Interchangeable sets of complementary habitat variables and target values allow for flexible, site-adapted wildlife habitat management in forest ecosystems

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Abstract

1 Integrating biodiversity conservation into forest management is a major goal in
2 sustainable forestry. Hence, target values for forest structural and compositional
3 stand characteristics are required to ensure wildlife habitats of sufficient extent
4 and quality. Yet, the possibility to meet these targets depends on the patch
5 conditions, notably their initial state and future trajectory. Shaped by succession,
6 site conditions and management regime, not all forest stands can be readily
7 converted into a particular state, which calls for flexible management
8 prescriptions. Using the example of two forest grouse species, capercaillie and
9 hazel grouse, we sought complementary variable combinations – with quantitative
10 thresholds for any given crucial habitat feature – which would likewise offer
11 suitable habitat. Habitat variables were mapped in sampling plots within occupied
12 and non-occupied 1 km² grid cells distributed across three Swiss mountain
13 regions. Generalized Linear Mixed Models (GLMM) were combined with
14 Conditional Inference Trees (CIT) to identify species-relevant variable
15 combinations and variable thresholds. Important features for both species were the
16 proportion of bilberry (*Vaccinium myrtillus*) and the number of basal-branched
17 trees, as well as a low proportion of beech (*Fagus sylvatica*) in the canopy layer.
18 Hazel grouse additionally favoured rowans (*Sorbus aucuparia*) as feeding trees
19 and a high percentage of herbs in the ground layer, while the presence of inner
20 forest edges was additionally important for capercaillie. Thresholds were not
21 clear-cut: different values applied for a particular variable depending on other,
22 functionally similar habitat variables present at the site. By delivering information
23 about relevance, interactions and the required amount of crucial variables, we
24 provide alternative options for flexible species habitat management which allows
25 accounting for the prevailing stand conditions.

26 **Zusammenfassung**

27 Die Integration von Naturschutzzielsetzungen in die Waldbewirtschaftung ist
28 wesentliches Ziel einer nachhaltigen Waldwirtschaft. Um Wildtierlebensräume in
29 ausreichendem Umfang und Qualität zu gewährleisten werden waldstrukturelle
30 Zielwerte benötigt. Die Möglichkeit diese Zielwerte zu erreichen hängt jedoch
31 maßgeblich von den Ausgangsbedingungen und dem Entwicklungspotential eines
32 Waldbestandes ab. Je nach Sukzessionsstadium, Standortbedingungen und
33 Bewirtschaftungsform können nicht alle Bestände gleichermaßen in einen
34 gewünschten Zustand überführt werden. Dies macht flexible
35 Managementvorgaben erforderlich. Am Beispiel von zwei sympatrischen
36 Raufußhuhnarten, Auerhuhn und Haselhuhn, ermittelten wir Kombinationen
37 komplementärer Habitatvariablen und zugehöriger Schwellenwerte, die
38 gleichermaßen geeignete Lebensraumbedingungen bieten. Hierfür wurden
39 Flächen mit und ohne Artvorkommen in drei Bergregionen der Schweiz
40 verglichen und artrelevante Variablen, Variablenkombinationen sowie
41 Schwellenwerte durch Generalisierte Lineare Gemischte Modelle und Conditional
42 Inference Trees (CIT) identifiziert. Wichtige Lebensraummerkmale für beide
43 Arten waren der Anteil der Heidelbeere (*Vaccinium myrtillus*) sowie die Anzahl
44 tiefbesteter Bäume und ein geringer Anteil Buche (*Fagus sylvatica*) in der
45 Baumschicht. Das Vorkommen des Haselhuhns wurde zusätzlich durch die
46 Anzahl an Ebereschen (*Sobus aucuparia*) und einen hohen Anteil an krautigen
47 Pflanzen in der Bodenvegetation bestimmt, Randlinien zu offenen Flächen im
48 Wald waren ein wichtiger, zusätzlicher Habitatfaktor für das Auerhuhn. Die
49 ermittelten Schwellenwerte für Habitatvariablen waren meist nicht klar definiert,
50 vielmehr galten unterschiedliche Werte abhängig davon, welche anderen,
51 funktional ähnlichen Habitatmerkmale in einer Fläche vorhanden waren. Neben

52 der Identifikation artrelevanter Habitatvariablen kann die Bereitstellung
53 alternativer Variablenkombinationen und kombinationsabhängiger
54 Schwellenwerte eine wichtige Grundlage dafür liefern, Managementmaßnahmen
55 flexibel an die in einem Waldbestand gegebenen Ausgangsbedingungen
56 anzupassen.

57

58 **Keywords:** *Bonasa bonasia*, complementary habitat variables, Conditional
59 Inference Tree, habitat management, mountain forests, *Tetrao urogallus*,
60 thresholds

61

62 **Introduction**

63 In the human-dominated landscapes of Central Europe, where suitable wildlife
64 habitat is limited, conservation management needs quantitative and spatially
65 explicit prescriptions for biodiversity preservation and habitat restoration. In
66 forest ecosystems, where species occurrence and diversity largely depends on
67 characteristics of forest composition and structure (Bollmann et al., 2009;
68 Brombacher, 1999), enhancing or restoring forest structural diversity is a prime
69 goal of wildlife habitat management (Bergman et al., 2012; Lindenmayer & Luck,
70 2005). Yet, evidence-based, quantitative targets with regard to the amount, size
71 and configuration of crucial habitat features (e.g. Müller & Bütler, 2010) are still
72 rare. Moreover, even if quantitative management prescriptions exist, they are
73 often not equally applicable to all site conditions: Most forests are commercially
74 used ecosystems, characterized by a slow vegetation succession. Stand
75 composition and structure differ greatly depending on site conditions and mode of
76 exploitation (Bürgi, 1998), and thus provide variable conditions for habitat
77 management. Possibilities for habitat management are further constrained by the
78 objectives of commercial forestry, which may interfere with habitat management
79 goals (Bollmann & Braunsch 2013). While some measures can readily be
80 implemented, e.g. removing trees to create gaps, alter light conditions and
81 promote ground vegetation, other structural components such as tree species
82 composition or age structure can only be modified within long time frames, and in
83 strict consideration of the initial state and local site conditions. Given these
84 limitations, achieving the multiple functionalities of forests through integrative
85 management remains a big challenge. This is particularly true when the
86 requirements of different species with diverging ecological needs have to be met

