

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 km<sup>2</sup> 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 & Braunisch 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

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

118

## 119 **Materials and methods**

### 120 Study area

121 The study was conducted in Switzerland, with the study sites distributed across  
122 three mountain ranges representing a broad gradient of bioclimatic conditions: the  
123 Jura Mountains (47°00' N 6°40' E - 47°30' N 8°00' E), Northern Prealps (46°30'  
124 N 7°15' E - 47°00' N 9°30' E) and Inner Alps (46°30' N 9°00' E - 47°00' N  
125 10°30' E) (Fig. 1A). The Jura Mountains are characterized by a moderate climate  
126 with mild, damp summers and cold winters (MeteoSchweiz 2013,  
127 <http://www.meteoschweiz.admin.ch>). The mean annual ambient temperature is  
128 5.5°C with 180 frost days and, on average, 2000 mm of rain and 4 m of snow  
129 annually at an altitude of 1200 m (MeteoSchweiz 2013). The tree line is around  
130 1400 m a.s.l. (Steiger, 1994). The Northern Prealps are characterized by an  
131 Atlantic climate with high precipitation (2000-3000 mm/yr), cold-temperate  
132 winters and wet summers (MeteoSchweiz 2013). The tree line is at an elevation of  
133 approximately 2000 m (Steiger, 1994). The open and diversely structured forests  
134 are often adjacent to pastures and interspersed with mires. In the Inner Alps, the  
135 prevailing climate conditions are continental, with low precipitation (800-  
136 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 km<sup>2</sup> 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 ( $\geq 5$  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*

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

230

### 231 *Variable thresholds*

232 Conditional Inference Trees (CIT) were used for the identification of variable  
233 thresholds explaining species presence. This method, similar to classification and  
234 regression trees, uses recursive partitioning to select significant predictor variables  
235 in a hierarchical way and to identify the best cut-off values that split the dataset so  
236 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

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

289 The canopy layer on sites with capercaillie presence was composed of spruce by  
290 at least 5 % (CI: 1 - 11%) which corresponded roughly to the lower limit of 10 –  
291 33% indicated by Suchant and Braunisch (2004). For hazel grouse, a minimum  
292 value of 10% (CI: 5-16%) was found. Furthermore, there was an upper limit for  
293 deciduous trees other than beech for both species, at 19% (CI: 12-28%) for  
294 capercaillie and 14% (CI: 0 – 18%) for hazel grouse. While these trees are rarely  
295 used as food resource and provide neither sight nor thermal protection in winter,  
296 the beech buds represent an important food resource in late winter and spring.  
297 Nevertheless, in our model both grouse species showed only little tolerance  
298 towards beech in the canopy (upper threshold of 3%) although the confidence  
299 intervals suggest that higher amounts of beech in the canopy layer are accepted.

300 Both grouse species required a minimum of 60% of ground vegetation cover (CI:  
301 28 – 60% for capercaillie; 38-60% for hazel grouse) which corresponded to  
302 literature specifications (Bollmann et al., 2008; Bollmann et al., 2005; Lieser &  
303 Roth, 2001; Storch, 1993a). For the hazel grouse, herbs covering the ground  
304 ideally exceeded 18 % (CI: 13 – 38 %); slightly higher values but with a greater  
305 variance were obtained for capercaillie (38 %, CI: 0 -62%). Very low threshold  
306 values were obtained for important food resources like bilberry cover and the  
307 proportion of resource trees in the shrub and the canopy layer (1% for both  
308 species and variables). Moreover, a minimum of one rowan ( $\geq 3$  m tall) and of one  
309 basal-branched tree was required per plot (900 m<sup>2</sup>), the former being a little lower  
310 than what Schäublin and Bollmann (2011) found for hazel grouse (2 rowans/900

311 m<sup>2</sup>). 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 900m<sup>2</sup> 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 km<sup>2</sup>  
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-

