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Abstract: European beech forests are of particular importance for biodiversity, although relatively little is known about how beech forest management impacts on invertebrate communities. In this paper we investigated the influence of beech forest management history [i.e. over-mature coppices (OC) and coppices in conversion to high forests (CCHF)], climatic, topographic and microhabitat characteristics on ground beetle diversity (measured as total relative abundance, species richness, Shannon diversity and abundance of the endangered endemic species *Carabus olympiae*) in northern Italy. The diversity of forest specialist carabids was higher in OC and in forest stands characterized by a higher mean temperature and lower relative humidity. Moreover, we detected a positive response of several diversity variables to coarse wood debris cover or volume, herb cover, and the standard deviation of tree diameter. Currently, OC seems to be a more favorable habitat for forest carabids, including *Carabus olympiae*, although succession over time can lead to a progressive homogenization of the vegetation structure, with negative consequences for the conservation of the forest carabid assemblage.

Based on our results, we suggest that the traditional management of beech coppice and its conversion to high forest be modified by including practices aimed at promoting structural and microhabitat diversity such as retention of large trees, creation of canopy gaps, retention of coarse wood debris and the preservation of 'islands' of older trees in the managed stands.

Dear Dan Binkley
Editor-in-Chief
Forest Ecology and Management

we return the revised version of our paper entitled “Effects of forest management on ground beetle diversity in alpine beech (*Fagus sylvatica* L.) stands”. The text has been modified to conform to the journal’s format and according to the referees’ suggestions. Whilst we have attempted to address the referees’ comments as far as possible, we are also mindful of the need to reduce the length of the paper – for some points raised we have therefore been fairly brief. We hope we have managed to maintain the right balance between relevant additions and excessive detail. We have managed to reduce the text from 8679 to 7800 words. If the text is still too long, we would greatly appreciate some editorial guidance on where best to shorten the paper.

We give our detailed responses in the “Reply to the viewers” file.

Best regards

Matteo Negro .

1 **Effects of forest management on ground beetle diversity in alpine**
2 **beech (*Fagus sylvatica* L.) stands**

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19 **Abstract**

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21 known about how beech forest management impacts on invertebrate communities. In this paper
22 we investigated the influence of beech forest management history [i.e. over-mature coppices
23 (OC) and coppices in conversion to high forests (CCHF)], climatic, topographic and microhabitat
24 characteristics on ground beetle diversity (measured as total relative abundance, species richness,
25 Shannon diversity and abundance of the endangered endemic species *Carabus olympiae*) in
26 northern Italy. The diversity of forest specialist carabids was higher in OC and in forest stands
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29 cover, and the standard deviation of tree diameter. Currently, OC seems to be a more favorable
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34 conversion to high forest be modified by including practices aimed at promoting structural and
35 microhabitat diversity such as retention of large trees, creation of canopy gaps, retention of
36 coarse wood debris and the preservation of ‘islands’ of older trees in the managed stands.

37

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39 ecology, retention, ageing islands

40

41 **1. Introduction**

42 In Europe, Beech *Fagus sylvatica* forests are of particular importance for biodiversity. Annex 1
43 of the "Habitats Directive" (92/43/EEC) lists eight habitat types characterized by beech forests as
44 worthy of conservation. Current threats to beech forest ecosystems include climate change
45 (Gessler et al., 2007; Di Filippo et al., 2012), increased likelihood of drought and fire damage
46 (Piovesan et al., 2008; Ascoli et al., 2013), impact of tourism (Negro et al., 2009; Rolando et al.,
47 2013), habitat loss and fragmentation (Kunstler et al., 2007), grazing by domestic or wild
48 ungulates (Vandenberghe et al., 2007; Olesen and Madsen, 2008) and changes in forest
49 management (Mund and Schulze, 2006; Wagner et al., 2011).

50 There are few studies concerning the effect of forest management on biodiversity in beech
51 forests (e.g. Moning and Müller, 2009; Spiecker, 2003), and most of these focus on plant or
52 mycorrhizal diversity (e.g. Van Calster et al., 2007; Bartha et al., 2008; Di Marino, 2008; Radtke
53 et al., 2013). However, such information is a necessary pre-requisite for management of this
54 habitat given the various environmental pressures to which it is subject. A case in point are the
55 beech forests which characterize the landscape of many mountain areas in Italy (Nocentini,
56 2009). Most beech forests are currently managed as coppice, i.e., by repeatedly cutting back
57 shoots to ground level to stimulate vegetative growth and provide firewood on a short rotation
58 basis (20 to 40 years). High forests where trees are regenerated by seed are rare. However, many
59 coppices are now transitioning to a high-forest structure, due to either the abandonment of
60 regular management, or silvicultural conversion by thinning (Nocentini, 2009), yet the impacts
61 of such management changes on biodiversity are not as yet fully understood.

62 Insects respond to stand structural complexity at different temporal and spatial scales, and they
63 are strongly influenced by natural and anthropogenic disturbance (Kraus and Krumm, 2013). In

64 particular, ground beetles (Coleoptera: Carabidae) cover a wide range of life histories and
65 microhabitat requirements, and therefore they have been widely recommended as bioindicators
66 of forest management (Rainio and Niemelä, 2003). They are relatively easy and cost-efficient to
67 assess with standardized methods (i.e., pitfall trapping), and are sensitive to environmental
68 factors such as temperature, humidity and vegetation structure (Stork, 1990; Butterfield, 1996;
69 Lövei and Sunderland, 1996). Furthermore, changes in carabid abundance and species richness
70 can be useful tools to evaluate the effects of human disturbance in forest ecosystems (Brandmayr
71 et al., 2009).

72 Most of the studies of carabid diversity in forest habitats have focused on the effects of habitat
73 fragmentation (Davies and Margules, 1998; Niemelä, 2001; Koivula and Vermeulen, 2005), edge
74 effects (Heliölä et al., 2001; Koivula et al., 2004; Negro et al., 2009), or forestry practices
75 (Werner and Raffa, 2000; Pearce and Venier, 2006; Taboada et al., 2006). The latter affect
76 particularly large-sized and brachypterous (short or reduced wings) habitat specialists, which
77 have limited dispersal capacity (Kotze and O'Hara, 2003). Indeed, several authors have
78 demonstrated that flight capability, and therefore dispersal ability, is a function of carabid wing
79 form (Den Boer, 1970; Den Boer, 1990; Lovei and Sunderland, 1996). For example, radio-
80 telemetry in the same beech forest stands considered in this study has shown that the endangered
81 *Carabus olympiae* has very low dispersal (Negro et al., 2008).

82 We focused on a group of localized, medium and large-bodied brachypterous ground beetles
83 inhabiting beech forests in the north western Italian Alps. The study site, located in the Sessera
84 Valley, is part of Natura 2000 ecological network. In particular, the site houses *Carabus*
85 *olympiae*, classified as a priority species in Annexes II and IV of the "Habitats Directive"

86 (92/43/EEC) and considered Vulnerable according to the IUCN red list of Threatened species
87 (<http://www.iucnredlist.org/>).

88 In this study, we considered the response of forest carabid beetles to management history (i.e.
89 coppice or coppice in conversion to high forest), habitat structure and micro-climate in beech
90 forests in northern Italy, in order to understand the factors affecting their abundance and
91 diversity, and hence to better inform management strategies for their conservation. The specific
92 aims were: (1) to test whether two different management histories [i.e., over-mature coppice
93 (OC) and coppice in conversion to high forests (CCHF)], in the same beech forest ecosystem,
94 have different effects on the abundance, species richness, diversity and composition of forest
95 carabid assemblages; (2) to assess which vegetation and stand structure parameters are more
96 important in driving forest carabid abundance and diversity, and (3) to evaluate which are the
97 best forest management practices, if any, for long-term conservation of the endemic species
98 *Carabus olympiae*.

99

100 **2. Methods**

101 2.1 Study area

102 The study area was the Upper Sessera Valley (Fig. 1), about 108 km² wide, located in north-east
103 Piedmont, Italy (45°40' N, 8°16' E). It includes the upper part of the River Sessera basin, a
104 mountainous catchment, from the valley bottom up to an elevation of 2556 m a.s.l. (average
105 elevation: 1350 m). Annual rainfall is 1700 mm with two equinoctial maxima, and mean annual
106 temperature is 7°C. Snow cover lasts about 5 months (November to March).