87 within the same area. Yet, species rarely require similar habitat conditions
88 throughout their range, but avail themselves of a mosaic of different habitat
89 features and resources that offer complementary functionalities, such as food
90 supply, cover against predators, roosting or breeding sites. Thereby, different
91 habitat features may be interchangeable across a species' home range. Identifying
92 sets of important and complementary variables is thus a key for a flexible multi-
93 species habitat management.

94 In Europe, the hazel grouse (*Bonasa bonasia*) and the capercaillie (*Tetrao*
95 *urogallus*) are two forest grouse species of conservation concern (Storch, 2000)
96 which often occur sympatrically. Being considered as indicators for structural
97 diversity of boreal and mountain forest ecosystems (Pakkala et al., 2003; Suter et
98 al., 2002), they have suffered from habitat loss and degradation during the last
99 century mainly due to changes in forest management (Klaus, 1991). While
100 qualitative habitat requirements for these two tetraonids have been well described
101 (e.g. Glutz von Blotzheim et al., 1973; Müller, 1973), recent studies also provide
102 quantitative target values for particular habitat features, including variable
103 thresholds, which allow for targeted habitat management (Mathys et al., 2006;
104 Müller et al., 2009; Sachot et al., 2003; Schäublin & Bollmann, 2011; Suchant &
105 Braunisch, 2004). However, habitat recommendations vary considerably between
106 studies and areas, providing evidence for their limited generality.

107 In this study we analyse the habitat requirements of the two species from a novel
108 perspective: using multivariate classification and regression trees, we seek for
109 different combinations of habitat variables as well as quantitative thresholds
110 thereof that similarly promote species presence at the forest stand scale. In this
111 context we explore if and to what extent the required amount of one habitat

variable depends on the occurrence and amount of another, complementary habitat feature. Thereby we hypothesize that different threshold values apply for a given habitat feature which vary within the range of threshold-values found in literature. The quantitative prescriptions drawn for our analyses provide refined guidance for a flexible management and restoration of suitable forests for declining populations of the two tetraonids.

Materials and methods

Study area

The study was conducted in Switzerland, with the study sites distributed across three mountain ranges representing a broad gradient of bioclimatic conditions: the Jura Mountains (47°00' N 6°40' E - 47°30' N 8°00' E), Northern Prealps (46°30' N 7°15' E - 47°00' N 9°30' E) and Inner Alps (46°30' N 9°00' E - 47°00' N 10°30' E) (Fig. 1A). The Jura Mountains are characterized by a moderate climate with mild, damp summers and cold winters (MeteoSchweiz 2013, <http://www.meteoschweiz.admin.ch>). The mean annual ambient temperature is 5.5°C with 180 frost days and, on average, 2000 mm of rain and 4 m of snow annually at an altitude of 1200 m (MeteoSchweiz 2013). The tree line is around 1400 m a.s.l. (Steiger, 1994). The Northern Prealps are characterized by an Atlantic climate with high precipitation (2000-3000 mm/yr), cold-temperate winters and wet summers (MeteoSchweiz 2013). The tree line is at an elevation of approximately 2000 m (Steiger, 1994). The open and diversely structured forests are often adjacent to pastures and interspersed with mires. In the Inner Alps, the prevailing climate conditions are continental, with low precipitation (800-2000mm/yr), cold winters and warm and dry summers (MeteoSchweiz 2013).

137 Large, continuous forests belts are found along the valley slopes with the tree line
138 being located at 2300m a.s.l. (Steiger, 1994). The altitudinal-climatic gradient is
139 also reflected in the tree species composition, consisting of European beech
140 (*Fagus sylvatica*), silver fir (*Abies alba*) and Norway spruce (*Picea abies*) in the
141 montane zone with larger proportions of larch (*Larix decidua*) and Swiss stone
142 pine (*Pinus cembra*) present in the most continental conditions of the subalpine
143 zone.

144

145 Model species

146 The capercaillie is declining throughout its European distribution range (Storch
147 2007), being classified as “endangered” in Switzerland (Keller et al. 2010) where
148 the number of displaying males was estimated between 450 and 500 in 2001 (half
149 the size of the population in 1968/71; Mollet et al., 2003; Müller, 1973).

150 Capercaillie prefers mature, open, coniferous or conifer-dominated mixed stands
151 with an intermediate canopy cover (Bollmann et al., 2005; Suchant & Braunisch,
152 2004) and a rich ground vegetation cover, ideally including a high proportion of
153 bilberry (Storch, 1993a). The species is considered to be an indicator for structural
154 diversity in boreal and mountain forests, and plays the role of an umbrella species
155 for some associated animal communities, as its presence is positively associated
156 with the diversity and abundance of highly specialized mountain forest birds and
157 forest-dwelling mammals (Pakkala et al., 2003; Suter et al., 2002). The hazel
158 grouse is a territorial forest bird which requires semi-natural forests with young
159 seral stages and old-growth stands with gaps (Desbrosses, 1997; cited in: Sachot,
160 Perrin & Neet 2003). In the year 2001, 7500-9000 breeding pairs were estimated
161 for Switzerland (Maumary et al., 2007). The hazel grouse is not threatened in

162 Europe (IUCN 2012, <http://www.iucnredlist.org>), however it is considered to be
163 “near threatened” in Switzerland (Keller et al., 2010). Probably due to major
164 differences in body size and mating system, home range and habitat preferences
165 (in terms of forest structure and stand density) diverge between the two focal
166 species. Distinct winter feeding habits also lead to discrepancies between the
167 trophic niches, especially as regards resource trees. Local sympatric occurrence
168 might arise from a patchy distribution of suitable hazel grouse habitat being
169 embedded within a suitable capercaillie habitat matrix.