387 dominated stands in the lower altitudes otherwise representing structurally  
388 suboptimal habitat conditions, which may explain this result. Hazel grouse has  
389 been shown to prefer mixed or coniferous stands over pure deciduous stands  
390 (Klaus, 1991; Montadert & Léonard, 2006), which is corroborated in this study.  
391 Although several deciduous trees act as important resource trees, coniferous trees  
392 in the shrub layer remain essential as they provide better sight protection from  
393 predators and enhanced thermal benefits, especially in winter (Swenson et al.,  
394 1995; Swenson & Olsson, 1991). Yet, despite explaining species presence very  
395 well, our variable set may not fully represent the two species' requirements, since  
396 large-scale habitat characteristics such as stand mosaic heterogeneity, forest gaps  
397 and linear structural elements cannot be sufficiently captured by a plot-based  
398 sampling design. Area-wide structural variables obtained from remote sensing,  
399 such as Airborne Laser Scanning, aerial or satellite images have been shown add  
400 valuable complementary information which can substantially improve the  
401 predictive performance of habitat models (Zellweger et al., 2014) and - in our case  
402 - may have revealed greater species-specific differences in habitat selection.

403

#### 404 Variable thresholds

405 While the threshold-ranges obtained for most variables encompassed the values  
406 found in literature, for some relevant habitat variables our thresholds were  
407 strikingly lower. This concerns for instance the proportion of bilberry in the field  
408 layer, a feature relevant for both species. Former studies indicated 15 – 70%  
409 bilberry cover for capercaillie and 40% for hazel grouse (Baines et al., 2004;  
410 Schäublin & Bollmann, 2011), which contrasts with our > 0% for capercaillie and  
411 >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 km<sup>2</sup> 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 km<sup>2</sup> 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 km<sup>2</sup> 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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704 **Tables**

705 Table 1. The number of presence and absence grid cells (1 km<sup>2</sup>) per species, as  
706 well as the number of embedded sampling plots (30 x 30 m) (in parentheses) used  
707 for the analysis.

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	<b>Presence</b>	<b>Absence</b>
Capercaillie	50 (609)	50 (526)
Hazel Grouse	72 (771)	71 (627)

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708

709



710 Table 2. List of habitat variables with the reference area (R.area) at which they  
711 were collected: P = Plot (30 x 30 m), NS = Nested square (15 x 15 m), GV =  
712 Nested square quarters (7.5 x 7.5 m) for ground vegetation (see Fig. 1C). DBH:  
713 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 (≥ 3tr. ≥60cm DBH) 6 = multi-age stands	categorical (1-6)	P
		Stand structure		
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
	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 ≥3m ( <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

716 Table 3. Habitat variables explaining the presence of capercaillie, obtained from a  
717 Generalized Linear Mixed Model (GLMM) with “grid cell-pair” as random factor.  
718 Variable estimates, as obtained from averaging the four best models according to  
719 the AIC-ranking, are presented and the relative variable importance is provided in  
720 parentheses. The composition and ranking of the included models is specified in  
721 the lower part of the table. Asterisks indicate significance levels with \*\*\*  $p <$   
722 0.001, \*\*  $p < 0.01$ , \*  $p < 0.05$ , n.s. = non-significant. Variable codes are explained  
723 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.
<b>Grouping factor (random effect)</b>		<b>Variance</b>	<b>CI</b>	
1	Pair_ID (Intercept)	1.933	1.339-3.032	
<b>Rank</b>	<b>Incl. Variables (No.)</b>	<b>AICc</b>	<b><math>\Delta</math>AICc</b>	<b><math>\Delta</math>AICc weight</b>
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

724

725

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.