107 Due to its position at the outer margins of the Alps, the Upper Sessera Valley provided a glacial
108 refugium for many plant and animal genera, and is now a local hotspot for biodiversity. The most
109 common land cover classes are pasture (dominated by graminaceous plants), shrubland (alpen
110 rose *Rhododendron ferrugineum* L. and blueberry *Vaccinium myrtillus* L.), secondary forest on
111 former pastures (birch *Betula pendula* L. and common hazel *Corylus avellana* L.), and beech
112 (*Fagus sylvatica* L.) forest (belonging to the association *Luzulo-Fagetum*). Moreover, large
113 portions of the site were afforested by conifer plantations (Norway spruce *Picea abies* (L.) Karst)
114 and other conifers before and after World War II.

115 In the study area, beech was traditionally coppiced to produce firewood and charcoal. Over the
116 last decades, forest management has been progressively abandoned. The last harvest in privately
117 owned coppice stands was carried out in 1960. The sprouts are 53 years old and most of the
118 standards are about 80 years old. On the other hand, most coppices on public properties have
119 been actively converted to high forest since the 1980s. The traditional treatment applied to
120 coppice was the coppice with standard (an average of 100 standards per hectare) and the
121 conversion has been applied with a gradual thinning of sprouts (Giannini and Piussi, 1976). This
122 method requires a first thinning in an over-mature coppice, and 2-3 further thinnings before
123 reaching the final step defined as “temporary high forest” (a forest that has the structure of a
124 monolayered high forest, but that, at the same time, originated from sprouting). The application
125 of a seeding cut (i.e. to provide growing space for the regeneration to establish and shelter for the
126 young developing seedlings) on the temporary high forest represents the end of the conversion
127 process, producing an even-aged high forest stand. Most of the CCHF plots are currently
128 between the second and the third thinning and the trees are 70-75 years old, with some standards
129 > 100 years old.

130 2.2 Sampling design

131 Monitoring and conservation actions were carried out in a study area of 54 ha, including beech
132 forest, afforestation, and shrubland. Among beech forests, 24% were publicly owned (CCHF) and
133 76% were private (OC that have passed the traditional rotation period). Therefore, a stratified
134 sampling design was used to select plots managed as OC and CCHF. A total of 31 plots,
135 established at the nodes of a 100x100m grid overlaid by beech forest cover, were selected. The
136 number of plots was set in relation to the area occupied by each management system, i.e., 10 in
137 CCHF and 21 in OC stands (Fig. 1).

138 We used baited pitfall traps to sample the carabid community in the study area. Catches with
139 pitfall traps can be used to estimate the density of carabid beetles (Baars, 1979), but as stressed
140 by several authors (e.g. Niemela et al., 1993; Kinnunen et al., 2001), they are better adapted for
141 comparing species richness, abundance and Shannon diversity between different habitats
142 (Andorkó and Kádár, 2006; Máthé, 2006) or, as in our case, between different forest management
143 systems (du Bus de Warnaffe and Lebrun, 2004).

144 In each sampling plot, five pitfall traps were arranged according to a Latin square design, i.e., at
145 the four vertices and at the center of a 20 m-wide square. Pitfall traps were placed at the end of
146 May 2013 and emptied on average every four days (ranging from three to six) until the end of
147 August (equal to 18 sampling periods). Each trap (7.5 cm diameter and 9 cm deep) was
148 assembled with a double bottom in order to keep animals alive, and filled with 150 ml of vinegar
149 as an attractant (van den Berghe, 1992). A flat stone was positioned 3 cm above each trap to
150 prevent flooding. Identification of the carabids was carried out in the field following the
151 nomenclature of Audisio and Vigna Taglianti (2004).

152 *Thermo/Hygro Button 23* loggers (Maxim Integrated Products, Inc., Sunnyvale, CA, U.S.A.)
153 were used to record temperature and relative humidity in each sampling point. The buttons were
154 fixed to wooden poles (2 cm above the soil surface) and were sheltered from rain by means of a
155 plastic roof. The data loggers measured the temperature and the relative humidity every 1 h and
156 were run for the entire sampling period (about three months). In the lab, we computed mean,
157 minimum, and maximum temperature and relative humidity for each of the 18 sampling periods.
158 Topography was characterized by extracting the elevation, slope, and ‘southness’ (i.e., a
159 linearization of aspect: Chang et al., 2004) from a 10-m gridded digital terrain model. Elevation
160 was not considered in statistical analysis because differences among sampling points were very
161 small (ranging from 1090 to 1450 m a.s.l.).

162 At each plot, forest and vegetation structure was described by measuring: species and diameter at
163 130 cm height (diameter at breast height, DBH) of all living trees with DBH > 2.5 cm; diameter,
164 length and decay class (Motta et al., 2006) of all standing dead trees (snags) with DBH > 2.5 cm;
165 length and decay class of logs (diameter > 5 cm, length > 100 cm) and stumps (diameter at the
166 ground level > 2.5 cm, height < 130 cm); and, canopy cover by means of two hemispherical
167 photographs taken from the plot center at a height of 80 cm from the ground (digital camera set
168 at 400 ISO and F8). The images were masked for terrain and automatically thresholded (Nobis
169 and Hunziker, 2005). Canopy cover was computed as the ratio of (1 - sky pixels) to the total
170 number of pixels, and averaged between the two images; species and height of regenerating trees
171 (DBH < 2.5 cm and height > 10 cm).

172 Additionally, the following variables were measured: percent cover of each plant species (Braun-
173 Blanquet, 1932); percent cover of the regeneration layer, shrubs, herbs, bare soil, and litter; fine
174 (branches, twigs, logs with diameter <5cm, FWD) and coarse woody debris (logs with DBH>5

175 cm, CWD); rocks in four size classes (<10 cm, 10-40 cm, 40-100 cm, and > 100 cm in mean
176 diameter) within a concentric 5m radius circular plot; and, species and number of seedlings
177 (height < 10 cm) within four 1x1m square subplots, located at the outer edge of the regeneration
178 plot along four orthogonal directions.

179

180 2.3 Data analysis

181 We computed standard forest structure descriptors for each plot, i.e., tree density, basal area,
182 quadratic mean diameter (QMD), and relative beech abundance in the total basal area. Tree size
183 heterogeneity was assessed by computing the range, standard deviation, skewness, and kurtosis
184 of the DBH distribution of live trees. The volume of CWD (standing dead trees, logs and stumps)
185 was computed by applying National Forest Inventory yield tables for beech (Castellani et al.,
186 1984) in the case of standing dead trees, and Smalian's formula (Bruce and Schumacher, 1950)
187 for logs and stumps. Vegetation structural parameters were compared between coppice and high
188 forest by means of Kruskal-Wallis two-sample tests, with a correction for multiple comparisons
189 (Benjamini and Hochberg, 1995).

190 Characteristic carabid species in OC and CCHF were identified by means of the Indicator Value
191 (IndVal) procedure (Dufrière and Legendre, 1997). This method identifies quantitatively the
192 characteristic species of each forest management system, and generates a significance value (p)
193 for the strength of association using a randomized resampling technique. The IndVal of a species
194 is expressed as a product of the specificity and fidelity measures. In our study, it reaches a
195 maximum (100) when all individuals of a species are found within a single management system

196 (high specificity), and when the species occurs at all plots of that type (high fidelity) (Dufrêne
197 and Legendre, 1997). IndVal was calculated by means of the R package *labdsv* (Roberts, 2013).

198

199 2.3.1 Effect of macrohabitat variables

200 For each sampling point and sampling period we pooled data because of equal sampling effort
201 across points (i.e. no pitfall trap was lost). The effects of forest management history, topographic
202 and climatic variables were therefore run on a matrix with 558 observations (i.e. 31 points x 18
203 periods). Afterwards we computed the sum of relative abundances for each species (hereafter
204 total abundance or N), species richness (S), abundance of the endemic species *Carabus olympiae*
205 (CO_N), and Shannon diversity (i.e., the exponential of the Shannon-Weaver index - Shannon
206 entropy; Jost, 2006) for each observation.