170

171 Species data

172 The presence data of the two focal species were drawn from the database of the
173 Swiss Ornithological Institute (<http://www.ornitho.ch>) which compiles the data of
174 the Swiss National Bird Monitoring programme. Direct (sightings) and indirect
175 (feathers, faeces) species observations are collected year-round by a dense and
176 area-wide network of species specialists and ornithologists, validated by experts
177 of the Swiss Ornithological Institute, and allocated to the respective 1 km² cell of
178 the Swiss National Grid. This cell size also corresponds to the size of a small
179 capercaillie home range (100-1000 ha; Storch, 1995a) and to the double or triple
180 of the home range of a hazel grouse (30-40 ha; Rhim & Lee, 2001). A pairwise
181 sampling scheme was applied, selecting pairs of grid cells with species presence
182 or absence (Table 1). Presence grid cells were chosen according to the following
183 selection criteria: (1) there were at least three observations of the species within
184 the years 2007 – 2010, (2) the sample contained different types of cells, namely
185 cells with both single and sympatric occurrence of the two species, (3) the grid
186 cells were distributed as evenly as possible within the respective study area and

187 along the altitudinal gradient (Fig. 1A). Absence grid cells with a forest cover of
188 at least 50% were randomly selected within 1 km up to maximum 4 km distance
189 to the corresponding presence cells to make sure that they could potentially be
190 reached by the species. Although absence cells were only selected when there
191 were no species records (indirect or direct) within the last 10 years, species
192 presence could not be entirely ruled out, so that absence grid cells were in fact
193 pseudo-absences. Yet, for reasons of simplicity they are referred to as “absence”
194 here.

195

196 Habitat variables

197 Habitat variables were collected from June to August 2011 at 16 sampling plots of
198 30 x 30 m in size, regularly distributed within each grid cell (Fig. 1B,C, Table 1).
199 The variables included information on stand structure, successional stage, tree
200 species composition, ground vegetation and species-specific habitat features
201 (Table 2). Depending on the spatial extent required to capture the respective
202 structural attribute in sufficient detail, habitat variables were mapped at different
203 reference areas within the sampling plot. Whereas variables describing stand
204 structure and tree species composition in the canopy (≥ 5 m) and shrub layer ($\geq$
205 1.3 and < 5 m) were collected across the whole plot area, special resources like
206 rowans (*Sorbus aucuparia*) and anthills were quantified within a 15 x 15 m nested
207 square located around the plot centre (Fig. 1C), the two diagonal corners of which
208 were used to assess the ground vegetation.

209

210 Statistics

211 *Habitat selection*

Habitat selection was analysed using Generalized Linear Mixed Models (GLMMs, R-package lme4; Bates et al., 2014) with a binomial error distribution (logit link) and “grid cell pair” as random factor. First, univariate models were run with all potentially relevant variables. From pairs of correlated explanatory variables (Spearman’s $r_s \geq |0.7|$) the variable with the higher predictive performance in univariate models was retained. Multivariate models were then generated with the remaining set of significant variables, using a backward selection procedure until the model was reduced to twelve variables. Then, the “dredge” function (R-package MuMIn; Barton, 2012) was applied to identify the most parsimonious model from all possible combinations of the remaining variables according to Akaike’s Information Criterion (AIC) (Burnham & Anderson, 2002). In case of non-significant differences between the top-ranked candidate models (ΔAIC of ≤ 2), model averaging was applied. The models were evaluated by assessing their discrimination ability using the area under the receiver operating characteristic (ROC) curve (AUC) (R-package pROC, Robin et al., 2011) as well as their calibration, i.e. the extent to which the observed proportion of species presence equates to the model’s estimated presence probabilities (sensu Jiménez-Valverde et al., 2013).

230

231 *Variable thresholds*

Conditional Inference Trees (CIT) were used for the identification of variable thresholds explaining species presence. This method, similar to classification and regression trees, uses recursive partitioning to select significant predictor variables in a hierarchical way and to identify the best cut-off values that split the dataset so as to predict species presence and absence (Hothorn et al., 2006). It is therefore a

237 valuable tool for deriving quantitative variable thresholds for habitat management
238 (Müller & Bütler, 2010). The model starts with univariately testing for
239 independence between the response and each of the predictor variables. If this
240 hypothesis cannot be rejected, the calculation stops - otherwise the split for the
241 variable with the strongest association is applied. The procedure is recursively
242 repeated with each of the remaining subsets until no significant split is found. A
243 Bonferroni correction was used to account for multiple testing.

244 Variable thresholds were first calculated univariately for all variables that had
245 been identified as being significant in the GLMMs. The 95% confidence interval
246 of each threshold value was quantified by bootstrapping and the obtained value-
247 ranges compared to the threshold values provided by other studies.

248 Multivariate CIT were then generated to identify variable combinations and
249 threshold thereof that provide suitable structural conditions at the plot-level so as
250 to guide the management of forest stands. Based on the results, we also calculated
251 the percentage of suitable plots per grid cell (i.e. plots with a predicted probability
252 of species' presence > 0.5) to obtain information about the required proportion of
253 suitable habitat in the stand mosaic. Conditional Inference Trees were calculated
254 with the R-package party (Hothorn et al., 2011) setting the minimum sum of
255 weights for splitting (minsplit-criterion) to 100. The models' predictive
256 performance and consistency were evaluated by calculating AUC (package
257 pROC, (Robin et al., 2011)) and calibration. All statistical analyses were done
258 with the Software R (R Development Core Team 2011).

