 50% and had a mean height over 17–18 m. In 2011, it is relatively evident that the species avoid slopes lower than 20%, without having preference for steep slopes.

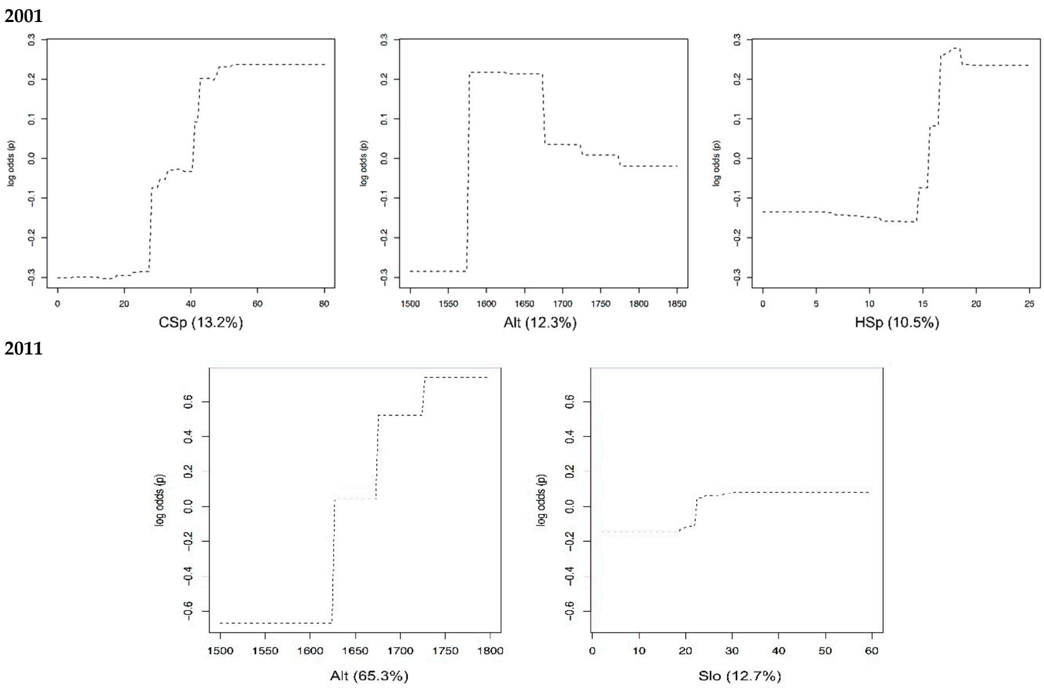

Figure 5. Relationship of the most influential variables (relative influence ≥ 10%) with capercaillie summer occurrence in 2001 and 2011, obtained by integrating out all other variables in a generalized boosted regression model. A logistic regression was used, and y-axes report the fitted values on log-odds scale (explanatory variables, with their codes, are reported in Table 2).

4. Discussion

We observed an altitudinal shift of capercaillie based on the comparison of presence–absence data between 2001 and 2011. Even if altitude gained the highest relative influence in 2011, habitat features, particularly those associated with spruce canopy cover, played an important role in both years.

4.1. Species-Habitat Relationships

In our study area, capercaillie presence seemed to be influenced by a series of habitat factors, which have also previously been reported in the literature. For instance, the absence of wild berries seemed to have a deterrent effect on capercaillie presence. Availability of this food source is recognized as an essential feature for the bird's diet [41] as it is thought to determine brood survival [13]. In general, abundance of dwarf shrubs—possibly with more than 20% bilberry cover [42]—is a characteristic that defines a good capercaillie habitat [7,12,14,41]. Spruce had a positive influence on the bird species presence. For instance, the lower branches of spruce can provide roosts and shelters [12]. Furthermore, the positive relationship between capercaillie presence and spruce mean height is consistent with its preference for mature stands [14].

The importance of altitude together with a preference for higher altitudes in 2011 than in 2001 indicated a shift in capercaillie presence. This was also observed for capercaillie in neighboring regions [43].

In 2011, slope appeared as an explanatory variable for capercaillie presence with a negative influence of slopes lower than 20% and no preference for steep slopes. Accordingly, Graf et al. [11] recorded capercaillie more often on gentle slopes, mountain ridges, or upper slopes, rather than on very steep topography, toe slopes, or valley bottoms. In both years, the cover of the herbaceous layer was positively related to capercaillie presence, and this might be due to the fact that grass cover can favor *V. myrtillus* [44]. However, the herbaceous layer height had a negative influence, as this may have negatively influenced berries and the type and amount of invertebrates, in turn impacting on food availability for the chicks [45]. Lastly, grazing and silvicultural activities did not have an influence in our study because their intensity is currently moderate [46].

4.2. Management Implications

Even though changes in the relationships between capercaillie and its habitat may not be seen as negative *per se*, we agree with other authors [15,23] that the maintenance of suitable habitats for local populations is strongly recommended. Data for 2001 highlighted the necessity of maintaining both mature and over-mature stands. Therefore, actions should integrate conservation measures for multiple benefits [47], thus address both forests and open habitats such as shrublands. In the first case, recommended actions include low-impact forestry practices that emulate natural disturbances and ensure the presence of not too dense stands, where there are mature development stages [46]. In the second case, several studies and applications, conducted in the southern Alps [48–52], agreed in suggesting different actions, depending on the successional stage.