207 To test for differences in abundance and diversity (N, S, CO_N and H') between management
208 systems, we used Generalized Additive Mixed Models (GAMMs) (Equation 1). We specified
209 management system, mean temperature, mean humidity, aspect and southness as fixed factors.
210 Sampling plot was specified as a random factor to account for repeated measures of the same
211 plots over successive visits. Visual inspection of scatter plots suggested highly non-linear
212 seasonal trends, so sampling period was fitted with a smoother. The GAMM models were
213 compared to linear mixed models (GLMMs), and were found to provide a much better fit (ΔAIC
214 > 2 , Burnham and Anderson, 2002), hence justifying their use.

215 The optimal degree of smoothing was identified by cross-validation, and a gamma value of 1.4
216 was specified in order to minimise overfitting (Zuur et al., 2009) and provide a more
217 conservative estimated degrees of freedom (edf). The higher the edf, the more non-linear is the
218 smoothing spline (a GAMM with edf = 1 is a straight line). A log-transformed offset term was

219 included to account for the variable number of hours in which the traps were active for each
220 sampling period.

221 (1)

222 $y = \text{intercept} + \text{offset}(\log(\text{hours sampling})) + \text{management} + TM + HM + \text{slope} + \text{southness} + f(\text{period}) + 1 | \text{plot}$
223

224 For the only categorical fixed factor in the models (i.e. management history), CCHF was chosen
225 as the reference category. GAMMs were run using the R packages *mgcv* and *MASS* (Venables
226 and Ripley, 2002; Wood, 2011).

227

228 2.3.2 Effect of vegetation and structural variables

229 In order to identify which vegetation and/or structural variables were driving carabid total
230 abundance and diversity (and so which may have explained overall differences tested for above),
231 we fitted a series of generalized linear models (GLM) to each of the response variables (N, S,
232 CO_N and H'). Vegetation structure was measured only once for each sampling point, therefore
233 GLMs were run on a matrix with 31 observations (i.e. the sampling 31 points), and response
234 variables were calculated over the whole period. Predictors were selected by running a
235 regression-based Random Forest, an ensemble machine learning method which extends
236 classification and regression trees (Breiman, 2001). Random Forests have been successfully
237 applied for variable reduction in datasets with high dimensionality and correlated predictors
238 (Genuer et al., 2010). We used the *randomForest* package for R (Liaw and Wiener, 2002), with
239 the following settings: number of trees to build = 999, minimum size of terminal nodes = 3, size
240 of predictor subset = $\frac{1}{3}$ (number of original predictors). For each dependent variable, we fitted a

241 random forest and computed the permutation importance index (incMSE) associated with each
242 predictor, i.e., the percent increase in mean square error of a tree in the random forest when the
243 values of that predictor are randomly permuted. Predictors with incMSE >0 were retained and
244 entered in to GLMs; each GLM was fitted with a stepwise algorithm using 99 maximum
245 iterations. We assessed a model's explanatory power by the percent deviance explained, and
246 effect size and direction of each predictor by its standardized regression coefficient.

247 For count data (both in GAMMs and in GLMs), on the basis of the outcomes of an
248 overdispersion test (via the *qcc* package for R, Scrucca, 2004), we chose a Poisson error
249 distribution for R and a negative binomial error distribution for N and CO_N. H', being a
250 continuous response variable that has always positive values, was modeled by a Gamma
251 distribution with a log link function (McIntyre and Lavorel, 1994; Zuur et al., 2009). Note that
252 the estimate of total abundance will likely overestimate true abundance as it is possible that
253 some individuals were caught on successive occasions. Nevertheless, given that sampling effort
254 was constant across plots, pooling all visits provides a relative measure of abundance between
255 sites. We constructed variograms to assess the degree of spatial autocorrelation in the data. There
256 was no strong evidence of spatial autocorrelation (Appendix I), hence this was not considered
257 further.

258 All analyses were carried out using the R statistical framework, version 3.0.2 (R Core Team,
259 2014).

260

261

262

263 **3. Results**

264

265 *3.1 Vegetation and structure of OC and CCHF*

266 Despite the two different forest management histories, most beech forests had a high
267 compositional (beech > 80%) and structural homogeneity, full canopy cover (> 85%), and very
268 limited regeneration, understory or herbaceous layers (soil cover by strata: 0.5%, 4%, and 3% on
269 average) (Table 1). Only two variables were significantly different, OC stands having higher tree
270 density and lower QMD than CCHF (Table 1). CWD was higher in OC stands, but not
271 significantly so after correction for multiple comparisons. Most variables, however, had a similar
272 range of variability between management systems and a large coefficient of variation within each
273 (25 to 540%, except canopy cover, % beech and QMD), indicating that micro-environmental
274 conditions can assume different characteristics regardless of forest management.

275

276 *3.2 Ground beetle assemblage and effect of macrohabitat variables*

277 A total of 13 species (3073 individuals) of three sub-families (Carabinae, Pterostichinae and
278 Platyninae) were collected during the eighteen sampling periods. All trapped species were
279 medium and large-bodied predators and, except macropterous *Platynus complanatus*, they were
280 brachypterous (Brandmayr et al., 2005). Five species preferred OC to CCHF: *C. olympiae*
281 (IndVal = 14.1; $p < 0.01$), *C. depressus* (25.8; $p < 0.001$), *P. flavofemoratus* (33.1; $p < 0.001$), *P.*
282 *spinolae* (26.9; $p < 0.01$), and *P. appeninus* (30.2; $p < 0.001$). *A. exaratus* (37.6; $p < 0.05$) and *A.*
283 *continuus* (7.1; $p < 0.001$) preferred CCHF.

284 Management system affected total abundance, species richness, abundance of *C.olympiae* and
285 Shannon diversity: all dependent variables were significantly higher in OC stands than in CCHF
286 (Table 2, Fig. 2). Total abundance and species richness responded positively to mean temperature
287 and negatively to mean relative humidity, whereas abundance of *C.olympiae* was positively
288 related to humidity. All response variables were negatively associated with slope, while
289 southness had a negative effect only on total abundance.

290 The smoother for sampling period was significant for all dependent variables ($P < 0.001$, Table 1).
291 The models fitted to total abundance, species richness and Shannon diversity showed a non-
292 linear decreasing trend. The smoothing curve for the abundance of *C.olympiae* showed a
293 different shape with a clear peak in the central part of the sampling season (Fig. 3).

294

295 *3.3 Effect of vegetation and structural variables*

296 After variable reduction by random forest (Fig. 4), we entered seven predictors in the GLM for
297 *Carabus olympiae* relative abundance (i.e., CWD volume, QMD, tree density, canopy cover, bare
298 soil, FWD and CWD cover), six for species richness (beech abundance, DBH standard deviation,
299 DBH range, regeneration density, CWD volume and CWD cover), four for total abundance
300 (DBH standard deviation, regeneration density, herb cover, and regeneration cover), and nine for
301 Shannon diversity (CWD volume, QMD, basal area, tree density, rocks, bare soil, CWD, herb
302 cover, and management system).

303 Total abundance, Shannon diversity and abundance of *C.olympiae* were strongly influenced by
304 several vegetation and forest structural variables; deviance explained was 44.8%, 55.7%, and
305 34.8%, respectively. Conversely, no variables could explain carabid species richness.

306 Volume or cover of CWD played an important role in forest carabid diversity, having a strong
307 positive effect on total abundance, Shannon diversity and abundance of *C.olympiae* (Table 3).
308 Total carabid abundance was also associated with higher tree size variability and herb cover.
309 *Carabus olympiae* abundance was negatively affected by bare soil cover and positively by
310 canopy cover. Finally, Shannon diversity was negatively associated with QMD (Table 3).

311

312

313 **4. Discussion**

314 *4.1 Vegetation and structure of OC and CCHF*

315 OC stands had significantly higher density, significantly lower QMD, and higher CWD and tree
316 size variability than CCHF, due to their different management histories. In OC, stems sprouted in
317 1960 have undergone intense light competition, which has produced, together with the retention
318 of larger seed trees, a higher size differentiation, and greater competition-induced mortality.
319 Conversion to high forest is carried out by selecting the best stems on each stump, so tree sizes in
320 CCHF were much more uniform, tree density was lower, and mortality did not occur. Other
321 microhabitat variables, however, had a similar range of variability between management systems
322 and a large coefficient of variation within each, indicating that micro-environmental conditions
323 can assume different characteristics regardless of forest management.