259

260 **Results**

261 **Habitat selection**

262 The important habitat variables identified for both grouse species resembled those
263 of former studies: The probability of capercaillie occurrence was best explained
264 by the following variables: The number of basal-branched trees, the cover of
265 ground vegetation, particularly of bilberry, as well as the presence of inner forest
266 edges positively influenced the occurrence probability of capercaillie, while the
267 proportion of fir and beech in the canopy layer was negatively related to species
268 presence (Table 3). The presence probability of hazel grouse was positively
269 affected by the number of basal-branched trees, the number of rowans (*Sorbus*
270 *sp.*), the bilberry cover and the proportion of herbs and ferns in the ground
271 vegetation. A high proportion of beech and deciduous trees other than feeding
272 trees (s. Table 2) in the canopy layer, as well as outer forest edges negatively
273 affected the presence probability (Table 4). With an AUC of 0.85 and 0.86 for
274 capercaillie and hazel grouse, respectively, and a consistent calibration (Fig. 2)
275 both models performed very well in predicting species presence (Hosmer &
276 Lemeshow, 2000).

277

278 Variable thresholds

279 The two target species showed a similar selection pattern for several crucial
280 habitat variables. Confidence intervals largely overlapped between species and
281 mostly encompassed the species-specific threshold values provided by other
282 studies (Table 5):

283 The canopy cover threshold for capercaillie indicated an upper limit at 81% (95%
284 confidence interval [CI] of the threshold: 60 – 83%) which was rather high
285 compared to the values of 25 – 70% obtained in other studies (Bollmann et al.,
286 2008; Bollmann et al., 2005; Lieser & Roth, 2001; Storch, 1993a). For hazel

grouse this threshold was lower with 60% (CI: 60 – 81%), but still exceeded the results of Mathys (2000)(40 – 50%).

The canopy layer on sites with capercaillie presence was composed of spruce by at least 5 % (CI: 1 - 11%) which corresponded roughly to the lower limit of 10 – 33% indicated by Suchant and Braunisch (2004). For hazel grouse, a minimum value of 10% (CI: 5-16%) was found. Furthermore, there was an upper limit for deciduous trees other than beech for both species, at 19% (CI: 12-28%) for capercaillie and 14% (CI: 0 – 18%) for hazel grouse. While these trees are rarely used as food resource and provide neither sight nor thermal protection in winter, the beech buds represent an important food resource in late winter and spring. Nevertheless, in our model both grouse species showed only little tolerance towards beech in the canopy (upper threshold of 3%) although the confidence intervals suggest that higher amounts of beech in the canopy layer are accepted.

Both grouse species required a minimum of 60% of ground vegetation cover (CI: 28 – 60% for capercaillie; 38-60% for hazel grouse) which corresponded to literature specifications (Bollmann et al., 2008; Bollmann et al., 2005; Lieser & Roth, 2001; Storch, 1993a). For the hazel grouse, herbs covering the ground ideally exceeded 18 % (CI: 13 – 38 %); slightly higher values but with a greater variance were obtained for capercaillie (38 %, CI: 0 -62%). Very low threshold values were obtained for important food resources like bilberry cover and the proportion of resource trees in the shrub and the canopy layer (1% for both species and variables). Moreover, a minimum of one rowan (≥ 3 m tall) and of one basal-branched tree was required per plot (900 m²), the former being a little lower than what Schäublin and Bollmann (2011) found for hazel grouse (2 rowans/900

311 m²). While outer forest edges were avoided, both species showed a preference for
312 inner forest edges which is in accordance with Bollmann (2006).

313

314 Complementary variable combinations

315 The multivariate CIT for capercaillie (Fig. 3A) and hazel grouse (Fig. 3B) showed
316 that suitable habitat (defined here as sites with a probability of species presence
317 $p \geq 0.5$) can be obtained by different variable combinations.

318 The multivariate tree for capercaillie provided four possible combinations of
319 explanatory variables that resulted in a probability of species occurrence greater
320 than 50% (see Fig. 3A). If, in a given plot, bilberry is available, the ground
321 vegetation cover exceeds 53%, and at least one basal-branched tree per 900m² is
322 present, the probability that capercaillie occurs is 83% (option 1). In the absence
323 of basal-branched trees this probability decreases to 68% (option 2), and with a
324 ground vegetation cover of less than 53%, the presence probability is further
325 reduced to 50% (option 3). With no bilberry present, at least three basal-branched
326 trees have to be available to obtain a 61% probability of capercaillie presence. The
327 model showed a good ability to correctly discriminate between species presence
328 and absence (AUC = 0.75).

329 To obtain a probability of hazel grouse presence of at least 50%, again four
330 possible variable combinations could be prescribed according to the multivariate
331 CIT (see Fig. 3B): if bilberry cover is present, and at least one basal-branched tree
332 is present, the probability of hazel grouse occurrence is 83% (option 1); without
333 such a tree but with bilberry cover of more than 31% there is still a 79%
334 probability that the hazel grouse occurs under such habitat conditions (option 2).
335 In sites with a lower or no bilberry cover a probability of presence of 57% will

336 still be reached (options 3 and 4). With an AUC of 0.76, this CIT showed good
337 discrimination ability

338 The probability of capercaillie occurrence was over 70% in grid cells of 1 km²
339 with sampling plots having of suitable habitat in more than 63% (CI: 0.33 - 0.91)
340 (Fig. 4A). More than 75 % (CI: 0.25 - 0.90) of the plots within a grid cell had to
341 be suitable for hazel grouse in order to increase its probability of presence from
342 30% to almost 80% (Fig. 4B).

