

UNIVERSITÄT BERN

**Identifying combined sets of crucial habitat
variables and providing quantitative
thresholds for flexible wildlife habitat
management in forest ecosystems**

Masterarbeit der Philosophisch-naturwissenschaftlichen
Fakultät der Universität Bern

vorgelegt von

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2013

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Identifying combined sets of crucial, site-specific habitat variables and providing quantitative thresholds for flexible wildlife habitat management in forest ecosystems

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Key words: *Bonasa bonasia*, Conditional Inference Tree, complementary habitat variables, Swiss mountain forests, *Tetrao urogallus*, thresholds

Abstract

1 1. In the human-dominated landscapes of Central Europe, where
2 wildlife habitat has become scarce, sustainable biodiversity
3 conservation requires quantitative management prescriptions for
4 ensuring habitats for wildlife that are of sufficient extension and
5 quality. Yet, the possibility to meet these prescriptions depends on
6 habitat patch conditions, notably its initial state and predicted future
7 trajectory. In forests, where succession is typically slow and
8 commercial management affects species assemblage and dynamics,
9 stand conditions vary greatly and not all stands can be readily
10 converted into a particular state, which calls for pragmatic, flexible
11 management prescriptions.

12 2. Using the example of two forest grouse species, the capercaillie and
13 the hazel grouse, we sought different combinations of habitat variables
14 – with quantitative thresholds for any given crucial habitat feature –
15 which would likewise offer suitable habitat. For that purpose, habitat
16 variables were mapped within occupied and non-occupied 1 km² grid
17 cells distributed across three Swiss mountain regions: the Jura
18 Mountains, the Northern Prealps and the Inner Alps. Habitat selection
19 was analysed using Generalized Linear Mixed Models and Conditional
20 Inference Trees (CIT) were used to identify combinations of habitat
21 variables providing suitable conditions and to estimate quantitative
22 thresholds for crucial habitat features.

23 3. Important resources for both species were the proportion of bilberry
24 in the field layer and the number of basal-branched trees, as well as
25 the absence of outer forest edges. Hazel grouse additionally favoured a
26 high proportion of feeding trees in the shrub layer, particularly rowans

27 (*Sorbus aucuparia*), and a high percentage of herbs in the ground
28 vegetation layer. For capercaillie, patchily distributed ground
29 vegetation, indirectly reflecting forest canopy cover and heterogeneity,
30 was also very important.

31 4. Quantitative thresholds for habitat features where not clear-cut:
32 multivariate CIT furthermore yielded different thresholds depending on
33 the conditions of other, complementary habitat variables present at
34 the site.

35 5. CIT not only delivers primary information about the relevance of a
36 given habitat variable and variables interaction, which eases
37 interpretation, it also provides different option sets for flexible
38 management prescriptions.

39 **326 words**

40

41 **Introduction**

42 In the human-dominated landscapes of Central Europe, where the area
43 available for wildlife is nowadays limited, conservation management
44 needs quantitative and spatially explicit prescriptions for biodiversity
45 preservation and restoration. This is particularly challenging when the
46 requirements of different species with diverging ecological needs have
47 to be met within the same area. Forests are commercially used
48 ecosystems, characterized by a slow vegetation succession. Forest
49 stand composition and structure thus differ greatly depending on the
50 local environmental conditions and mode of exploitation, and provide
51 different framework conditions for habitat management. In addition
52 the possibilities for habitat management are constrained by the
53 objectives of commercial forestry, which may interfere with habitat
54 management goals, notably biodiversity preservation. Achieving the
55 multiple functionalities of forests through adaptive management
56 remains a big challenge. While trees can easily be removed, e.g. to
57 alter light conditions and promote ground vegetation, other factors
58 such as tree species composition, stand structure or age can only be
59 modified within long timeframes, and in strict consideration of the local
60 site conditions. In such relatively inert ecosystems, quantitative,
61 flexible management prescriptions are required that maximize habitat
62 suitability for target species, accounting for the natural forest
63 dynamics and local environmental constraints, while maintaining
64 exploitation potential. Species rarely require similar habitat conditions
65 throughout their range, but avail of a mosaic of different habitat
66 features and resources that offer complementary functionalities, such
67 as food supply, cover against predators, roosting or breeding sites.

68 Thereby, different habitat features may be interchangeable across a
69 species' home range. Identifying such sets of complementary variables
70 is thus a key for instating pragmatic, flexible habitat management for
71 wide-range species preservation.

72 The hazel grouse (*Bonasa bonasia*) and the capercaillie (*Tetrao*
73 *urogallus*) are two often sympatrically occurring forest grouse species
74 which are of conservation concern in Europe (Storch 2000). Being
75 considered as indicators for structural diversity of boreal and mountain
76 forest ecosystems, they have suffered from habitat loss and
77 degradation during the last century mainly due to changes in forest
78 management (Klaus 1991). Qualitative habitat requirements for these
79 two tetraonids are well described (e.g. Glutz von Blotzheim 1973,
80 Müller 1973), and quantitative management prescriptions for particular
81 habitat features have been provided (Sachot et al. 2003, Braunisch &
82 Suchant 2004, Müller et al. 2009, Schäublin & Bollmann 2011),
83 however, they vary considerably between studies and areas (Bollmann
84 et al. 2008).

85 The capercaillie is declining throughout its European distribution range
86 (Storch 2007), being classified as "endangered" in Switzerland (Keller
87 et al. 2010) where the number of cocks was estimated between 450
88 and 500 in 2001 (half the size of the population in 1968/71; Müller
89 1973; Mollet et al. 2003). Capercaillie prefers mature, open, coniferous
90 or conifer-dominated mixed stands with an intermediate canopy cover
91 (50-70%, Suchant & Braunisch 2004; 25-65%, Bollmann et al. 2005)
92 and a rich ground vegetation cover, ideally including a high proportion
93 of bilberry (Storch 1993). The species is highly sensitive to human
94 disturbance (Thiel et al. 2008). It is also considered to be an indicator

95 for structural diversity in boreal and mountain forests, and plays the
96 role of an umbrella species for some associated animal communities
97 (Suter et al. 2002, Pakkala et al. 2003).

98 The hazel grouse is a territorial forest bird which requires semi-natural
99 forests with young seral stages and old-growth stands with gaps
100 (Sachot 2003). In the year 2001, 7500-9000 breeding pairs were
101 estimated for Switzerland (Maumary et al. 2007). The hazel grouse is
102 not threatened in Europe (IUCN 2012), however it is considered to be
103 "near threatened" in Switzerland (Keller et al. 2010).