	<b>Variable</b>	<b>Estimate</b>	<b>SE</b>	<b>Sign.</b>
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.
<b>Grouping factor (random effect)</b>		<b>Variance</b>	<b>CI</b>	
	Pair_ID	1.554	1.398-2.243	
<b>Rank</b>	<b>Incl. Variables (No.)</b>	<b>AICc</b>	<b><math>\Delta</math>AICc</b>	<b><math>\Delta</math>AICc weight</b>
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 <sup>1,2</sup>	
	<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 <sup>2</sup> )	>0 (0-2)	>0 (0-1)		2/900m <sup>2</sup> [11]
BB_TREE (no./900m <sup>2</sup> )	>0 (0-1)	>0 (0-5)		
E1 (0;1)	=1	=1	The more the better [9]	
E2 (0;1)	=0	=0		

<sup>1</sup>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

<sup>2</sup>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, 64m<sup>2</sup>; [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  $\geq 0.5$ ) 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

Figure 1  
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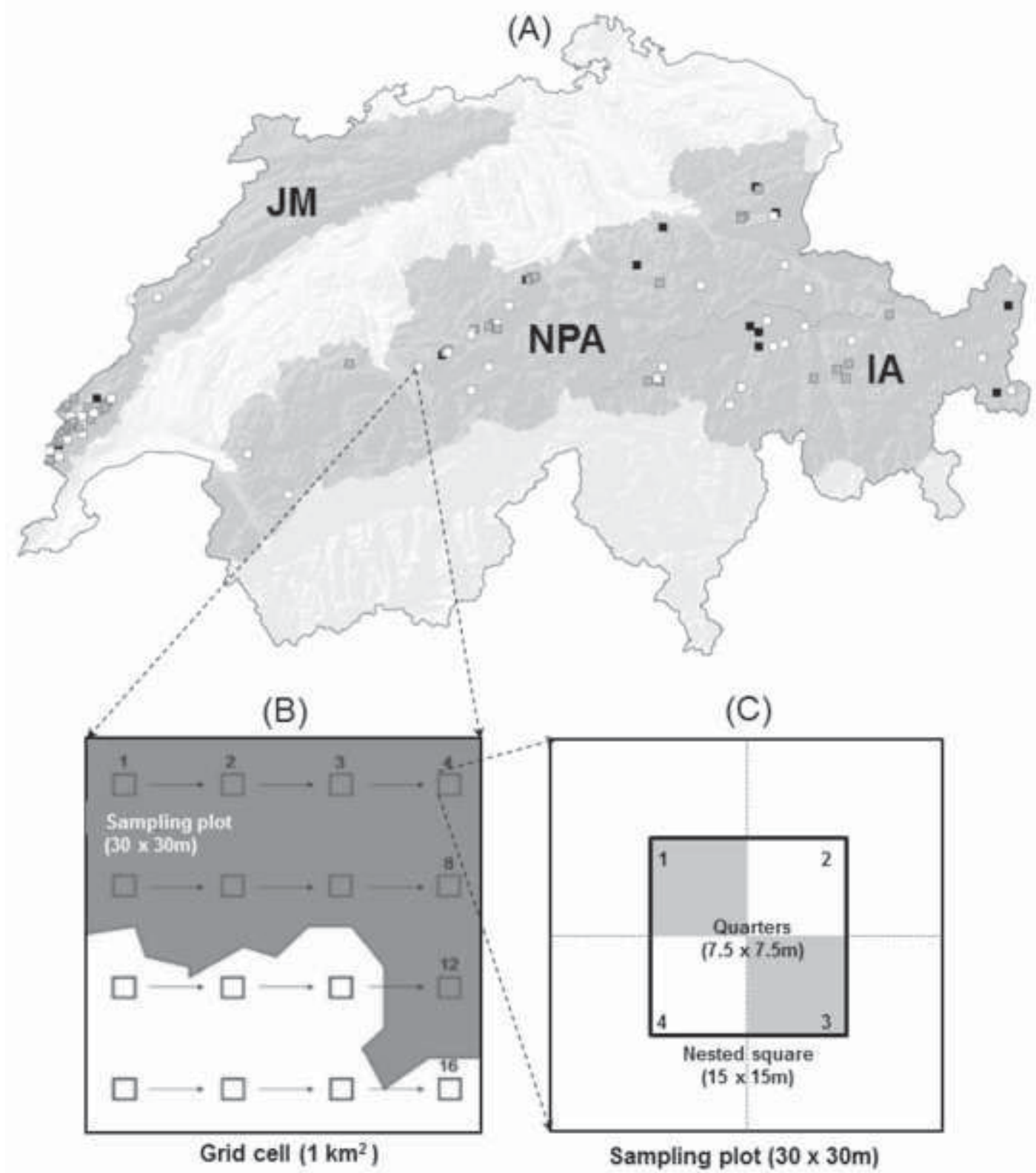