343

344 **Discussion**

345 Similar habitat associations of the two species

346 Even if this study overall corroborates previous findings about habitat selection of
347 capercaillie and hazel grouse, it indicates less contrasting habitat associations than
348 previously established. The novelty of our research lies in the finding of
349 combinations of habitat variables that all provide acceptable if not suitable habitat
350 conditions for both grouse species. This increases the flexibility of managers in
351 developing area-specific solutions for species conservation.

352 A previously established major difference in the ecological association of the two
353 grouse species is a preference for different seral stages. While hazel grouse is
354 considered to prefer younger forests (Klaus, 1991; Mathys et al., 2006),
355 capercaillie is generally associated with old growths (Rolstad & Wegge, 1987).

356 We could not find a clear cut preference for any given successional stage, neither
357 for hazel grouse nor for capercaillie. This might be due to the fact that our study
358 sites mainly consisted of multi-aged stands without extended old growths. The
359 variable with the strongest association with capercaillie presence was bilberry
360 cover. Another important variable was ground vegetation cover, which decreases

361 as the canopy becomes denser. A well-developed field layer provides shelter
362 against predators to chick-rearing hens and food supply in the form of buds and
363 berries (e.g. *Vaccinium myrtillus*, Lakka & Kouki, 2009). When the field layer
364 was limited, basal-branched trees took over as shelter and vice versa. According
365 to Bollmann et al. (2005) and Lanz and Bollmann (2008), basal-branched Norway
366 spruce *Picea abies* typically represent the favourite resting trees for capercaillie,
367 especially when these trees are situated in forest stands with two or more aisles as
368 this eases soaring and landing (Lanz & Bollmann, 2008). Therefore it is also not
369 surprising that capercaillie preferred the presence of inner forest edges. There is a
370 trade-off, however, between woodland openness and closure due to an increased
371 predation risk when the habitat is too open, as demonstrated for other grouse
372 species (Signorell et al., 2010). Especially the hazel grouse avoided outer forest
373 edges. Edge effects typically caused by increased habitat fragmentation have been
374 shown to augment the risk of egg-predation in grouse that nest on the ground
375 (Storch, 1995b). Moreover, the hazel grouse is the poorest disperser among grouse
376 species, which renders it very vulnerable to patch isolation (Åberg et al., 1995;
377 Sahlsten, 2007): gaps larger than 150 - 250 m in diameter already represent a
378 serious obstacle to dispersal (Åberg et al., 1995; Montadert & Léonard, 2006;
379 Sahlsten, 2007). While both species' avoidance of beech-dominated stands was
380 not surprising, capercaillie presence was also negatively related to the proportion
381 of white fir (*Abies alba*). This is in contrast with previous studies demonstrating a
382 preference for this tree species, particularly as food resource in winter (e.g., Lanz
383 & Bollmann, 2008), although preferences for particular conifer species (Storch,
384 1993b) have been found to vary greatly between regions (Lanz & Bollmann,
385 2008; Lieser, 1996; Siano, 2011; Storch, 1993b). Across our study area the
386 abundance of white fir was overall low and frequently associated with beech-

dominated stands in the lower altitudes otherwise representing structurally suboptimal habitat conditions, which may explain this result. Hazel grouse has been shown to prefer mixed or coniferous stands over pure deciduous stands (Klaus, 1991; Montadert & Léonard, 2006), which is corroborated in this study. Although several deciduous trees act as important resource trees, coniferous trees in the shrub layer remain essential as they provide better sight protection from predators and enhanced thermal benefits, especially in winter (Swenson et al., 1995; Swenson & Olsson, 1991). Yet, despite explaining species presence very well, our variable set may not fully represent the two species' requirements, since large-scale habitat characteristics such as stand mosaic heterogeneity, forest gaps and linear structural elements cannot be sufficiently captured by a plot-based sampling design. Area-wide structural variables obtained from remote sensing, such as Airborne Laser Scanning, aerial or satellite images have been shown add valuable complementary information which can substantially improve the predictive performance of habitat models (Zellweger et al., 2014) and - in our case - may have revealed greater species-specific differences in habitat selection.

403

404 Variable thresholds

While the threshold-ranges obtained for most variables encompassed the values found in literature, for some relevant habitat variables our thresholds were strikingly lower. This concerns for instance the proportion of bilberry in the field layer, a feature relevant for both species. Former studies indicated 15 – 70% bilberry cover for capercaillie and 40% for hazel grouse (Baines et al., 2004; Schaublin & Bollmann, 2011), which contrasts with our > 0% for capercaillie and >1% for hazel grouse. Regional variation in both food supply and diet (i.e. the

412 availability and use of other, complementary food resources), can explain this
413 divergence. For example, in the dry Eastern part of the study area the abundance
414 of bilberry is generally low and replaced by other food items (Bollmann et al.
415 2005). Still, methodological issues cannot entirely be ruled out: Small patches
416 with locally high proportions of *Vaccinium myrtillus* may be sufficient within an
417 individual's home range, but may have been missed by our plot-based sampling.
418 Differences in variable thresholds may further result from different statistical
419 methods (Manel et al., 2001), sampling resolutions, study regions as well as
420 varying seasons (Table 5). Moreover, most of the studies were conducted within
421 small study regions with limited representativeness (Braunisch & Suchant, 2010;
422 Graf et al., 2006).