104 Probably due to major differences in body size and mating system,
105 home range [30-40 vs 100-1000 ha for hazel grouse and capercaillie,
106 respectively (Blattner & Perrenoud 2001; Storch 1995)] and habitat
107 preferences (in terms of forest structure and stand density) diverge
108 between the two focal species. Distinct winter feeding habits also lead
109 to discrepancies between the trophic niches, especially as regards
110 resource trees. Local sympatric occurrence might lay in a patchy
111 distribution of suitable hazel grouse habitat being embedded within a
112 suitable capercaillie habitat matrix.

113 In this study we analyse the habitat requirements of the two species
114 from a novel perspective: using multivariate classification and
115 regression trees, we seek for different combinations of habitat
116 variables as well as quantitative thresholds thereof that similarly
117 promote species presence at the forest stand scale. In this context we
118 explore if and to what extent the required amount of one habitat
119 variable depends on the presence and quantity of another,
120 complementary habitat feature. Since both species are indicators for
121 structural diversity, with partially diverging requirements, we consider

122 them as ideal model organisms for testing the applicability of these
123 methods to conservation management of sympatric species. The
124 quantitative prescriptions drawn for our analyses also provide refined
125 guidance for a flexible management and restoration of suitable forests
126 for these two declining tetraonoids.

127

128 **Material & Methods**

129 Study area

130 The study was conducted in Switzerland, with the study sites
131 distributed across three mountain ranges representing a broad
132 gradient of bioclimatic conditions: the Jura Mountains (47°00' N 6°40'
133 E - 47°30' N 8°00' E), Northern Prealps (46°30' N 7°15' E - 47°00' N
134 9°30' E) and Inner Alps (46°30' N 9°00' E - 47°00' N 10°30' E) (Fig.
135 1A). The Jura Mountains are characterized by a moderate climate with
136 mild, damp summers and cold winters (MeteoSchweiz 2013). The
137 mean annual ambient temperature is 5.5°C with 180 frost days and,
138 on average, 2000 mm of rain and 4 m of snow annually at an altitude
139 of 1200 m (MeteoSchweiz 2013). The tree line is around 1400 m a.s.l.
140 (Steiger 1994). The Northern Prealps are characterized by an Atlantic
141 climate with high precipitation (2000-3000 mm/yr), cold-temperate
142 winters and wet summers (MeteoSchweiz 2013). The tree line is at an
143 elevation of approximately 2000 m (Steiger 1994). The open and
144 diversely structured forests are often adjacent to pastures and
145 interspersed with mires. In the Inner Alps, the prevailing climate
146 conditions are continental, with low precipitation (800-2000mm/yr),
147 cold winters and warm and dry summers (MeteoSchweiz 2013). Large,
148 continuous forests belts are found along the valley slopes with the tree

149 line being located ca. at 2300m a.s.l. (Steiger 1994). The altitudinal-
150 climatic gradient is also reflected in the tree species composition,
151 consisting of European beech (*Fagus sylvatica*), silver fir (*Abies alba*)
152 and Norway spruce (*Picea abies*) in the montane zone with larger
153 proportions of larch (*Larix decidua*) and Swiss stone pine (*Pinus*
154 *cembra*) present in the most continental conditions of the subalpine
155 zone.

156

157 Species data

158 The presence data of the two focal species were drawn from the
159 database of the Swiss Ornithological Institute, which compiles
160 observations made by volunteers at a spatial resolution of 1 km²,
161 corresponding to the Swiss National Grid. This cell size also
162 corresponds to the average size of a capercaillie home range and to
163 the double or triple of the home range of a hazel grouse.

164 A pairwise sampling scheme was applied, selecting pairs of grid cells
165 with species presence or absence (Table 1). Presence grid cells were
166 chosen according to the following selection criteria: (1) there were at
167 least three observations of the species within the years 2007 – 2010,
168 (2) the sample contained different type of cells, namely cells with both
169 single and sympatric occurrence of the two species, (3) the grid cells
170 were distributed as evenly as possible within the respective study area
171 and along the altitudinal gradient (Fig. 1A). Absence grid cells with a
172 forest cover of at least 50% were randomly placed within 1 km up to
173 maximum 4 km distance to the corresponding presence cells to make
174 sure that they could potentially be reached by the species. Although
175 absence cells were only selected when there were no species records

176 (indirect or direct) within the last 10 years, species presence could not
177 be entirely ruled out, so that absence grid cells were in fact pseudo-
178 absences. Yet, for reasons of simplicity they are referred to as
179 "absence" here.

180

181 Habitat variables

182 Habitat variables were collected from June to August 2011 at 16
183 sampling plots of 30 x 30 m in size, regularly distributed within each
184 grid cell (Fig. 1B,C, Table 1) and included information on stand
185 structure, age, tree species composition, ground vegetation and
186 species-specific habitat features (Table 2). For a matter of precision,
187 the habitat variables were mapped on different reference areas within
188 the sampling plot. Whereas variables describing stand structure and
189 tree species composition in the canopy (≥ 5 m) and shrub layer (≥ 1.3
190 and < 5 m) were collected across the whole plot area, special
191 resources like rowans (*Sorbus aucuparia*) and anthills were quantified
192 within a 15 x 15 m nested square located around the plot center (Fig.
193 1C), the two diagonal corners of which were used to assess the ground
194 vegetation.

195

196 Statistics

197 *Habitat selection*

198 Habitat selection was analysed using Generalized Linear Mixed Models
199 (GLMMs) with a binomial error distribution and "grid cell pair" as
200 random factor. First, univariate models were run with all potentially
201 relevant variables. From pairs of correlated explanatory variables
202 (Spearman's $|r_s| \geq 0.7$) the variable with the higher predictive

203 performance in univariate models was retained (Fielding & Haworth
204 1995). Multivariate models were then generated with the remaining
205 set of significant variables, using a backward selection procedure until
206 the model was reduced to twelve variables. Then, the "dredge"
207 function (R-package MuMIn (Barton 2012)) was applied to identify the
208 best model from all possible combinations of the remaining variables
209 according to Akaike's Information Criterion (AIC) (Hurvich & Tsai
210 1989). In case of non-significant differences between the top-ranked
211 candidate models (ΔAIC of ≤ 2), model averaging was applied. Model
212 fit was evaluated by calculating the area under the receiver operating
213 characteristic (ROC) curve (AUC) using the R-package pROC (Robin et
214 al. 2012).