324

325 *4.2 Microclimate and topography*

326 The occurrence of ground beetles may depend on microclimatic factors such as humidity
327 (Epstein and Kulman, 1990, Niemelä et al, 1992) and air temperature (Thiele, 1997). Usually,

328 forest species prefer cooler and moister sites, characterized by small fluctuations over time
329 (Pearce and Venier, 2006). These conditions occur in stands characterized by limited natural or
330 anthropogenic disturbance, where a closed canopy moderates ground surface conditions. Within
331 this microclimatic framework, we have unexpectedly found that relative abundance and species
332 richness responded positively to mean temperature and negatively to mean relative humidity.
333 Conversely, *Carabus olympiae* relative abundance increased with mean humidity.
334 Mean humidity and temperature could be used as indirect measures of habitat complexity. Lower
335 percentages of canopy cover cause an increase in mean temperature and a decrease in mean
336 humidity, but can also promote the growth of grasses and shrubs that are important for providing
337 hunting and foraging niches and protection from predator and desiccation.
338 The occurrence of ground beetles may also depend on topographic features (Negro et al., 2007).
339 In particular, carabid diversity was negatively associated with slope, as found by Thiele (1977)
340 and Lövei and Sunderland (1996). In our study area, beech forests characterized by steep slopes
341 had low structural variability, due to the lower amount of coarse wood debris and leaf litter that
342 are removed by gravity and surface runoff water (Johnson and Lewis, 1995). Therefore, we
343 believe a lack of shelters and the reduced presence of favorable microhabitats reduces the
344 diversity of carabids.

345

346 *4.3 Management systems*

347 Much research has found that ground beetles respond to different forest management systems
348 (Werner and Raffa, 2000; du Bus de Warnaffe and Lebrun, 2004; Pearce and Venier, 2006). In
349 this study, the diversity of forest specialist carabids was higher in OC. The last harvest of coppice
350 stands in our study site was carried out more than 50 years ago, whereas conversion to high

351 forests began about 20 years ago. It may therefore appear that, irrespective of the management
352 type, the long period of absence or low intensity of forest management has enhanced ground
353 beetle diversity. The five species (*C. olympiae*, *C. depressus*, *P. flavofemoratus*, *P. spinolae* and
354 *P. appeninus*) that significantly selected OC stands (IndVal analysis) are wingless with low
355 dispersal power which may prevent them from quickly recolonizing recently harvested stands
356 (Niemela et al., 1993; Spence et al., 1996).

357 The cessation of silvicultural disturbances may benefit forest specialist carabids (du Bus de
358 Warnaffe and Lebr, 2004; Toigo et al., 2013), as well as other animal groups such as birds
359 (Laiolo et al., 2004) and amphibians (Hicks and Pearson, 2003). When abandonment of forest
360 management results in more heterogeneous light conditions on the ground, open-habitat species
361 may also be favored (Toigo et al., 2013). However, in our case, canopy cover was very high, both
362 in OC and in CCHF (89% on average). This has hindered the colonization by species that select
363 neighboring open areas (Negro et al., 2013) which could disfavour typical forest species by
364 competition (du Bus de Warnaffe and Lebr, 2004).

365

366 *4.4 Structural Variables*

367 Carabids are strongly sensitive to changes in forest heterogeneity and respond to structural
368 variables (Taboada et al., 2010). Microhabitat complexity was a powerful predictor of the total
369 abundance of pitfall-trapped beetles. We detected a positive response of several diversity
370 variables to CWD cover or volume, herb cover, and standard deviation of tree diameter
371 distribution. In a similar study, coarse woody debris, snag volume, gap area, understory
372 vegetation and forest floor depth were all critical in structuring beetle communities (Latty et al.,
373 2006).

374 Volume or cover of coarse woody debris had a strong positive effect on N, CO₂ and H₂. CWD
375 volume ha⁻¹, in particular, was about twice as large in OC stands (11 m³ on average) than in
376 CCHF stands (6.8 m³), although the difference was not significant after correcting for multiple
377 comparisons. Woody debris, such as branches, logs, and twigs, is a major habitat feature on
378 forest floors (Jonsson et al., 2005). In mature or restored forests, it provides a set of microsites
379 that offer food and habitat resources to several arthropods, such as saproxylic organisms
380 (Siitonen, 2001; Komonen et al., 2014), soil mites (Johnston and Crossley, 1993) and carabids
381 (Hanula et al., 2009). In particular, it is an important resource for many ground beetle species as
382 an overwintering site, and for ovipositioning and larval development (Larochelle and Lariviere,
383 2003; Bousquet, 2010). In fact, in sampling points characterized by higher levels of CWD, we
384 also trapped seven *Carabus olympiae* in the third instar larval stage.

385 Shannon diversity was negatively associated with mean tree diameter, which was significantly
386 larger in CCHF. A more diverse array of tree sizes and a mosaic of patches covered by trees and
387 herbs may provide a greater number of potential ecological niches, for both carabids and their
388 prey (e.g., snails: Müller et al., 2005), than in less complex forests (Klopfer and MacArthur,
389 1960; Day and Carthy, 1988). This, together with CWD, may partly contribute to explaining why
390 the diversity of ground beetles was lower in CCHF.

391 *Carabus olympiae* abundance was negatively related to bare soil cover. Bare ground, defined as
392 exposed soil deprived of vegetation, is not considered a suitable habitat (Fry and Lonsdale, 1991;
393 Key, 2000) for many insect groups. Often, it is the result of the erosive action of rainwater, which
394 is particularly strong on steeper slopes, that leads to a reduction of vegetation and microhabitat
395 complexity (Fayt et al., 2006).

396 The previous results can be used to formulate management recommendations to maintain carabid
397 diversity in beech stands of Northern Italy. Currently, abandoned coppices are a more favorable
398 habitat. However, succession will lead to more homogenous stand structures, due to the natural
399 tendency of beech to form closed and monolayered canopies. Since coppicing beyond rotation
400 age (30 years) has not been allowed in the region since 2011, because beech is known to lose the
401 capability to regenerate vegetatively after 40 years (Hofmann, 1963), this dynamic could be
402 avoided by silvicultural interventions aimed at increasing structural and microhabitat diversity.
403 Conversion to high forest should therefore be carried out by avoiding traditional gradual thinning
404 and: 1) retaining large trees or whole stumps in order to favor tree size differentiation (Barbalat
405 and Getaz, 1999) and the creation of future large snags (Motta et al., Submitted); 2) creating
406 canopy gaps in order to maintain a mosaic of patches covered by trees, herbs, and shrubs as a
407 consequence of varying light conditions on the ground; 3) releasing standing dead trees and
408 woody debris of all sizes (e.g. $> 20 \text{ m}^3 \text{ ha}^{-1}$: Brunet et al., 2010; Paillet et al., 2010).

409 Nevertheless, any intervention of forest management can result in strong local impacts on
410 carabid assemblages due to tree-cutting and logging. Gunnarsson et al. (2004) found that
411 extensive logging residue removal leads to impoverished species richness of Coleoptera at a
412 local scale due to the reduction of microhabitat complexity. For this reason, the establishment of
413 some small ageing stands, managed as strict reserves, where any kind of human intervention is
414 banned, should provide refuges for specialized forest carabid species characterized by low
415 vagility (Kotze and O'Hara, 2003).

416 More research needs to be carried out to elucidate the tradeoffs between positive and negative
417 impacts of silvicultural interventions on carabid diversity, i.e., mechanical disturbance as

418 opposed to the opportunity of regulating the mosaic of patches and producing woody debris of
419 multiple decay classes.

420

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422

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430

431 **Table captions**

432

433 Table 1: Descriptive statistics of vegetation and structure in over-mature coppices (OC; N = 21
434 sampling plots) and coppices in conversion to high forests (CCHF; N = 10 sampling plots).
435 p: significance of a two-sample Kruskal-Wallis test, corrected for multiple comparisons
436 (Benjamini and Hochberg, 1995).

437

438 Table 2: Coefficients for GAMM of *Carabus olympiae* abundance and carabid diversity indices
439 (n= 558 = 31 plots x 18 sampling periods). For the categorical fixed factor (i.e. management
440 system) CCHF was chosen as the reference category.

441

442 Table 3: Standardized regression coefficients from GLM of *Carabus olympiae* abundance and
443 carabid diversity indices (n= 31 plots).