Alpine scrub, mainly consisting of dwarf mountain pine (*Pinus mugo* Turra), is the dominant land cover type above the timberline (Figure 6). It is encroaching abandoned pastures. It is a habitat not suitable for capercaillie, because of the lack of berries and its dense structure which hinders easy movement in and through the canopy [53]. This means that the habitat available to capercaillie inside this Natura 2000 site is under pressure. The observed altitudinal shifts of capercaillie close to unsuitable mountain pine scrublands confirms the relevance of habitat restoration actions. For example, in pastures not completely encroached by mountain pine, it is appropriate to promptly intervene, making openings according to an irregular design and subsequently mowing them, so that a mosaic of bushes and open areas is kept for as long as possible. These actions may be in conflict with the limitations imposed by environmental regulations, such as the Habitats Directive [47,54]. For example, any land use change that involves trimming of dwarf mountain pine may contrast with the need to protect the priority European Union habitat 4070 * "Bushes with *Pinus mugo* and *Rhododendron hirsutum* (*Mugo-Rhododendretum hirsuti*)".

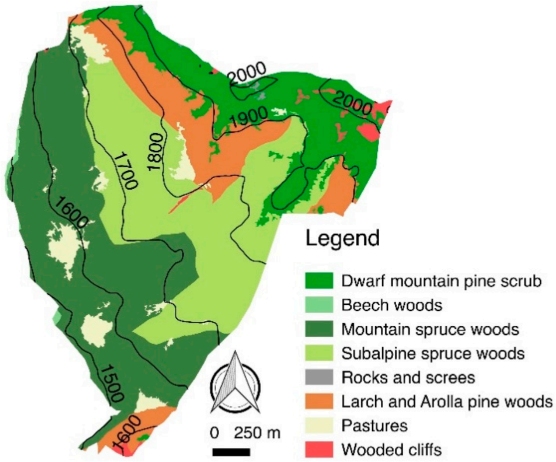

Figure 6. Distribution of land cover types in the Scanuppia Natura 2000 site. The altitudinal distribution of capercaillie in 2011, currently centered at 1620 to 1750 m a.s.l., is closer than in 2001 to the dwarf mountain pine scrub, which is unsuitable to capercaillie (source: Provincia Autonoma di Trento, Servizio Sistemazione Montana, 2001).

4.3. Conclusions and Further Research

Spatial requirements of capercaillie are large, a lively population of capercaillie might require around 250 km^2 [55]. Moreover, number and size of suitable habitat patches and the distance between them determine capercaillie occupancy and dispersal [15,17]. The observed shift in capercaillie altitudinal distribution could therefore be restricted to our study area. In fact, a possible drawback of our study is the limited area investigated and the relatively small number of surveyed plots. Nevertheless, models of this species built with regional-scale data may not be appropriate for understanding habitat preferences and the effects of their changes [56], and proposing restoration actions at the stand scale. Periodic stand-level monitoring would thus improve the understanding of regional trends, because we observed that the variables with the highest predictive powers changed across time.

In addition to what was observed in our study, other factors may have played a role. For example, changes in ungulate populations might also influence habitat use by capercaillie [57]. Human disturbance might be another contributing factor. Tourism and forest management [19,46] at lower altitudes could have emphasized the effects of land cover changes pushing capercaillie upwards in the post-breeding season. Lastly, being a key factor in other European contexts, increased predation at lower altitudes may have been driven by habitat cover changes [18,58,59] and capercaillie mobility might have been an adaptation to avoid predation [13].

This study focused on data recorded in two years during one season. However, while land use changes likely played a major role, it must be emphasized that additional studies over longer time-spans are needed to detect consistent trends and exclude short-term phenological effects related to the summer growing season. Additional research should focus on linking the observed altitudinal shift to other likely drivers.

Author Contributions: Conceptualization, S.M.M. and T.S.; Methodology, S.M.M. and T.S.; Formal Analysis, M.D. and T.S.; Investigation, F.D., S.M.M. and T.S.; Writing-Original Draft Preparation, A.P., T.C., T.S.; Writing-Review & Editing, all authors; Visualization, A.P., T.C., M.D., T.S.

Funding: The 2001 survey was funded by the Autonomous Province of Trento within a service contract with S.M.M., M.D. was supported by a postdoctoral research fellowship "Grant" (Dept. TESAF Decree no. 36/Protocol no. 1006/2011), T.C. was supported by a postdoctoral research fellowship (Dept. TESAF Decree no. 35/Protocol no. 2010/2017), A.P. was supported by a PhD grant from the Fondazione Cariparo.

Acknowledgments: The authors thank the Autonomous Province of Trento for supporting this study and three anonymous referees for the comments received on previous versions of this manuscript.

Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, nor in the decision to publish the results.

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