215

216 *Variable thresholds*

217 Conditional Inference Trees (CIT) were used for the identification of
218 variable thresholds explaining species presence. This method, similar
219 to classification and regression trees, uses recursive partitioning to
220 select significant predictor variables in a hierarchical way and to identify
221 the best cut-off values that split the dataset so as to predict species
222 presence and absence (Hothorn et al. 2006), and is therefore a
223 valuable tool for deriving quantitative variable thresholds for habitat
224 management (Müller & Bütler 2010). The model starts with
225 univariately testing for independence between the response and each
226 of the predictor variables. If this hypothesis cannot be rejected, the
227 calculation stops - otherwise the split for the variable with the
228 strongest association is applied. The procedure is recursively repeated

229 with each of the remaining subsets until no significant split is found. A
230 Bonferroni correction was used to account for multiple testing.

231 Although our species data were recorded for 1 km² grid cells, we
232 applied the CIT to the plot-data to capture the full variety of different
233 variable combinations within an individuals' home range, without
234 smoothing out the heterogeneity between sampling plots, e.g. by
235 averaging the variable values across the grid cell. This was possible as
236 the variance between the plots of the same grid cell did not differ from
237 those between randomly chosen plots of different grid cells of the
238 same category (presence/absence).

239 Variable thresholds were first calculated univariately for all variables
240 that had been identified as being significant in the GLMMs. The 95 %
241 confidence interval of each threshold value was quantified by
242 bootstrapping and the obtained value-ranges compared to the results
243 of other studies.

244 Multivariate CIT were then generated to identify variable combinations
245 and threshold thereof that provide suitable structural conditions at the
246 plot-level so as to guide the management of forest stands. The model
247 fit was evaluated by means of the AUC (package pROC, Robin et al.
248 2012). Based on the results, we also calculated the percentage of
249 suitable plots per grid cell (i.e. plots with a predicted probability of
250 species' presence > 0.5) to obtain information about the required
251 proportion of suitable habitat in the stand mosaic. Conditional
252 Inference Trees were calculated with the R-package party (Hothorn et
253 al. 2011) setting the minimum sum of weights for splitting (minsplit-
254 criterion) to 100. All statistical analyses were done with the Software R
255 (R Development Core Team 2011).

256

257 **Results**

258 Habitat selection

259 The probability of capercaillie occurrence, as identified with the
260 GLMMs, was explained by the following variables: The number of
261 basal-branched trees, the proportion of spruce in the canopy, the
262 cover of bilberry, the number of rowans and the quantity of pine in the
263 shrub layer, the ground vegetation cover and its patchy distribution
264 (not too small grained), as well as the proportion of herbs covering the
265 ground positively influenced the occurrence probability of capercaillie,
266 while the presence of outer forest edges had a negative effect (Table
267 3). According to the classification of Hosmer & Lemeshaw (2004), the
268 model had a good discrimination ability with an AUC of 0.76.

269 The presence probability of hazel grouse was positively affected by the
270 number of basal-branched trees, proportion of herbs covering the
271 ground, a patchily, but not too fine-grained ground vegetation
272 distribution, the number of rowans, the fraction of resource trees [i.e.
273 rowan (*Sorbus* sp.), willow (*Salix* sp.), birch (*Betula* sp.), alder (*Alnus*
274 sp.), hazel (*Corylus* sp.) and elder (*Sambucus* sp.)] in the shrub layer,
275 the bilberry cover and the amount of ferns in the ground vegetation.
276 As in the case of capercaillie, outer forest edges were avoided by hazel
277 grouse. With an AUC of 0.733 the model also showed a good
278 discrimination ability (Table 4).

279

280 Variable thresholds

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

285 The canopy cover threshold for capercaillie indicated an upper limit at
286 81 % (95 % confidence interval [CI] of the threshold: 60 – 83 %)
287 which was rather high compared to the values of 50 – 70 % obtained
288 in other studies (Storch 1993, Lieser & Roth 2001, Bollmann et al.
289 2005, Bollmann et al. 2008). For hazel grouse this threshold was a
290 little lower with 59 % (CI: 56 – 79 %), but still exceeded the results of
291 Mathys et al. 2006 (40 – 50 %).

292 The canopy layer in sites with capercaillie presence, was at least to
293 7 % (CI: 1 - 11%) composed of spruce which corresponded roughly to
294 the lower limit of 10 – 33% indicated by Suchant & Braunisch 2004.
295 Further, a maximum of 30 % (CI: 1 – 38 %) deciduous regeneration
296 appeared to be tolerated, while there was an upper limit for deciduous
297 trees other than beech both in the shrub (6 %, CI: 0 – 18 %) and in
298 the canopy layer (23 %, CI: 13 – 28 %). While these trees can rarely
299 be used as food resource and provide neither sight nor thermal
300 protection in winter, the beech buds represent an important food
301 resource in late winter. Nevertheless, in our model capercaillie showed
302 only little tolerance towards beech in the canopy compared to the
303 hazel grouse: the upper limit of 3 % (CI: 1 – 4 %) was ca ten times
304 lower than the one for the hazel grouse (33.75 %, CI: 3 – 73 %).

305 Furthermore, according to the confidence interval, it seems that hazel
306 grouse may accept an even higher amount of beech in the canopy
307 layer.

308 Capercaillie required a minimum of 60 % (CI: 28 – 60 %) of ground
309 vegetation cover, the threshold for the hazel grouse was within the
310 same range (CI: 25 - 60%) but with a lower mean (40 %) and
311 corresponded to what is found in literature (Storch 1993, Lieser & Roth
312 2001, Bollmann et al. 2005, Mathys et al. 2006, Bollmann et al. 2008,
313 Ehrbar et al. 2011). Both species also preferred patchily distributed
314 ground vegetation over a homogenous or strongly clumped ground
315 vegetation pattern. Ground vegetation height, not less than 7 cm (CI:
316 5 - 20 cm), was only found important for hazel grouse, whereas other
317 studies also give recommendations for capercaillie (30 – 50 cm
318 (Bollmann 2006) and < 40 cm (Storch 1993). For the hazel grouse,
319 herbs covering the ground ideally exceeded 25 % (CI: 3 – 53 %);
320 similar values were obtained for capercaillie (20 %, CI: 8 -53 %). Very
321 low threshold values were obtained for important food resources like
322 bilberry cover (1 % for both species, CI: 0 – 3 %) and the proportion
323 of resource trees in the shrub and the canopy layer (only significant for
324 hazel grouse: > 0 % (CI: 0 – 2 %, shrub) and > 1% (CI: 0 – 2 %,
325 canopy). Moreover, for both species a minimum of one rowan (≥ 3 m
326 tall) and of one basal-branched tree was required per plot (900 m²),
327 the former being a little lower than what Schäublin & Bollmann (2011)
328 found for hazel grouse (2 rowans/900 m²). While outer forest edges
329 were avoided by both species, capercaillie showed a preference for
330 inner forest edges which is in accordance with Bollmann (2006).