444

445

446 **Figure captions**

447

448 Fig. 1 Study area (geographical reference system: UTM WGS 1984, zone 32N) and location of
449 sampling plots [black circles: over-mature coppices (OC), black triangles: coppices in conversion
450 to high forests (CCHF)].

451

452 Fig. 2 *Carabus olympiae* abundance and carabid diversity indices as a function of forest
453 management system.

454

455 Fig. 3 GAMM smoothing plots for *Carabus olympiae* abundance and carabid diversity indices.

456

457 Fig. 4 Standardized variable importance scores (incMSE) from Random Forest regression for
458 *Carabus olympiae* abundance and carabid diversity indices.

459

460

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697 **Table 1**

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Variable	Description	CCHF			OC		p
		units	mean	std.err.	mean	std.err.	
canopy	% canopy cover by hemispherical photography	%	89.29	0.62	90.29	0.7	0.662
regeneration	% soil covered by regeneration	0-1	0.01	0	0	0	0.662
shrubs	% soil covered by shrubs	0-1	0.03	0.03	0.05	0.03	0.878
herbs	% soil covered by herbaceous vegetation	0-1	0.02	0.01	0.04	0.03	0.878
litter	% soil covered by litter	0-1	0.78	0.05	0.77	0.04	0.878
CWD	% soil covered by coarse woody debris	0-1	0.02	0	0.02	0	0.966
FWD	% soil covered by fine woody debris	0-1	0.04	0.01	0.03	0	0.29
bare soil	% soil covered by bare soil	0-1	0.04	0.01	0.03	0.02	0.29
rocks	% soil covered by rocks (all sizes)	0-1	0.07	0.03	0.04	0.01	0.897
tree density	trees per hectare	ha ⁻¹	894.92	59.97	2182.08	180.12	0.001*
seedlings	seedlings per hectare	ha ⁻¹	519.35	305.45	517.07	170.8	0.662
basal area	cumulative tree basal area	m ² ha ⁻¹	28.3	1.52	31.08	1.6	0.426
QMD	quadratic mean diameter	cm	20.36	0.77	13.79	0.45	0.001*
tree volume	comulative aboveground tree volume	m ³ ha ⁻¹	243.11	17.04	217.29	10.73	0.29
CWD volume	comulative volume of coarse woody debris	m ³ ha ⁻¹	6.84	1.18	11.13	1.72	0.29
dbh range	range of tree diameters	cm	31.77	1.63	34.88	2.26	0.662
dbh skewness	skewness of tree diameter distribution	-	0.8	0.1	1.3	0.1	0.101
dbh kurtosis	kurtosis of tree diameter distribution	-	3.8	0.3	5.4	0.7	0.29
dbh st. dev.	standard deviation of tree diameter distribution	cm	7	0.48	6.62	0.3	0.878
% beech	percent beech by basal area	0-1	0.97	0.01	0.95	0.01	0.29

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702 **Table 2**

Carabus olympiae abundance
Family: Negative binomial
Link: log

	Estimate	SE	P
intercept	-7.02	0.24	<0.001
management : OC	0.62	0.26	<0.05
mean humidity	0.33	0.14	<0.05
slope	-0.35	0.12	<0.01
smooth term	edf	F	P
period	3.25	11.12	<0.001

Total abundance
Family: Negative binomial
Link: log

	Estimate	SE	P
intercept	-3.69	0.17	<0.001
management : OC	0.58	0.20	<0.01
mean temperature	0.14	0.07	<0.05
mean humidity	-0.14	0.05	<0.01
slope	-0.21	0.09	<0.05
southness	-0.20	0.09	<0.05
smooth term	edf	F	P
period	7.78	32.45	<0.001

Species richness
Family: Poisson
Link: log

	Estimate	SE	P
intercept	-4.30	0.10	<0.001
management : OC	0.40	0.12	<0.001
mean temperature	0.14	0.04	<0.001
mean humidity	-0.06	0.02	<0.01
slope	-0.14	0.05	<0.05
smooth term	edf	F	P
period	2.74	66.20	<0.001

Shannon Diversity
Family: Gamma
Link: log

	Estimate	SE	P
intercept	-4.28	0.06	<0.001
management : OC	0.23	0.07	<0.01
slope	-0.10	0.03	<0.01
smooth term	edf	F	P
period	2.23	42.6	<0.001

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707 **Table 3**

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***Carabus olympiae* abundance**

Family: negative binomial
Link: log

	Estimate	SE	P
intercept	1.24	0.11	< 0.001
bare soil	-0.73	0.18	< 0.001
canopy	0.27	0.09	< 0.01
CWD volume	0.19	0.08	< 0.05

Deviance explained = 55.7%

Total abundance

Family: negative binomial
Link: log

	Estimate	SE	P
intercept	4.55	0.07	< 0.001
herbs	0.17	0.07	< 0.05
CWD cover	0.21	0.08	< 0.01
seedlings	0.12	0.07	N.S.
dbh st. dev.	0.28	0.07	< 0.001

Deviance explained = 44.8%

Shannon diversity

Family: Gamma
Link: log

	Estimate	SE	P
intercept	1.44	0.04	< 0.001
CWD cover	0.10	0.04	< 0.05
QMD	-0.10	0.04	< 0.05

Deviance explained = 34.8%

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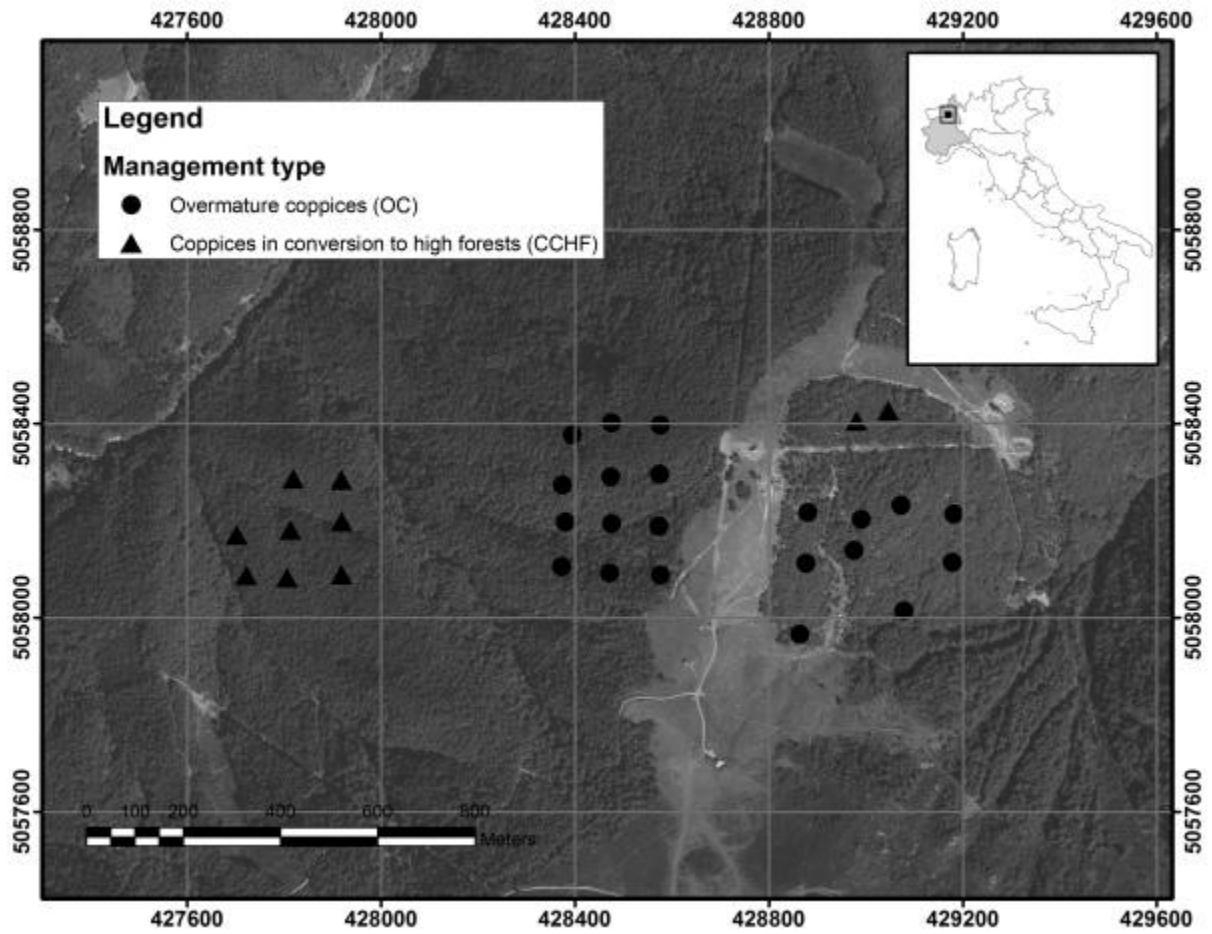
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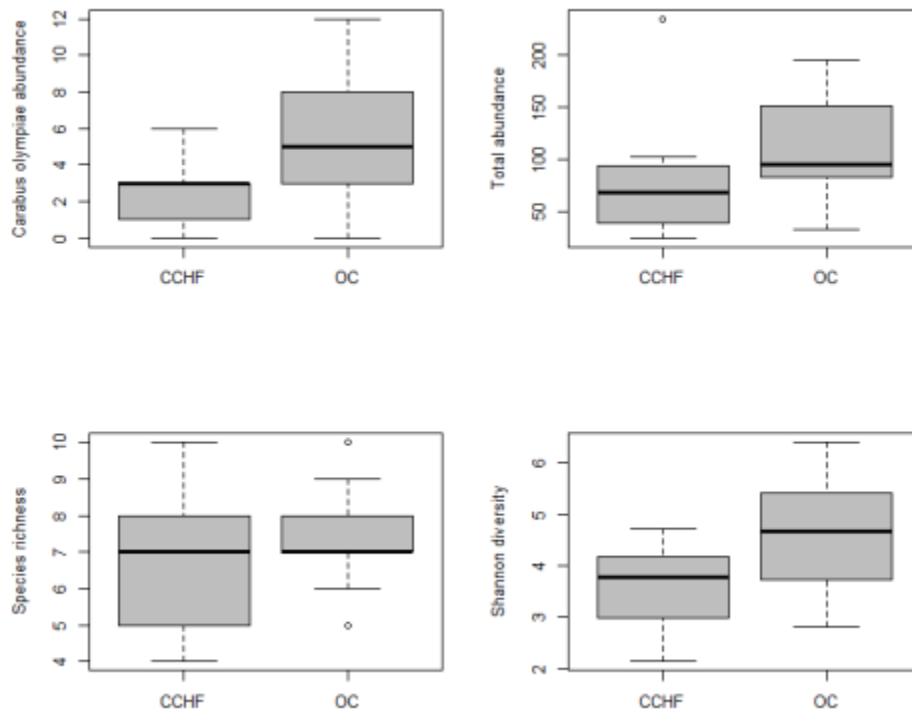
718 **Fig. 1**