423 The effects of grain and extent upon the generality of habitat selection analyses
424 have been subject to several studies (Braunisch & Suchant, 2010; Graf et al.,
425 2006; Thuiller et al., 2004). It is widely acknowledged that increasing the spatial
426 extent of the study area generally increases the representativeness of the results
427 because one then encompasses a greater proportion of a species' distribution and
428 environmental gradient. In practice, however, the unavoidable trade-off between
429 sampling resolution and extent persists, mostly due to time constraints and limited
430 manpower. Braunisch and Suchant (2010) showed that coarse-grained data,
431 sampled over a wide representative area, outperform very precise data
432 systematically collected from a restricted, less representative region. As our data
433 was collected over three Swiss mountain ranges at a 1 km² resolution, we are
434 confident about the generality of our results despite its fairly coarse resolution. In
435 addition, particularly in highly mobile species, a coarse sampling resolution
436 matching the species-specific home ranges, can even be advantageous for

437 appraising habitat selection, as the required habitat mosaic is also be taken into
438 account (Braunisch & Suchant, 2010).

439

440 Threshold ranges

441 Some of the habitat variable thresholds have broad confidence intervals. One may
442 argue that this is merely due to the variation between plots within the 1 km² grid
443 cells, and that narrower confidence intervals would have been obtained if
444 variables would have been mapped at a higher resolution (e.g. just around bird
445 sighting location). Actually, we tested for such an effect, mapping the habitat at a
446 25 x 25 m resolution within a subregion of 1772 ha (Forest Reserve Amden,
447 Northern Prealps, 1040 m a.s.l., 47°10'N 9°13'E): similar thresholds with equally
448 broad confidence intervals were obtained (Appendix A). Therefore, our large
449 confidence intervals indicate that there is not one clear-cut quantitative threshold,
450 but rather a “threshold zone” (Huggett, 2005) that may serve for habitat
451 management. The multivariate CIT finally show how, depending on the local
452 conditions (i.e. differences in presence and abundance of other variables), a single
453 variable can exhibit different threshold values, all falling within the confidence
454 intervals obtained from univariate CIT. A good example is provided by the
455 multivariate tree for capercaillie occurrence (Fig. 3A). Here, the variable “number
456 of basal-branched trees” has two thresholds: with a higher ground vegetation
457 cover, a lower number of such trees is required, and vice versa. Both thresholds
458 typically contribute to a capercaillie presence probability greater than 50% under
459 different conditions, which delivers flexible guidance for habitat management.

460

461 Combined habitat variable sets

462 Multivariate CITs enable visualizing, under the form of a classification tree, the
463 information about the importance and interaction of different variables. It
464 therefore provides a promising user-friendly tool that can deliver pragmatic,
465 flexible quantitative management criteria to practitioners by presenting different
466 pathways for receiving a favoured goal (e.g. a probability of species presence of at
467 least 50%). The probability of species presence resulting from a specific
468 combination of habitat variables is graphically depicted by branches of the tree,
469 which facilitates interpretation (Fig. 3).

470 Yet, one drawback of conditional inference trees is that one cannot account for
471 data clustering, e.g. by including spatial random factors in the models. Although
472 our species data were recorded for 1 km² grid cells, we applied the CIT to the
473 plot-data to capture the full variety of different variable combinations within an
474 individuals' home range, without smoothing out the heterogeneity between
475 sampling plots, e.g. by averaging the variable values across the grid cell.

476 Averaging all the plot values per grid cell and calculating the thresholds from the
477 averaged values may have biased the results towards intermediate values. Hence,
478 important information about species' preferences, for instance under more
479 marginal circumstances, would have been lost. This was possible as the variance
480 between the plots of the same grid cell did not differ from those between
481 randomly chosen plots of different grid cells of the same category
482 (presence/absence). Moreover, our grid cells do not correspond to the presence of
483 a single individual but rather an area where the species occurs. The area is hosting
484 at least one but most likely several individuals, with the plots in a grid cell thus
485 representing the gradient of species-specific environmental conditions. Our dual
486 approach, using a GLMM to pre-select the important habitat variables that were
487 entered in the CIT, nevertheless accounts for spatial clustering in the first analysis

488 step, which makes us confident that the plot-based results provide a useful
489 approximation of the variable thresholds at the forest stand level.

490

491 Conclusions

492 Our approach generates complementary, interchangeable habitat variable sets and
493 variable thresholds at both the forest stand (conditions per plot) and the forest
494 mosaic (proportion of suitable habitat per grid cell) scale that all deliver suitable
495 conditions for our model species. With that we provide applicable quantitative
496 prescriptions for habitat management that allow practitioners to take the local
497 conditions into account and to find a good solution for integrating timber
498 production and biodiversity preservation and restoration in multi-functional
499 forests. Our findings revealed that the two model species have less contrasting
500 habitat requirements as expected. This could be an indicator of their behavioural
501 and ecological congruence which may allow them to exploit similar habitats and
502 greatly simplifies management in areas of sympatric occurrence. Accompanied by
503 analyses of landscape suitability at the meta-population level, which allow priority
504 areas to be delineated (Bollmann et al., 2011; Braunisch & Suchant, 2007; Graf et
505 al., 2005), the approach used here advances the development of multiple-species
506 conservation strategies.

507

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515

516 **Appendix A. Supplementary data**

517 Supplementary data associated with this article can be found, in the online
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 703 23, 289-307.

704 **Tables**

705 Table 1. The number of presence and absence grid cells (1 km²) per species, as
 706 well as the number of embedded sampling plots (30 x 30 m) (in parentheses) used
 707 for the analysis.

	Presence	Absence
Capercaillie	50 (609)	50 (526)
Hazel Grouse	72 (771)	71 (627)

708

709

Table 2. List of habitat variables with the reference area (R.area) at which they were collected: P = Plot (30 x 30 m), NS = Nested square (15 x 15 m), GV = Nested square quarters (7.5 x 7.5 m) for ground vegetation (see Fig. 1C). DBH: stem diameter at breast height, p/a: presence/absence.