331

332 Complementary variable combinations

333 The multivariate CIT for capercaillie (Fig. 2A) and hazel grouse (Fig.
334 2B) showed that suitable habitat (defined here as sites with a

335 probability of species presence $p \geq 0.5$) can be obtained by different
336 variable combinations.

337 The multivariate tree for capercaillie provided three possible
338 combinations of explanatory variables if aiming at a probability of
339 species occurrence greater than 50 % (see Fig. 2A). If, in a given plot,
340 the ground vegetation cover is higher than 60 %, while the proportion
341 of bilberry covering the ground exceeds 0, and there is no outer forest
342 edge but a patchily distributed ground vegetation, then the probability
343 that capercaillie occurs is nearly 100 % (option 1). If the other
344 conditions remain the same, but the distribution of ground vegetation
345 is homogeneous or very coarsely clumped, the presence probability is
346 still above 50 % (option 2). Assuming less than 60 % of the ground is
347 covered with vegetation but there is at least one basal-branched tree
348 in a plot to provide cover, then the expected presence probability is
349 almost 60 % (option 3). The model showed a moderate fit (AUC =
350 0.65, Hosmer & Lemeshow 2004).

351 To obtain a probability of hazel grouse presence of at least 50 %, six
352 possible variable combinations could be prescribed according to the
353 multivariate CIT (see Fig. 2B): if bilberry cover is greater than 0.5 %,
354 plus the percentage of resource trees in the shrub is higher than 1.6 %,
355 and more than two basal-branched trees are present, then the
356 probability of hazel grouse occurrence is 80 % (option 1); with two or
357 less basal-branched trees the probability decreases to nearly 70 %
358 (option 2). In sites with a proportion of resource trees less than 1.6 %,
359 but a cover of herbs exceeding 53 %, a probability of presence of 80
360 % will also be reached, at least in the absence of forest edge (option
361 3). Where bilberry cover is absent, but the proportion of resource trees

362 in the shrub layer is more than 32 %, the likelihood that the hazel
363 grouse occurs is 100 % (option 4). If the fraction of shrub resource
364 trees is 32 % or less, at least two fructifying rowans are required to
365 maintain a 50 % chance that the hazel grouse is present (option 5). A
366 similar probability is obtained in plots without resource trees, but more
367 than four basal-branched trees present (option 6). With an AUC value
368 of 0.71, this CIT showed a good discrimination ability
369 With more than 55 % (CI: 0.50 - 0.75) of sampling plots with suitable
370 habitat per 1 km² the probability of capercaillie occurrence was nearly
371 90 % (Fig. 3A). More than 42 % (CI: 0.25 - 0.71) of the plots within a
372 grid cell had to be suitable for hazel grouse in order to increase its
373 probability of presence from 40 % to 65 % (Fig. 3B).

374

375 **Discussion**

376 Habitat selection

377 If this study overall corroborates previous qualitative and quantitative
378 findings about habitat selection by capercaillie and hazel grouse, it
379 indicates much more similar ecological requirements than previously
380 established. Capercaillie, however, shows more specific habitat
381 requirements than hazel grouse. The originality of our research lies in
382 that we found several combinations of habitat variables that all provide
383 acceptable if not suitable habitat conditions for these two grouse. This
384 provides the necessary flexibility for conservation management.

385 A previously established major ecological difference between the two
386 grouse species is a preference for different vegetation successional
387 stages. While hazel grouse prefer younger forests (11 - 40 years)

388 (Klaus 1991), capercaillie prefer old growths (60 - 70 yrs) (Rolstad &
389 Wegge 1987). Neither for hazel grouse nor for capercaillie could we
390 find a clear cut preference for any given successional stage, which
391 might be due to the fact that our study sites mainly consisted of multi-
392 aged stands without extended old growths. The variable which had the
393 strongest association with the presence probability of capercaillie was
394 ground vegetation cover, which decreases as the canopy becomes
395 denser. A dense field layer provides shelter against predators to chick-
396 rearing hens and food supply in the form of berries (e.g. *Vaccinium*
397 *myrtillus*; Lakka & Kouki 2009). Both species furthermore show a
398 preference for a patchy ground vegetation cover, however, because
399 horizontal heterogeneity offers a fine-grained mosaic that is crucial for
400 chick development, providing both rich food supplies and drier
401 conditions under adverse weather. When the field layer was limited,
402 basal-branched trees took over as shelter. According to Bollmann et al.
403 (2005) and Lanz & Bollmann (2008), basal-branched Norway spruce
404 *Picea abies* typically represent the favourite resting trees for
405 capercaillie, especially when these trees are situated in forest stands
406 with two or more aisles as this eases soaring and landing (Lanz &
407 Bollmann 2008). There is a trade-off, however, between woodland
408 openness and closure due to an increased predation risk when the
409 habitat is too open, as demonstrated for other grouse species
410 (Signorell et al. 2010). Capercaillie also avoided outer forest edges, as
411 already demonstrated by Braunisch & Suchant (2007), and we found
412 the same for hazel grouse. Edge effects typically caused by increased
413 habitat fragmentation have been shown to augment the risk of egg-
414 predation in grouse that nest on the ground (Storch et al. 2005).

415 Moreover, the hazel grouse is the poorest disperser among the grouse,
416 which renders it very vulnerable to patch isolation (Aberg et al. 1995,
417 Sahlsten 2007): gaps larger than 150 - 250 m already represent a
418 serious obstacle to dispersal (Aberg et al. 1995, Sahlsten 2007;
419 Montadert & Léonard 2006). Hazel grouse has been shown to prefer
420 mixed or coniferous stands over pure deciduous stands (Klaus 1991,
421 Montadert & Léonard 2011), which is corroborated in this study.
422 Although several deciduous trees act as important resource trees,
423 coniferous trees in the shrub layer remain essential as they provide
424 better sight protection from predators and enhanced thermal benefits,
425 especially in winter (Swenson and Olsson 1991; Swenson, Andreev &
426 Drovetski 1995). Our results further reveal that an even small
427 proportion of resource trees in a plot is not an issue, at least as long as
428 other crucial food resources (e.g. herbs in the ground layer) are
429 present. This is good news for conservation management.