Figure 2  
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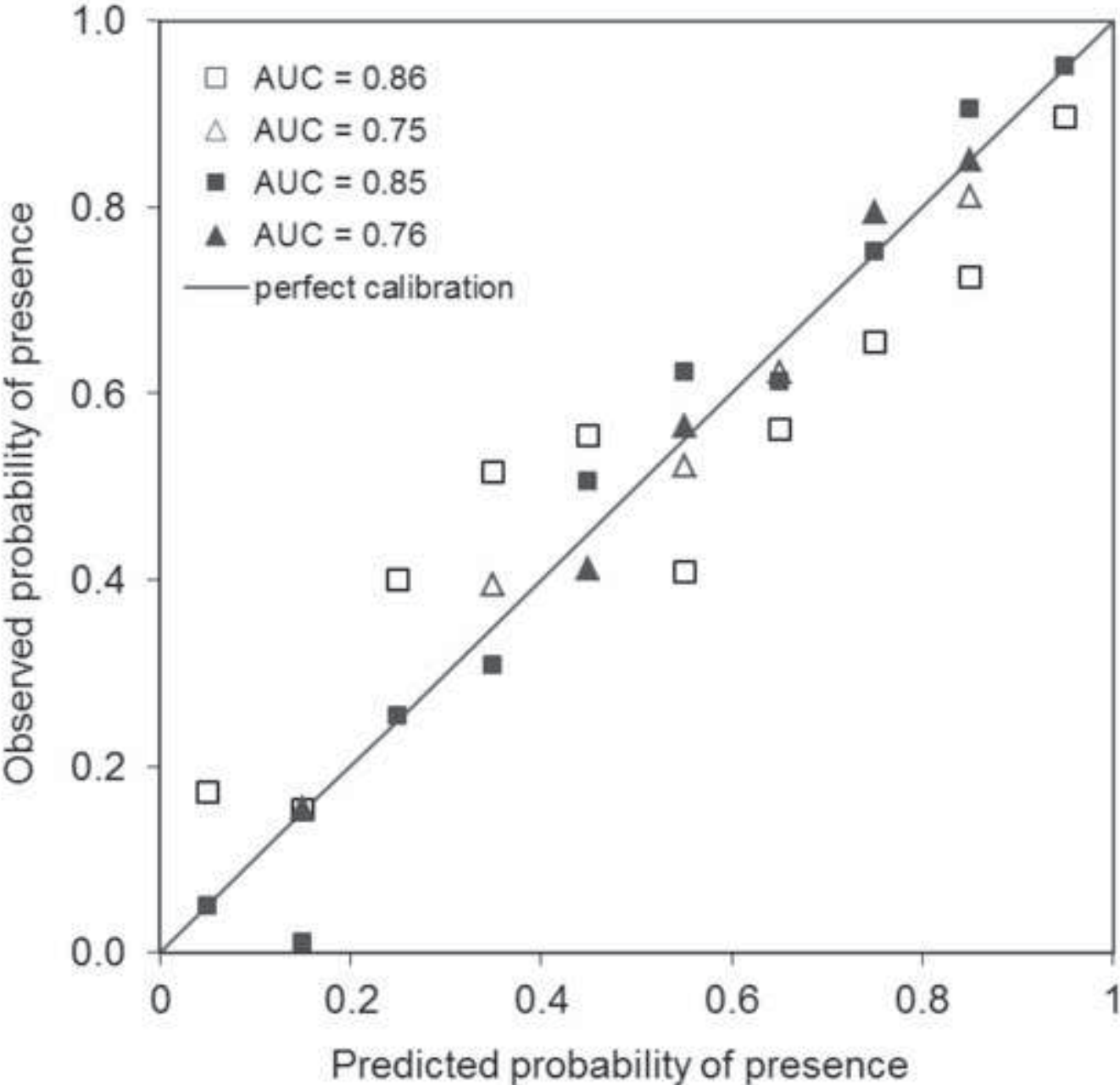