Category	Variable Code	Description	Unit	R.area
Successional stage	SUCC_STAGE	Age of the forest stands subdivided into 5 age-classes: 1 = regeneration (<1.3m height) 2 = thicket (<10cm DBH) 3 = pole stage (<30cm DBH) 4 = tree stage (<60cm DBH) 5 = „old“ forest (≥ 3 tr. ≥ 60 cm DBH) 6 = multi-age stands	categorical (1-6)	P
Stand structure	STAND_STRU	Vertical structure as number of layers, 1 = one, 2 = two 3 = multi layered	categorical (1-3)	P
Ground vegetation distribution	GV_DIS	Pattern of ground vegetation: 1=homogeneous, 2=patchy, 3=clumped	categorical (1-3)	P
Vegetation cover	CAN_COV	Canopy (≥ 5 m) cover	%	P
	SHRUB_COV	Shrub (≥ 1.3 m, < 5 m) cover	%	P
	GV_COV	Ground vegetation (<1.3m) cover	%	GV
Canopy composition	CAN_BEE	Percentage of beech (<i>Fagus sylvatica</i>)	%	P
	CAN_O_DEC	Percentage of deciduous trees (excluding beech and resource trees)	%	P
	CAN_FIR	Percentage of fir (<i>Abies alba</i>)	%	P
	CAN_LAR	Percentage of larch (<i>Larix decidua</i>)	%	P
	CAN_RES_TR	Percentage of resource trees (<i>Sorbus</i> sp., <i>Salix</i> sp., <i>Betula</i> sp., <i>Alnus</i> sp., <i>Corylus</i> sp. and <i>Sambucus</i> sp.)	%	P
	CAN_SPR	Percentage of spruce (<i>Picea abies</i>)	%	P
	CAN_PIN	Percentage of pine (<i>Pinus</i> sp.)	%	P
Shrub composition	SHR_BEE	Percentage of beech	%	P
	SHR_O_DEC	Percentage of deciduous trees (excluding beech and resource trees)	%	P
	SHR_FIR	Percentage of fir	%	P
	SHR_LAR	Percentage of larch	%	P
	SHR_RES_TR	Percentage of resource trees	%	P
	SHR_SPR	Percentage of spruce	%	P
	SHR_PIN	Percentage of pine	%	P
Ground vegetation	GV_HEI	Ground vegetation height	cm	GV
	COV_CON	Cover of coniferous regeneration	%	GV
	COV_DEC	Cover of deciduous regeneration	%	GV
	COV_HERB	Cover of herbs	%	GV
	COV_FERN	Cover of ferns	%	GV
	COV_GRAS	Cover of grasses	%	GV
	COV_BER	Cover of berry plants	%	GV
	COV_VAC	Cover of bilberry (<i>Vaccinium myrtillus</i>)	%	GV
Special Ressources	ROW_TOT	Number of Rowans ≥ 3 m (<i>Sorbus aucuparia</i>)	n	NS
	ANT_HILL	Number of ant hills	n	NS

Functional trees	BB_TREE	Basal-branched trees	n	P
Ecotones	E1	Presence/absence of inner forest edge	p/a	P
	E2	Presence/absence of outer forest edge	p/a	P

714

715

Table 3. Habitat variables explaining the presence of capercaillie, obtained from a Generalized Linear Mixed Model (GLMM) with “grid cell-pair” as random factor. Variable estimates, as obtained from averaging the four best models according to the AIC-ranking, are presented and the relative variable importance is provided in parentheses. The composition and ranking of the included models is specified in the lower part of the table. Asterisks indicate significance levels with *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, n.s. = non-significant. Variable codes are explained in Table 2.

No.	Variables (fixed effects)	Estimate	SE	Sign.
1	BB_TREE (1)	0.158	0.041	***
2	CAN_BEE (1)	-0.029	0.009	***
3	CAN_FIR (1)	-0.030	0.012	*
4	COV_HERB (0.81)	0.011	0.006	n.s.
5	COV_VAC (1)	0.045	0.008	***
6	E1 (1)	0.760	0.347	*
7	E2 (0.81)	-0.613	0.326	n.s.
8	GV_COV (1)	0.012	0.005	*
9	ROW_TOT (0.78)	0.056	0.033	n.s.
Grouping factor (random effect)		Variance	CI	
1	Pair_ID (Intercept)	1.933	1.339-3.032	
Rank	Incl. Variables (No.)	AICc	ΔAICc	ΔAICc weight
1	1/2/3/4/5/6/7/8/9	941.59	0	0.39
2	1/2/3/4/5/6/7/8	942.73	1.14	0.22
3	1/2/3/5/6/7/8/9	943	1.41	0.19
4	1/2/3/4/5/6/8/9	943.05	1.46	0.19

726 Table 4. Habitat variables explaining the presence of hazel grouse, obtained from
727 a Generalized Linear Mixed Model (GLMM) with “grid cell-pair” as random
728 factor. Variable estimates, as obtained from averaging the four best models
729 according to the AIC-ranking, are presented and the relative variable importance
730 is provided in parentheses. The composition and ranking of the included models is
731 specified in the lower part of the table. Asterisks indicate significance levels with
732 *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, n.s. = non-significant. Variable codes are
733 explained in Table 2.

	Variable	Estimate	SE	Sign.
1	BB_TREE (1)	0.268	0.047	***
2	CAN_BEE (1)	-0.023	0.006	***
3	CAN_O_DEC (1)	-0.032	0.012	**
4	COV_DEC (1)	-0.031	0.011	**
5	COV_FERN (1)	0.023	0.009	*
6	COV_HERB (1)	0.022	0.005	***
7	COV_VAC (1)	0.044	0.006	***
8	E2 (1)	-0.911	0.271	***
9	ROW_TOT (1)	0.099	0.035	**
10	SHR_O_DEC (1)	-0.053	0.019	**
11	SHR_RES_TR (0.68)	0.022	0.012	n.s.
<hr/>				
Grouping factor (random effect)		Variance	CI	
	Pair_ID	1.554	1.398-2.243	
Rank	Incl. Variables (No.)	AICc	ΔAICc	ΔAICc weight
1	1/2/3/4/5/6/7/8/9/10/11	1267.78	0	0.68
2	1/2/3/4/5/6/7/8/9/10	1269.28	1.5	0.32

734 Table 5. Thresholds for the variables significantly explaining the occurrence of
735 each of the two model species (see Table 3 and 4), calculated using univariate
736 Conditional Inference Trees (CIT) and compared to thresholds (indicated by </>)
737 and optimal variable ranges found in literature. n.s. = no significant split.