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720 **Fig. 2**

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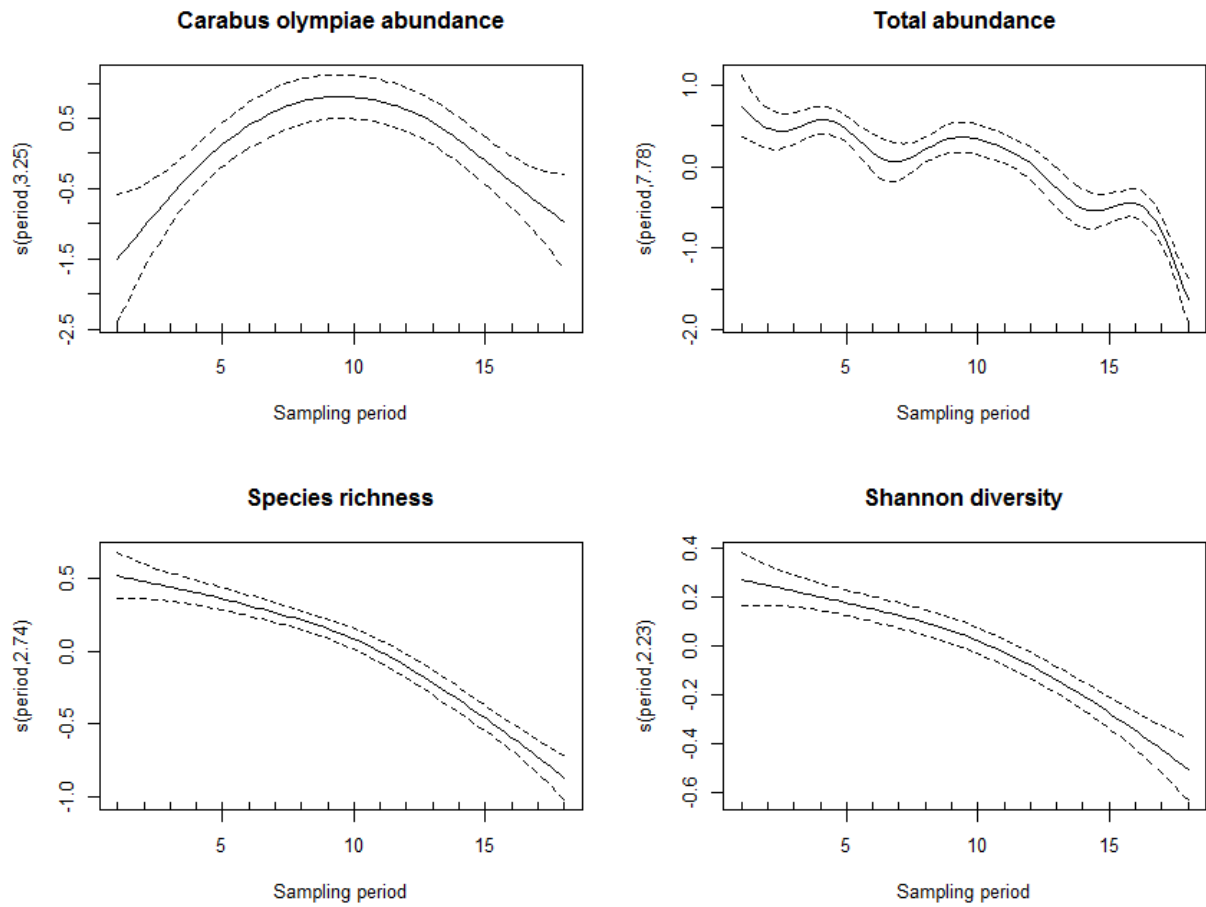
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725 **Fig. 3**

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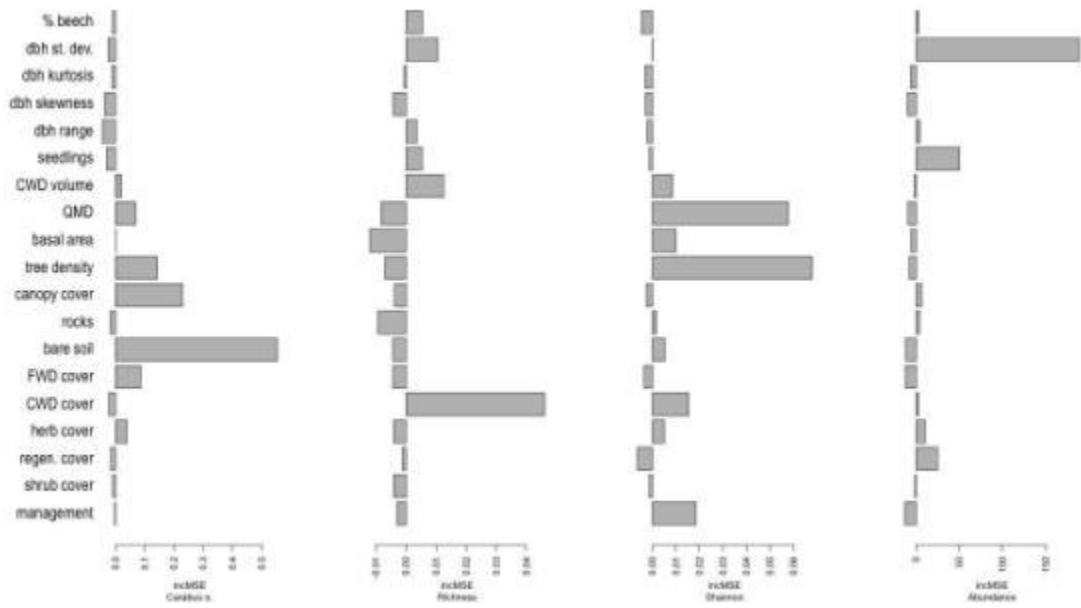
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729 **Fig. 4**

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**Dear Dan Binkley
Editor-in-Chief
Forest Ecology and Management**

we return the revised version of our paper entitled “Effects of forest management on ground beetle diversity in alpine beech (*Fagus sylvatica* L.) stands”. The text has been modified to conform to the journal’s format and according to the referees’ suggestions. Whilst we have attempted to address the referees’ comments as far as possible, we are also mindful of the need to reduce the length of the paper – for some points raised we have therefore been fairly brief. We hope we have managed to maintain the right balance between relevant additions and excessive detail. We have managed to reduce the text from 8679 to 7800 words. If the text is still too long, we would greatly appreciate some editorial guidance on where best to shorten the paper.