Figure 3A  
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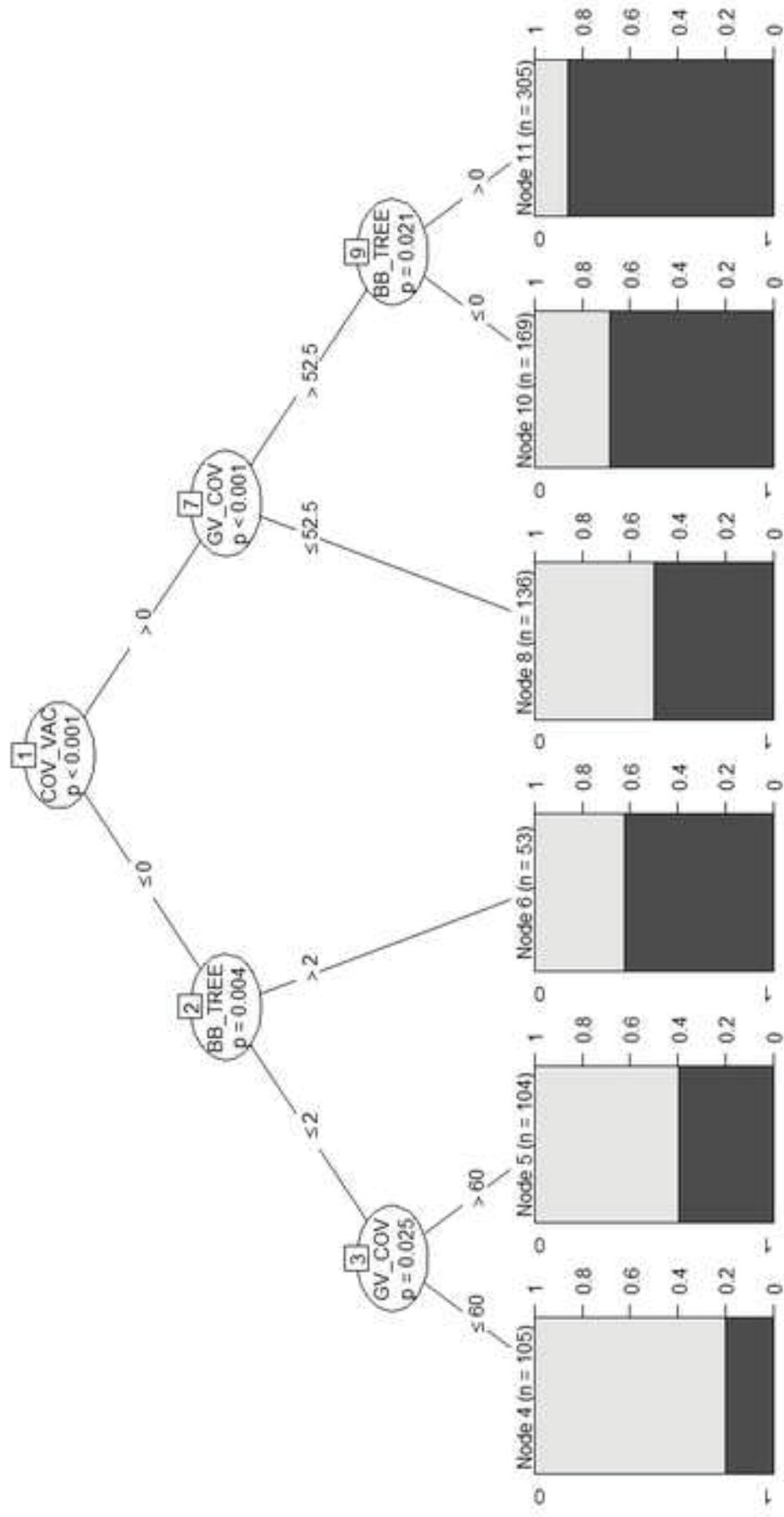