Explanatory variable	Thresholds		Literature ^{1,2}	
	<u>Capercaillie</u>	<u>Hazel grouse</u>	<u>Capercaillie</u>	<u>Hazel grouse</u>
n(presence/absence)	n(800/593)	n(477/667)		
CAN_COV (%)	≤81 (60-83)	≤60 (60-81)	25-65 [1] 40-60 [2] 50 [3] <60 [5] 50-70 [6]	40-50 [4]
CAN_SPR (%)	>5 (1-11)	>10 (5-16)	10-33 [6]	
CAN_FIR (%)	≤24 (3-33)	≤10 (1-33)		
CAN_BEE (%)	≤3 (2-26)	≤3(0-11)		
CAN_O_DEC (%)	≤19 (12-28)	≤14 (0-28)		
CAN_RES_TR (%)	>1(0-2)	>1 (0-5)		
SHRUB_COV (%)	n.s.	≤26 (15-40)		
SHR_RES_TR (%)	n.s.	>0 (0-2)		>10 [5]
SHR_O_DEC (%)	n.s.	≤6 (3-18)		
GV_COV (%)	>60 (28-60)	>60 (38-60)	>40 [6] 50-70 [7] >60 [5] [1] >70 [2] 90-100 [3]	30-45 [5] 60-100 [4]
COV_VAC (%)	>0 (0-3)	> 1 (0-1)	15-20 or more [8] >20 [5] ≥60 [10] >70-100 [7]	40 (+4) [11]
COV_HERB (%)	>38 (0-62)	>18 (13-38)		
COV_GRAS (%)	n.s.	>3 (1-17)		
COV_DEC (%)	n.s.	≤13 (8-25)		
ROW_TOT (no./900m ²)	>0 (0-2)	>0 (0-1)		2/900m ² [11]
BB_TREE (no./900m ²)	>0 (0-1)	>0 (0-5)		
E1 (0;1)	=1	=1	The more the better [9]	
E2 (0;1)	=0	=0		

¹**References:** [1] Bollmann et al. 2005, [2] Bollmann et al. 2008, [3] Storch, I. 1993, [4] Mathys et al. 2006, [5] Lieser and Roth 2001, [6] Suchant and Braunisch 2004, [7] Ehrbahr et al. 2011, [8] Baines et al. 2004, [9] Bollmann, K. 2006, [10] Müller, F. 1973, [11] Schäublin & Bollmann 2011

²**Season and spatial scale of the studies:** [1] spring, 25x25m plots; [2] winter&summer 25x25m; [3] plot with r=10m; [4] autumn, 0.8ha; [5] forest stand scale; [6] summer & winter, forest stand scale (1-50ha); [7] forest stand scale; [8] forest stand scale; [9] summer, Scotland, 64m²; [10] area not specified; [11] winter, 25x25m

738 **Figure captions**

739 Fig. 1. Sampling design. Distribution of presence grid cells (black: capercaillie
740 presence, white: hazel grouse presence and dark grey: sympatric occurrence)
741 within three biogeographic mountain regions (highlighted in grey) of Switzerland:
742 Jura mountains (JM), Northern Prealps (NPA) and Inner Alps (IA) (A). For each
743 presence grid cell, an absence grid cell (not depicted on this map) was selected
744 within 1 - 4 km distance. In each grid cell, habitat variables were collected in
745 every sampling plot which was located in the forest (maximum 16 per grid cell)
746 (B). In a sampling plot, variables were collected at different reference areas (C):
747 within the entire 30 x 30 m plot, within a nested square (15 x 15 m) (white) or
748 within the two diagonal quarters of the nested square (7.5 x 7.5 m). The variables,
749 their unit and corresponding reference area for sampling are listed in Table 2.

750

751 Fig. 2. Model evaluation: Calibration plot showing the modelled probabilities of
752 species presence (x-axis) against the observed proportion of presence points (y-
753 axis) for 10 equal-sized probability intervals. Open symbols: capercaillie, filled
754 symbols: hazel grouse, squares: Generalized linear mixed models (GLMM),
755 triangles: conditional inference trees (CIT), solid line: perfect calibration. As a
756 classification method, CIT returns probability classes instead of continuous
757 probability values. Consequently, the bins with values correspond to the
758 probability classes shown in Figs 3A and B. In addition, the AUC-values of the
759 corresponding models are indicated.

760

761 Fig. 3. Multivariate Conditional Inference Trees (CIT) (minsplit=100) explaining
762 the presence of (A) capercaillie and (B) hazel grouse. The columns at the end of
763 each branch illustrate the probabilities of species presence (values from 0 to 1 are

764 given on the right side of each bar) resulting from a specific variable combination.

765 Abbreviations of the habitat variables are explained in Table 2.

766

767 Fig. 4. CIT (minsplit = 10) depicting the thresholds for the proportion of suitable

768 habitat (i.e. proportion of plots with a probability of presence ≥ 0.5) per grid cell

769 explaining the presence of (A) capercaillie and (B) hazel grouse, respectively.

770 Presence probabilities (dark grey) are given in values from 0 to 1. The 95%

771 confidence intervals (CI) of the threshold values based on 1000 bootstrap

772 replicates are as follows: (A) CI: 0.33- 0.91 and (B) CI: 0.25 - 0.90).

773

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