We give our detailed responses to the comments raised below.

Reviewer #1: Comments:

The paper deals with beech forest in Northern Italy, and investigates the carabid fauna in two types of beech forest with different management history: over-mature coppice and coppices in conversion to high forest. It concludes that over-mature coppice is the most favourable habitat at present, but this will change as they too turn into more homogenous forests.

The study is interesting, the statistics rigorous and very sound and the manuscript is well written, although wordy. The discussion is well written and raises some important points.

* The main improvement potential is related to the length - it would gain in readability and impact by shortening and focusing the text.

We have attempted to shorten the text where possible (although given the additions requested by the referees, this was not always possible) and we have tried to be more focussed (in particular, stressing that the paper concerns forest-dwelling species with low dispersal power).

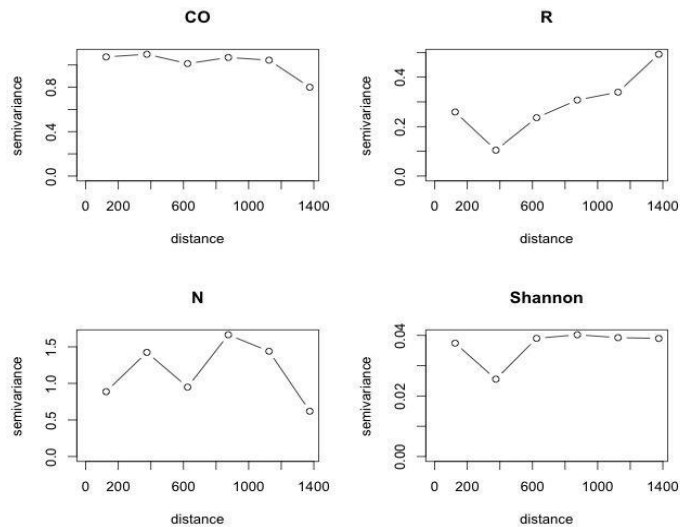
* But at the same time it is important to describe the relevant management systems properly, for readers not familiar with these types of forests. In my opinion, this can be improved. I miss a short, to-the-point description of this early in the paper - maybe move some of the description from Methods to Intro. I would also have liked some photos, maybe in Supplementary, to illustrate the two systems that are contrasted. It is important to remember that a limited proportion of the world's foresters or forest ecologists know this specific system.

We have described the beech management systems in the introduction adding these sentences: “Most beech forests in Italy are currently managed as coppice, i.e., by repeatedly cutting back shoots to ground level to stimulate vegetative growth and provide firewood on a short rotation basis (20 to 40 years). High forests where trees are

regenerated by seed are rare. However, many coppices are now transitioning to a high-forest structure, due to either the abandonment of regular management, or silvicultural conversion by thinning (Nocentini, 2009)". Furthermore, we have slightly re-structured the Introduction (see also Ref. #2) so reference to specific forest management practices comes earlier.

* The only other overall question I have is whether spatial autocorrelation should have been considered or at least discussed? The sites of the same type are mostly aggregated, to what degree could this represent a confounding factor?

We computed a variogram on residuals from all our GLM, and none showed evidence of spatial autocorrelation between plots, i.e., increasing variance with distance between plots. Only richness exhibited some degree of correlation, but since the richness model could not be fit with any of our predictors, we did not consider this finding further. The variograms are produced below, but we also add these in an Appendix (intended as online supplementary material) to the paper.



Minor points:

* l.52: a comma is missing after parenthesis

OK

* l. 63: mykorrhizal

The correct word is mycorrhizal

* l. 66: improve - e.g. by writing "different degrees of canopy closure and different age structures"

In shortening the paper, this part has been removed so is no longer relevant.

- * l. 70 : uneven-aged

OK

- * l. 87: rewrite, e.g. edges between forest and open habitat

We rewrote the sentence

- * l. 91-92 and l. 113-114: I find the use of "management" a bit confusing here, and several other places in the text. Is abandoned coppice still a management? Or would the wording "management history" be better?

For the most part, we have referred to management history, as we agree with the referee that 'management' implies something more current. However, we have sometimes used the term 'management' to give a better flow to the text.

- * what do you mean by ecological stability here?

We cut this part in order to shorten the introduction

- * l. 104-107: the % are a bit confusing. Are they supposed to sum to 100%?

We cut this part in order to shorten the introduction

- * l.126-138: lots of narrow scientific terms here - could they be interchanged for broader readability among non-specialists? Like steno-endemic, equinoctial, inceptisols, cambic, udic....

According to reviewer #1 and #2 we changed the word "steno-endemic" with the simpler word "endemic"

- * l. 138: Mycota. Maybe write fungi in parenthesis?

We deleted information provided on fungi as suggested by reviewer #2

- * l. 155: explain seeding cut in this system

We specified in the text that the meaning of seeding cut is "to provide growing space for the regeneration to establish, and shelter for the young developing seedlings"

- * l. 165: what do you mean by politically owned??

We changed "politically owned" to "publicly owned" as also suggested by the referee #2

* l. 175: why using attractants? Isn't there a risk that you get biased results, if it works differently in the different forest types or for different species? I would think you would be interested mainly in measuring the activity around the traps as such?

We report the same answer given to reviewer #2: In this study we used double-bottom pitfall traps to catch live insects, as *Carabus olympiae* is a conservation priority species, and using a preservative agent such as ethylene glycol would have been fatal. We used vinegar to slightly increase the capture efficiency of the traps; forest species are quite similar in their autoecology (they are all predators, medium or large-bodied and brachypterous) and so they were attracted alike. Moreover our comparisons were always relative (differences between management systems, etc.), and never absolute. We have not, for example, provided density values in the results. We now provide further justification of our method in relation to measurement of abundance in the text (sections 2.3.1 and 2.3.2).

Finally, this technique is standard, as evidenced by its use in several recent papers on carabids (e.g. Yu et al., 2006; Yu et al., 2007; Gobbi et al., 2007; Brandmayr et al., 2009; Giglio et al., 2011; Bettacchioli et al., 2012; Brigić et al., 2014 and so on)

* l. 196-198: I don't understand the coupling between the first and last sentence here

We changed the sentence to: “Additionally, the following variables were measured:...”

* l. 315: to, not than

OK

* l. 317 and 397: is it correct to use the term "actively selected"? You did not measure an active selection, like if you had done a 'cafeteria set-up' in lab? rather a distribution pattern?

OK, we deleted "actively selected"

* l. 360: no need to repeat the details - change the wording

We deleted details between brackets

* l. 398-400: This is confusing - why would they have to recolonize a CCHF stand - would they necessarily go locally extinct the because of the conversion cutting?

We changed the wording of the sentence

* l. 445: has not hass (and, curious: why is coppicing not allowed after 30 years?)

OK. We added in the text: “,because beech is known to lose the capability to regenerate vegetatively after 40 years (Hofmann, 1963),”

* l 454: there are several, newer studies on this that should be quoted here, e.g. from Sweden

We have quoted a number of relevant studies. We are not sure exactly to which study the referee is referring. We would be happy to include further relevant references if they could be specified.