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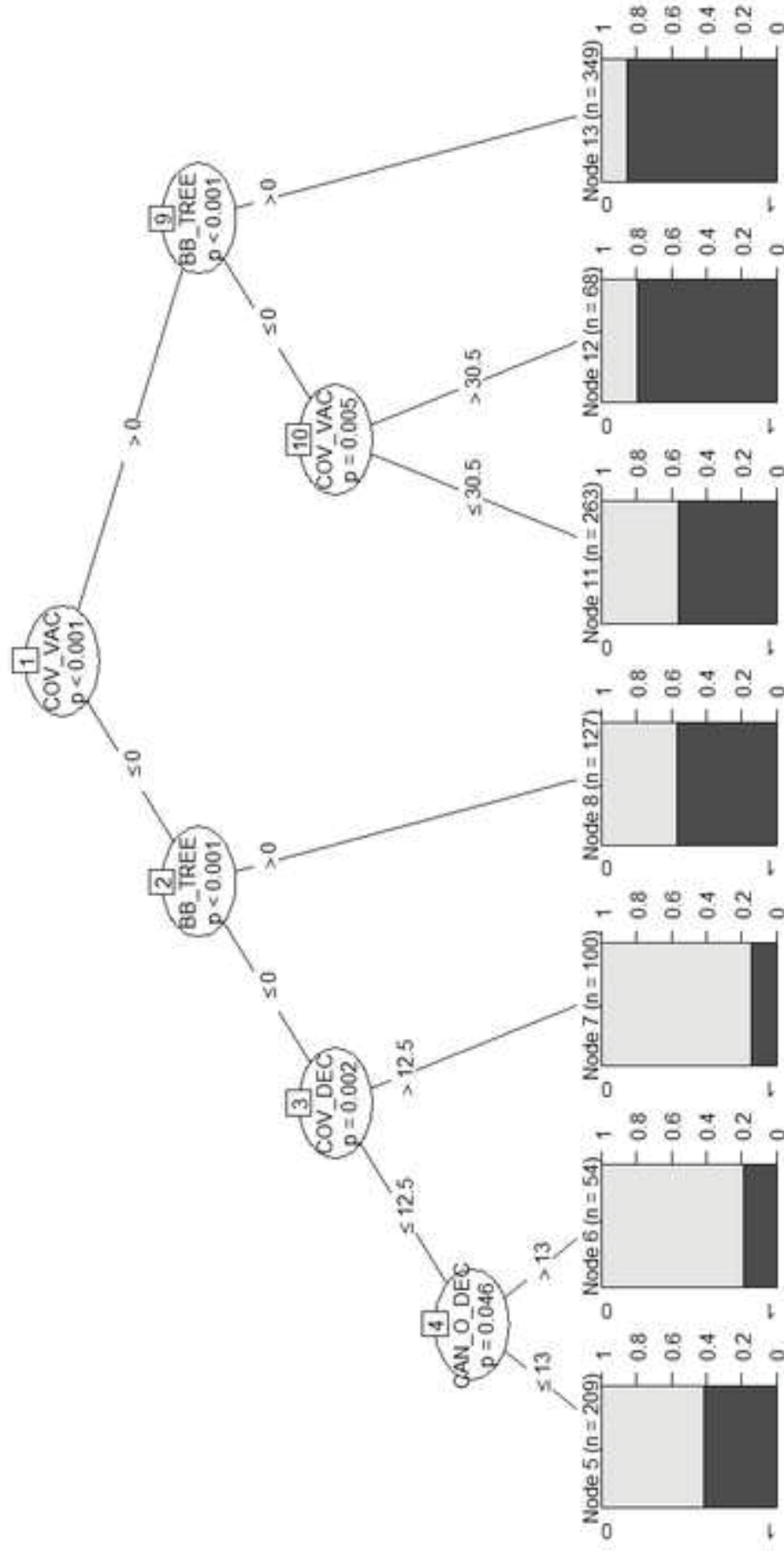