430

431 Variable thresholds

432 The quantitative thresholds we obtained for some relevant habitat
433 variables were in general strikingly lower than in other studies. This
434 concerns for instance the proportion of bilberry in the field layer, a
435 feature relevant for both species, as well as the quantity of resource
436 trees for hazel grouse. Former studies indicate 40 % and 15 – 70 %
437 bilberry cover for hazel grouse and capercaillie, respectively (Schäublin
438 & Bollmann 2011; Baines et al. 2004; Ehrbar et al. 2011), which
439 contrasts with our > 1 % for each species. Although regional variation
440 in both food supply and diet can explain this divergence (e.g. in the
441 dry Eastern part of the study area the abundance of bilberry is

442 generally low and replaced by other food items Bollmann et al. 2005)
443 methodological issues may also play a role: Small patches with locally
444 high proportions of *Vaccinium myrtillus* may be sufficient within an
445 individual's home range, but may have been missed by our plot-based
446 sampling. The variable thresholds for the two target species vary
447 greatly between studies, as resulting from different statistical methods
448 (Manel 2001), sampling resolutions, study regions as well as varying
449 seasons (Table 5). Moreover, most of the studies were conducted
450 within small study regions with limited representativeness (Graf 2006,
451 Braunisch 2010).

452 The effects of grain and extent upon the generality of habitat selection
453 analyses have been subject to several studies (Thuiller 2004, Graf et
454 al. 2006, Braunisch & Suchant 2010). It is widely acknowledged that
455 increasing the spatial extent of the study area generally increases the
456 representativeness of the results because one then encompasses a
457 greater proportion of a species' distribution and environmental
458 gradient. In practice, however, persists the unavoidable trade-off
459 between sampling resolution and extent, mostly due to time
460 constraints and limited manpower. Braunisch & Suchant (2010)
461 showed that coarse-grained data, sampled over a wide representative
462 area, outperform very precise data systematically collected from a
463 restricted, less representative region. As our data was collected over
464 three Swiss mountain ranges at a 1 km² resolution, we are confident
465 about the generality of our results despite its fairly coarse resolution.
466 In addition, particularly in highly mobile species a coarse sampling
467 resolution matching the species-specific home ranges, can even be

468 advantageous for appraising habitat selection, as the required habitat
469 mosaic is also be taken into account (Braunisch & Suchant 2010).

470

471 Threshold zones

472 Our quantitative habitat variable thresholds have broad confidence
473 intervals. One may argue that this is merely due to the variation
474 between plots within the 1 km² grid cells, and that narrower confidence
475 intervals would have been obtained if variables would have been
476 mapped at a higher resolution (e.g. just around bird sighting location).
477 Actually, we tested for such an effect, mapping the habitat at a
478 25 x 25 m resolution within a small subregion of 1772 ha (Northern
479 Prealps, Amden Forest Reserve, 1040 m a.s.l., 47°10'N 9°13'E):
480 similar thresholds with equally broad confidence intervals were
481 obtained (Appendix 1). Therefore, our large confidence intervals
482 indicate that there is not one clear-cut quantitative threshold, but
483 rather a "threshold zone" (Huggett 2005) that may serve for habitat
484 management. The multivariate CIT finally show how, depending on the
485 local conditions (i.e. differences in presence and abundance of other
486 variables), a single variable can exhibit different threshold values, with
487 the latter always falling within the confidence intervals obtained from
488 univariate CIT. A good example is provided by the multivariate tree for
489 hazel grouse occurrence (Fig. 2B). Here, the variable "number of
490 basal-branched trees" has two thresholds: with a higher cover
491 provided by *Vaccinium myrtillus*, a lower number of such trees is
492 required, and vice versa. Both thresholds typically contribute under
493 different conditions to a hazel grouse presence probability greater than
494 50 %. This delivers flexible guidance for habitat management.

495

496 Combined habitat variable sets

497 Multivariate CITs enable visualizing, under the form of a classification
498 tree, the information about the importance and interaction of different
499 variables. It therefore provides a promising user-friendly tool that can
500 deliver pragmatic, flexible quantitative management criteria to
501 practitioners as different pathways represented by branches of the
502 tree, can be chosen to receive a favoured goal (e.g. a probability of
503 species presence of at least 50 %). The probability of species presence
504 resulting from a specific combination of habitat variables is graphically
505 depicted, which facilitates interpretation (Fig. 2).

506 Yet, one drawback of conditional inference trees is that one cannot
507 account for data clustering, e.g. by including spatial random factors in
508 the models. Although grid cell was our sampling unit for habitat
509 mapping, we did not summarize the data of all plots per grid cell. One
510 could therefore argue that our results may suffer from pseudo-
511 replication if not spatial autocorrelation. However, averaging all the
512 plot values per grid cell and calculating the thresholds from these
513 mean values may have biased the results towards intermediate values,
514 this by smoothing out the actual variance in the sample. As a result,
515 some important information about species' preferences, for instance
516 under more marginal circumstances, would have been lost. Since the
517 variance between the plots within a grid cell did not differ from the
518 variance between plots of different grid cells within a category
519 (presence/absence), spatial autocorrelation of the plots within a grid
520 cell-pair appeared not to be a relevant issue. In addition, our grid cells
521 do not represent the presence of a single individual but rather an area

522 where the species occurs, hosting at least one but most likely several
523 individuals. In conclusion, the plots in a grid cell better represent the
524 gradient of species-specific environmental conditions, despite a
525 residual risk of pseudo-replication. Our dual approach, using a GLMM
526 to pre-select the important habitat variables that were entered in the
527 CIT, makes us confident that the plot-based results provide a useful
528 approximation of the variable thresholds at the forest stand level.

529

530 **Implications for conservation**

531 The aim of this study was to generate applicable quantitative
532 prescriptions that provide practitioners with increased habitat
533 management flexibility, so that local conditions can be taken into
534 account. Thereby our objective was to enable managers to find an
535 acceptable compromise for habitat management in forests with
536 multiple functionalities, notably timber production and biodiversity
537 preservation and restoration. The quantitative thresholds we deliver
538 offer such alternative quantitative prescriptions at both the forest
539 stand (conditions per plot) and the forest mosaic (proportion of
540 suitable habitat per grid cell) scale. Our findings revealed that the
541 habitat requirements of the two focal species in terms of quality and
542 quantity do not differ as much as it was expected. In the contrary we
543 could mostly evidence complementary needs. This greatly simplifies
544 management in areas of sympatry. Accompanied by analyses of
545 landscape suitability at the meta-population level, which allow priority
546 areas to be delineated (Graf et al. 2005; Braunisch & Suchant 2007,
547 2008; Bollmann et al. 2011), the approach used here advances the
548 development of multiple-species conservation strategies.

549

550 *Acknowledgements* - Great thanks go to all the people who contributed
551 to the fieldwork: Maria Rusche, Florian Zellweger, Lucretia Deplazes,
552 Lisa Bitterlin, Joy Coppes, Karin Feller and Nino Maag. Pierrick Burri
553 and Jean-Yves Humbert provided support with data analysis. This
554 study was part of a research project funded by the Swiss Federal Office
555 for the Environment (FOEN) and the Swiss Federal Research Institute
556 for Forest, Snow and Landscape Research (WSL).

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771 **Tables**

772 Table 1. The number of presence and absence grid cells (1 km²), as
773 well as the number of embedded sampling plots (30 x 30 m) (in
774 parentheses) are listed for each species.

775

	PRESENCE	ABSENCE
CAPERCAILLIE	50 (800)	56 (593)
HAZEL GROUSE	38 (477)	62 (667)

776 Table 2. List of habitat variables with the reference area at which they
777 were collected: P = Plot (30 x 30 m), NS = Nested square (15 x 15
778 m), GV = Nested square quarters (7.5 x 7.5 m) for ground vegetation
779 (see Fig. 1C). *DBH: stem diameter at breast height. This Table
780 continues on the next page.

Variable Category	Variable Code	Description	Unit	Reference 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 (≥ 3tr. >60cm 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 (≥5m) cover	%	P
	SHRUB_COV	Shrub (≥1.3m, <5m) 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

781 Table 2 (continued). List of habitat variables with the reference area at
 782 which they were collected: P = Plot (30 x 30 m), NS = Nested square
 783 (15 x 15 m), GV = Nested square quarters (7.5 x 7.5 m) for ground
 784 vegetation (see Fig. 1C). *DBH: stem diameter at breast height.

785

Variable Category	Variable Code	Description	Unit	Reference area
Ground vegetation	COV_FERN	Cover of ferns	%	GV
	COV_GRAS	Cover of grasses	%	GV
	COV_BER	Cover of berry plants	%	GV
Special Ressources	ROW_TOT	Number of Rowans $\geq 3\text{m}$ (<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	1/0	P
	E2	Presence/absence of outer forest edge	1/0	P

786 Table 3. Habitat variables explaining the presence of capercaillie,
 787 obtained from a Generalized Linear Mixed Model (GLMM) with "grid
 788 cell-pair" as random factor. *** p < 0.001, ** p < 0.01, * p < 0.05,
 789 n.s. = non-significant. Variable codes are explained in Table 2.

790

Multivariate GLMM	Independent variables	Estimate (+SE)	Sign.
CAPERCAILLIE~	BB_TREE	0.1691 (+-0.0401)	***
	CAN_SPR	0.0169 (+-0.0046)	***
	COV_GRAS	0.0126 (+-0.0070)	n.s.
	COV_HERB	0.0153 (+-0.0070)	*
	COV_VAC	0.0464 (+-0.0081)	***
	E2	-1.0526 (+-0.2850)	***
	GV_DIS Type 2	0.8281 (+-0.3975)	*
	GV_DIS Type 3	-0.7890 (+-0.3218)	*
	GV_COV	0.0210 (+-0.0065)	**
	ROW_TOT	0.1055 (+-0.0331)	**
	SHR_FIR	-0.0551 (+-0.0337)	n.s.
	SHR_PIN	0.0883 (+-0.0337)	**

791 Table 4. Habitat variables explaining the presence of hazel grouse,
 792 obtained from a Generalized Linear Mixed Model (GLMM) with "grid
 793 cell-pair" as random factor. *** p < 0.001, ** p < 0.01, * p < 0.05,
 794 n.s. = non-significant. Variable codes are explained in Table 2.

Multivariate GLMM	Independent variables	Estimate (+SE)	Sign.
HAZELGROUSE~	BB_TREE	0.1571 (+- 0.0474)	***
	COV_HERB	0.0159 (+- 0.0069)	***
	COV_VAC	0.0323 (+- 0.0073)	*
	E2	-1.3422 (+-0.3555)	***
	GV_DIS Type 2	0.7063 (+-0.4452)	***
	GV_DIS Type3	-0.5589 (+-0.3701)	n.s.
	GV_COV	0.0157 (+-0.0056)	n.s.
	ROW_TOT	0.1088 (+-0.0455)	**
	SHR_RES_TR	0.0313 (+-0.0143)	*
	COV_FERN	0.0110 (+-0.0123)	*
COV_CON	-0.0146 (+-0.0241)	n.s.	

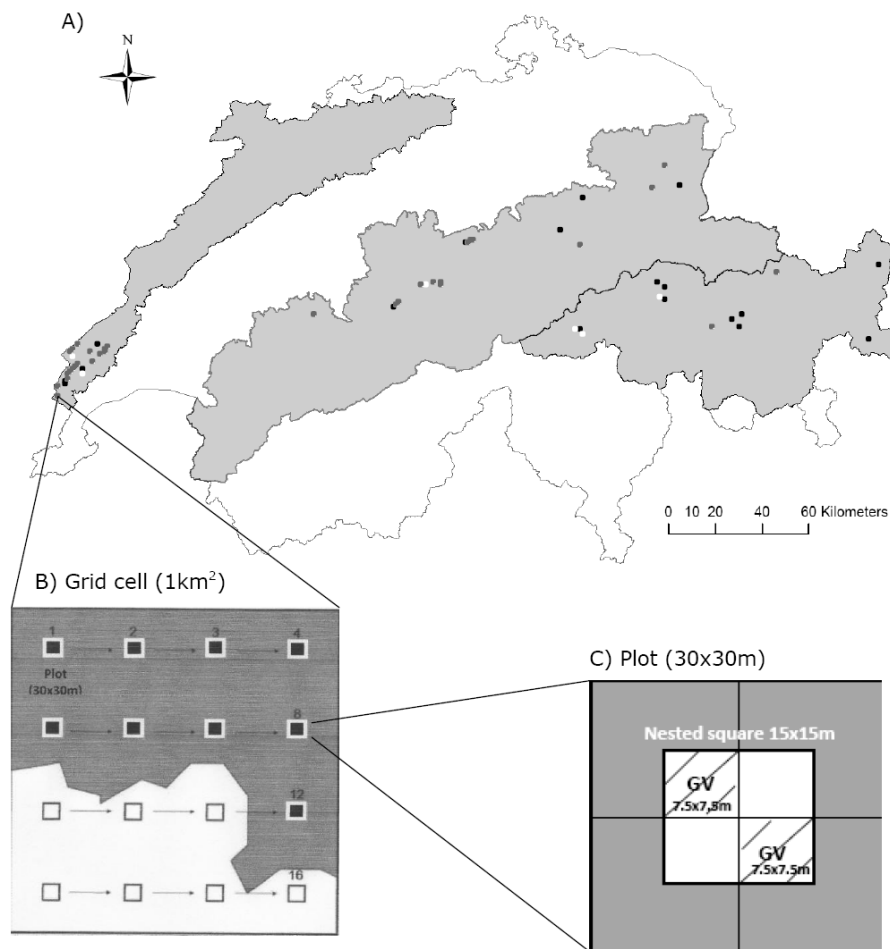
795 Table 5. Thresholds for the variables significantly explaining grouse-
 796 occurrence in Generalized Linear Mixed Models calculated using
 797 univariate Conditional Inference Trees (CIT) and compared to
 798 thresholds (indicated by </>) and optimal variable ranges found in
 799 literature. n.s. = non-significant (no split).