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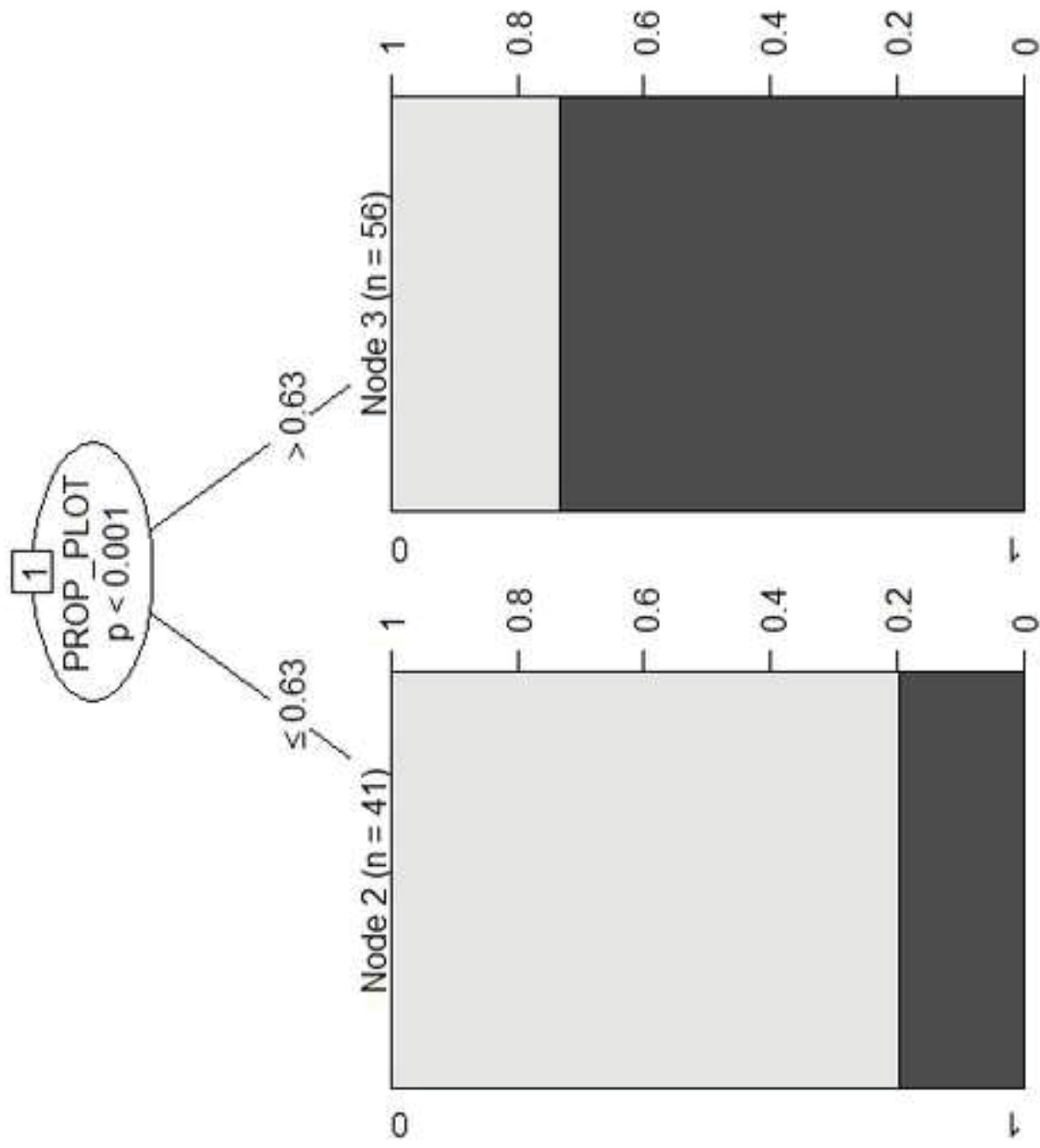
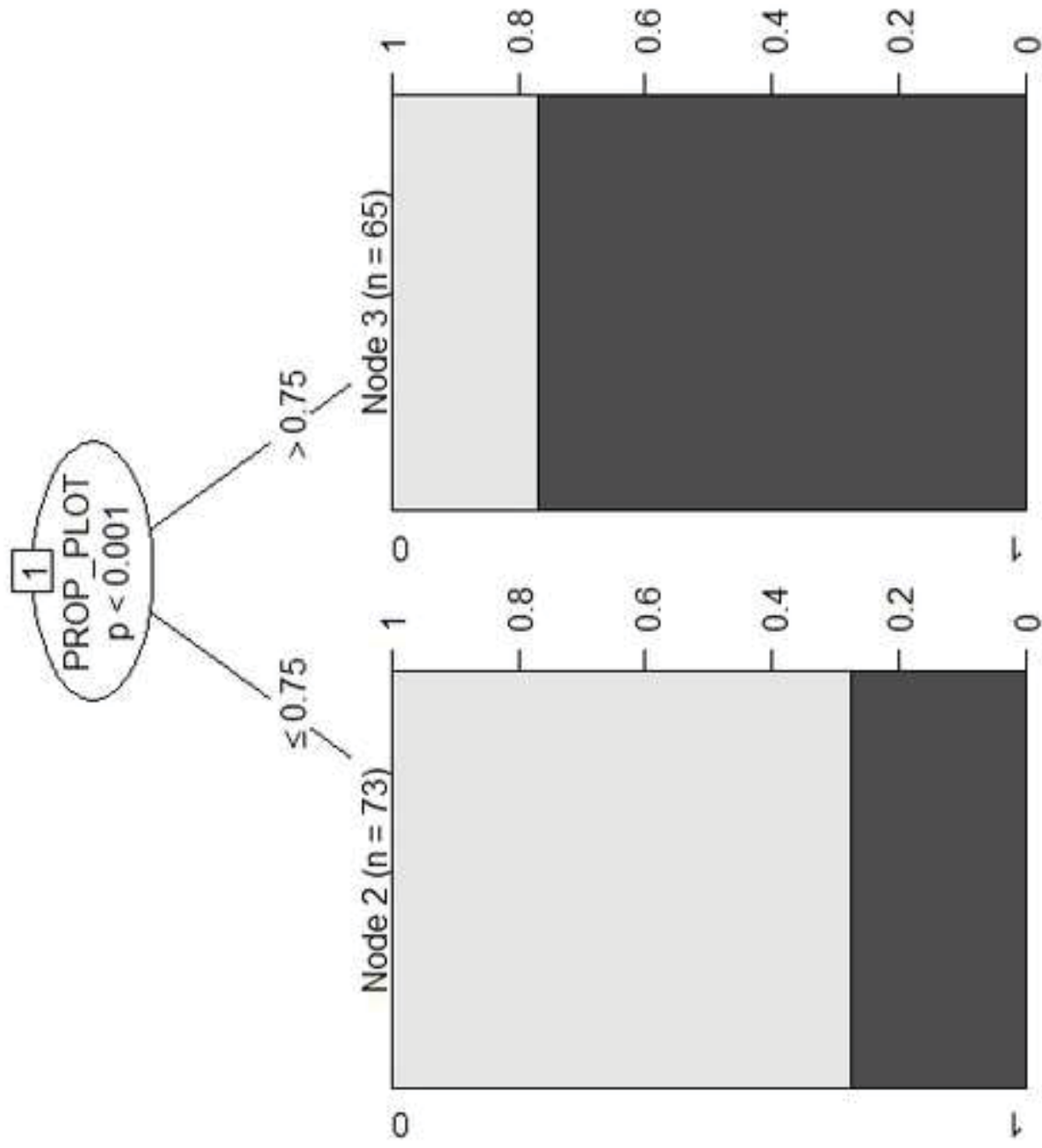


Figure 4B  
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**Supplementary material**

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