Explanatory variable	Thresholds		Literature	
	Capercaillie	Hazel grouse	Capercaillie	Hazel grouse
n(presence/absence)	n(800/593)	n(477/667)		
CAN_COV (%)	≤81 (60-83)	≤59 (56-79)	25-65 [1] 40-60 [2] 50 [3] <60 [5] 50-70 [6]	40-50 [4]
CAN_SPR (%)	>7 (1-11)	n.s.	10-33 [6]	
CAN_FIR (%)	≤7 (6-33)	≤21 (11-33)		
CAN_BEE (%)	≤3 (1-4)	≤34 (3-73)		
CAN_O_DEC (%)	≤23 (13-28)	n.s.		
CAN_RES_TR (%)	n.s.	>1 (0-2)		
SHR_RES_TR (%)	n.s.	>0 (0-2)		>10 [5]
SHR_O_DEC (%)	≤6 (0-18)	n.s.		
SHR_PIN (%)	>0 (0-10)	n.s.		
GV_COV (%)	>60 (28-60)	>40 (25-60)	>40 [6] 50-70 [7] >60 [5] [1] >70 [2] 90-100 [3]	30-45 [5] 60-100 [4]
GV_DIS (1;2;3)	=2	=2		
GV_HEI (cm)	n.s.	>7 (5-20)	30-50 [8] <40 [3]	
COV_VAC (%)	>1 (0-3)	> 1 (0-3)	15-20 or more [9] >20 [5] ≥60 [10] >70-100 [7]	40 (+-4) [11]
COV_HERB (%)	>20 (8-53)	>25 (3-53)		
COV_GRAS (%)	>1 (0-3)	n.s.		
COV_DEC (%)	≤30 (1-38)	n.s.		
ROW_TOT (no./900m ²)	>0 (0-2)	>0 (0,0)		2/900m ² [11]
BB_TREE (no./900m ²)	>0 (0-1)	>0 (0-5)		
E1 (0;1)	=1	n.s.	The more the better [8]	
E2 (0;1)	=0	=0		

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

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

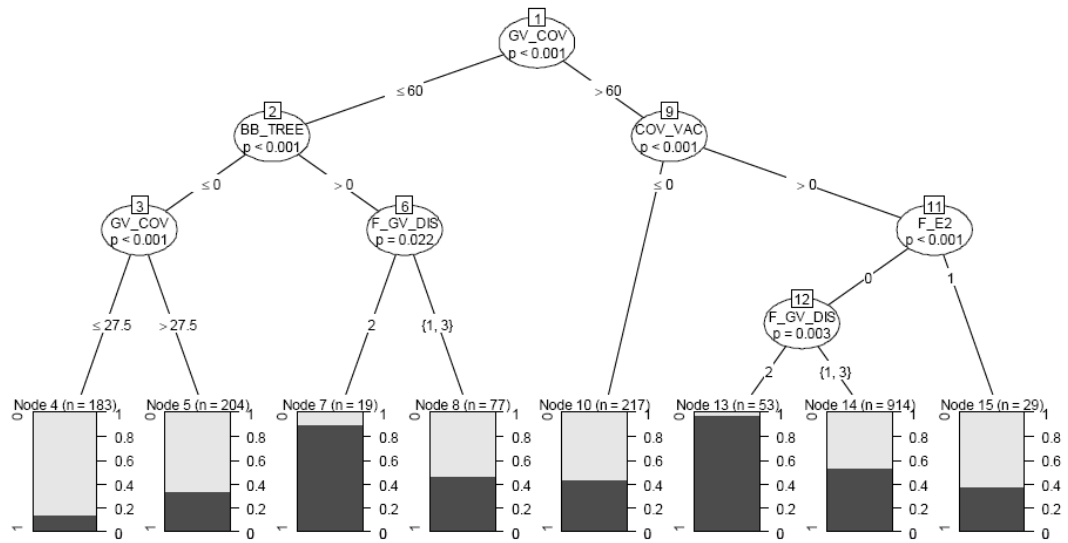
800 **Figures**



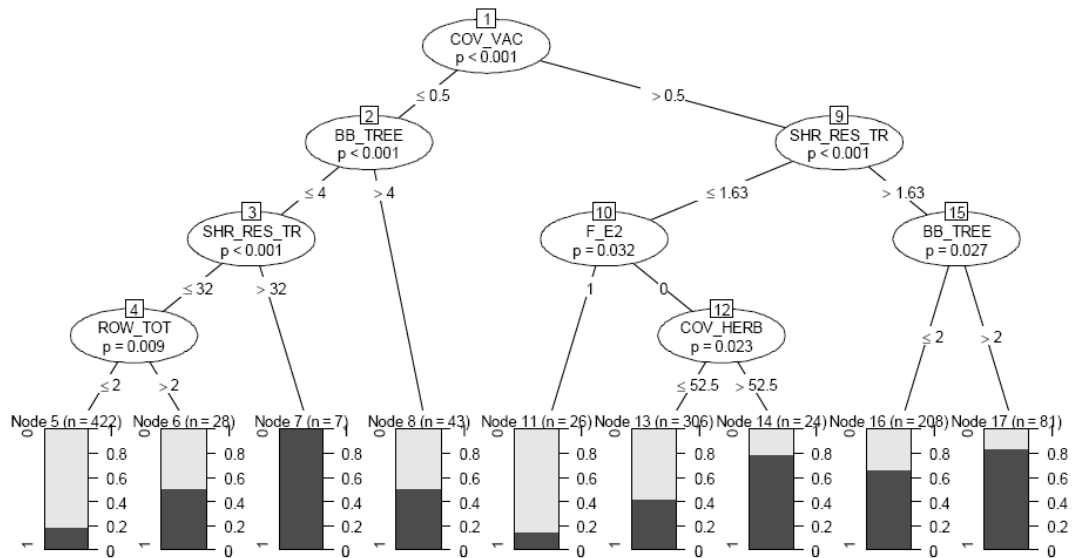
801

802 Figure 1. Sampling design. A) Distribution of presence grid cells (black:
803 capercaillie presence, white: hazel grouse presence and dark grey:
804 sympatric occurrence) within three biogeographic mountain regions
805 (highlighted in grey). For each presence grid cell, an absence grid cell
806 (not depicted on this map) was selected within 1 - 4 km distance. B) In
807 each grid cell, habitat variables were collected in those of the 16
808 sampling plots which were located in the forest. C) In a sampling plot,
809 variables were collected at different reference areas: within the entire
810 30 x 30 m plot, within a nested square (15 x 15 m) (white) or within
811 the two diagonal quarters of the nested square (7.5 x 7.5 m). The
812 variables, their unit and corresponding reference area for sampling are
813 listed in Table 2.

A) capercaillie



B) hazel grouse



814

815 Figure 2. Multivariate Conditional Inference Trees (CIT) (minsplit=100)

816 with the presence probability of A) capercaillie and B) hazel grouse as

817 dependent variable. The columns at branch end illustrate the

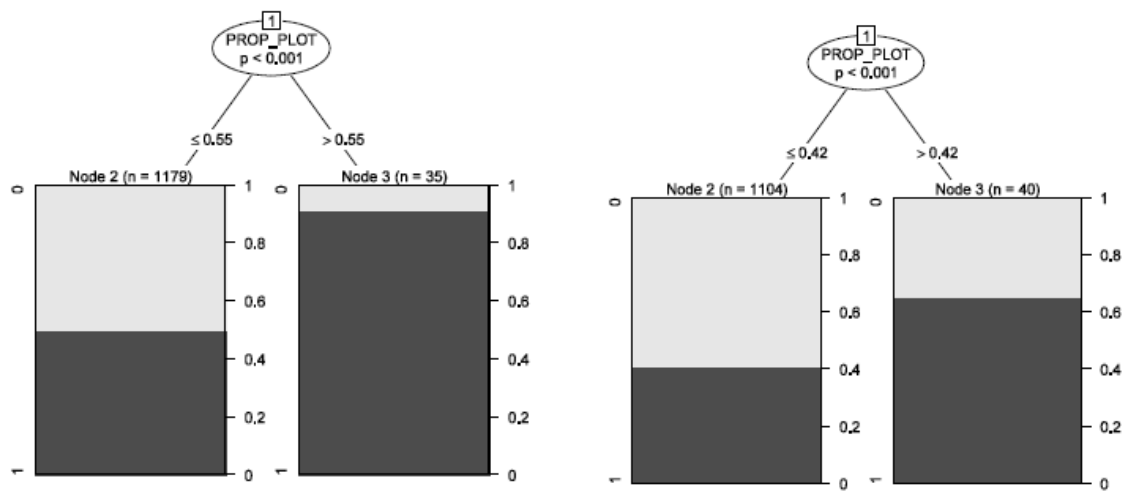
818 probabilities of presence (values from 0 to 1 are given on the right side

819 of each bar) resulting from a specific variable combination.

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

A) capercaillie

B) hazel grouse



821

822 Figure 3. CIT (minsplit = 10) depicting the thresholds for the
823 proportion of suitable habitat (i.e. plots with a probability of presence
824 ≥ 0.5) per grid cell. The dependent variables are the presence of A)
825 capercaillie and B) hazel grouse, respectively. Presence probabilities
826 (dark grey) are given in values from 0 to 1. The 95 % confidence
827 intervals (CI) of the threshold values based on 1000 bootstrap
828 replicates are as follows: A) CI: 0.50 - 0.75 and B) CI: 0.25 - 0.71.

829

830 **Appendix**

831 Appendix I. Variable thresholds obtained with univariate CITs (A)
 832 calculated for habitat variables collected at 16 sampling plots (30 x 30
 833 m) representing 1 km² grid cells at which species presence/absence
 834 was recorded, compared to (B) variable thresholds obtained from plots
 835 at precise locations of species presence/absence. Plots of (A) were
 836 representatively distributed across three mountain regions of
 837 Switzerland, whereas data of (B) were collected in a small region
 838 (Special Forest Reserve Amden, SG, Switzerland, 1772 ha).
 839 Abbreviations of the habitat variables are explained in Table 2. n.s. =
 840 non - significant, n.a. = non - available.

Explanatory variable	(A) Thresholds (plot-level)		(B) Thresholds (site selection)	
	capercaillie	hazel grouse	capercaillie	hazel grouse
n(presence/absence)	n(800/593)	n(477/667)	n(76/53)	n(61/63)
CAN_COV (%)	≤81 (60-83)	≤59 (56-79)	≤75 (10-80)	n.s.
CAN_BEE (%)	≤3 (1-4)	≤34 (3-73)	≤6 (2.21-31.82)	n.s.
CAN_FIR (%)	≤7 (6-33)	≤21 (11-33)	n.s.	n.s.
CAN_O_DEC (%)	n.s.	≤23 (13-28)	n.s.	n.s.
CAN_RES_TR (%)	n.s.	>1 (0-2)	n.s.	n.s.
CAN_SPR (%)	>7 (1-11)	n.s.	n.s.	n.s.
SHRUB_COV (%)	n.s.	n.s.	≤5 (2-25)	n.s.
SHR_RES_TR (%)	n.s.	>0 (0-2)	n.s.	>0.21 (0-4.78)
SHR_O_DEC (%)	≤6 (0 -18)	n.s.	n.s.	n.s.
SHR_PIN (%)	>0 (0-10)	n.s.	n.s.	n.s.
GV_COV (%)	>60 (28-60)	>40 (25-60)	>40 (20-50)	n.s.
GV_HEI (cm)	n.s.	>7 (5-20)	>25 (8-35)	n.s.
COV_VAC (%)	>1 (0-3)	> 1 (0-3)	n.s.	>50 (0-70)
COV_HERB (%)	>20 (8-53)	>25 (3-53)	n.a.	n.a.
COV_DEC (%)	≤30 (1-38)	n.s.	n.s.	n.s.
COV_GRAS (%)	>1 (0-3)	n.s.	n.a.	n.a.

841