* .l 480-481: no need to repeat ref's here

OK

Reviewer #2:

1. Overall justification for general investigation into species associations with forest management types is well-captured by the introduction, but the justification for focus on the specific measures used (e.g. abundance, diversity, and richness) of carabid beetle community are not well-explained. Rather than giving a broad overview of carabids as bioindicators (e.g. 77 - 90), the authors should try to extend our knowledge to more specific findings.

We justified the use of specific community parameter adding the following to the Introduction: "Furthermore, changes in carabid total abundance and species richness can be useful tools to evaluate the effects of human disturbance in forest ecosystems (Brandmayr et al., 2009)." and, with respect to the pitfall trapping method, this to the Methods: "Catches with pitfall traps can be used to estimate the density of carabid beetles (Baars, 1979), but as stressed by several authors (e.g. Niemela et al., 1993; Kinnunen et al., 2001), they are better adapted for comparing species richness, abundance and Shannon diversity between different habitats (Andorkó and Kádár, 2006; Máthé, 2006) or, as in our case, between different forest management systems (du Bus de Warnaffe and Lebrun, 2004)."

2. Given the implications of the study at the end, the introduction should really be refocused to have more on the ecology and habitat preferences of forest-dwelling species, particularly those that are large-bodied and 'with low dispersal power'. The introduction should provide more information on what other large-bodied species in this system have been worked on in detail, especially *Carabus olympiae*.

We have added more detail on forest-dwelling species with low dispersal power, citing a particular study on *Carabus olympiae*.

3. Use of the word steno-endemic - not a standard term that is widely used.

According to reviewer #1 and #2 we changed the word “steno-endemic” with the simpler word “endemic”

4. Multiple citations are provided for what are minor points (e.g. Lines 64 - 65), could probably trim these down in the next draft

We shortened the introduction and therefore reduced the number of citations

5. (Line 50) Reference for the EU Habitats Directive, I'm not sure about the format of this citation

We corrected the text with the reference from the website of european commission: "Habitats Directive" (92/43/EEC). We did the same thing with the "Birds Directive" (2009/147/EC) quoted in material and methods

6. (Lines 77 - 90) Authors are vague with the findings of other studies. E.g. Line 83 does not describe what 'sensitivity' to environmental factors actually means - do all species increase in abundance, or just some of them?

Responses in the carabid community that were evaluated by previous studies (e.g. richness, diversity, abundance) are lacking and could illuminate the reasons for selecting specific measures in this study. Need greater justification here.

We briefly quoted Brandmayr et al. (2006) in this regard, although we have not alluded to the findings of specific studies in the Introduction in the interests of shortening the text. We hope that the re-writing of the Introduction has made the general link between management and carabid community responses.

7. (Line 77) Use of the term 'integrity' is vague and normative. Not really clear what is implied here.

We agree with the reviewer's comment. We have changed the sentence.

8. (Lines 77 and 81-82) Some repetition of concept of indicator species here.

We simplified the sentence with: “Insects respond to stand structural complexity at different temporal and spatial scales, and they are strongly influenced by natural and anthropogenic disturbance (Kraus and Krumm, 2013). In particular, ground beetles (Coleoptera: Carabidae) cover a wide range...”

9. (Line 85) "Most of the studies..." should start as a new paragraph

OK

10. (Line 89 - 90) Final sentence in paragraph could be re-tooled to provide more insight into the species of interest for this paper. Opening phrase "Forestry affects mainly specialized forest species" sounds self-evident and could use a bit more punch.

This is re-worded as follows: " ...or forestry practices (Werner and Raffa, 2000; Pearce and Venier, 2006; Taboada et al., 2006). The latter affect particularly large-sized and brachypterous (short or reduced wings) habitat specialists, which have limited dispersal capacity (Kotze and O'Hara, 2003). "

11. At this point in the introduction would be a good place to introduce the issue of an endangered carabid beetle, while ecology of forest specialist species is being discussed.

We now make the initial reference to *Carabus olympiae* earlier (in the same paragraph as the above text).

12. (Lines 91 - 107) Paragraph on forest management and beech forests feels like it should come before the carabid beetle ecology paragraph, given the focus of this paper is leaning more towards the forestry management aspects than to the carabid beetle ecology (or ecology of endangered species). This would also make the final paragraph in the introduction (e.g. lines 108 - 119) seem less 'orphaned'.

We shortened the paragraph on forest management in beech forests and positioned it in the first part of the introduction (see also Ref #1).

13. Overview of next few comments - the references around endangered species and ecosystems are very European-centric and don't have the wider appeal or significance that the authors could aim for here. I would recommend less esoteric references and more reference links to widely-available policy.

We shortened the sentences and quoted the IUCN red list of Threatened species to give greater worldwide importance

14. (Line 109) "Site of Community Interest" reference and information provided around it [e.g. "Valsessera" (Biella province, Piedmont, north western Italy)] does not have any wider meaning and should be re-framed.

We rewrote the sentences in the text: "We focused on a group of localized, medium and large-bodied brachypterous ground beetles inhabiting beech forest in the north western Italian Alps. The study site, located in the Sessera Valley, The study site, located in the Sessera Valley, is part of Natura 2000 ecological network"

15. (Lines 111 - 112) Annexes II and IV of Habitats Directive doesn't bear much significance outside of the EU. Authors should also refer to the IUCN Red List, which *Carabus olympiae* is on, and which is of international importance and widely known.

We rewrote the sentence in the text: "... classified as a priority species in Annexes II and IV of the "Habitats Directive" (92/43/EEC) and considered Vulnerable according to the IUCN red list of Threatened species (<http://www.iucnredlist.org/>)"

16. (Lines 112) Reference to Bern and Washington (CITES) is not linked to any widely-available, specific policy document.

Reference to these has been deleted.

17. (Lines 133 - 134) Terminology and detail provided here is more appropriate to a soil ecology paper. Can possibly change the tone or omit if it's not in the direct line of investigation?

We omitted the sentences: "The bedrock is a complex overlay of metamorphic layers; soils are mostly inceptisols, deep and acidic, with a prevalence of cambic horizons and coarse textures. The moisture regime is udic."

18. (Line 138) Information provided on fungi would suggest a genera-level piece of information, not consistent with other elements in this sentence, which are only to larger taxonomic levels.

We deleted information provided on fungi

19. Reorganize first two paragraphs so that habitat description and rare species information occur in respective paragraphs. Same for information on the forest practices in the area. In general, paragraph structure in this section needs a bit of work.

We are not sure to which paragraphs the referee is referring – however, we hope that this comment is no longer relevant given the changes undertaken.

20. (Line 165) "Politically owned" means publicly or government owned?

We changed "politically owned" with "publicly owned"

21. (Line 175) Vinegar was used in traps for this study, which would not be recommended for a biodiversity study, as it would bias sampling towards those that are attracted to the smell. More recent papers (e.g. Schmidt et al. 2006) specifically recommend the use of ethylene glycol and water, though most other biodiversity surveys of arthropods use propylene glycol and water, owing to toxicity of ethylene glycol.

We report the same answer given to reviewer #1: In this study we used double-bottom pitfall traps to catch live insects, as *Carabus olympiae* is a conservation priority species,

and using a preservative agent such as ethylene glycol would have been fatal. We used vinegar to slightly increase the capture efficiency of the traps; forest species are quite similar in their autoecology (they are all predators, medium or large-bodied and brachypterous) and so they were attracted alike. Moreover our estimates were always relative (differences between management systems, etc.), and never absolute. We have not, for example, provided density values in the results.

Finally, this technique is standard, as evidenced by its use in several recent papers on carabids (e.g. Yu et al., 2006; Yu et al., 2007; Gobbi et al., 2007; Brandmayr et al., 2009; Giglio et al., 2011; Bettacchioli et al., 2012; Brigić et al., 2014 and so on).

We have not specifically addressed the use of the method, except to point out that it is very commonly used, and to stress that we consider relative measures. We could at the editor's request easily include a brief paragraph in the discussion which confronts the issues raised.

22. (Line 175) Animals were kept alive in the cup, which would lead to predation in the cup (even during the short collection time frame) and possibly result in an underestimation of some of the smaller-bodied or plant-eating species, further biasing results.

Animals were kept alive in the cup for a few minutes. We never saw any signs of predation in the cup (i.e. remains of predated individuals).

We did not underestimate the carabid diversity in the study site because the carabid assemblages inhabiting forest stands do not include plant eating species. These smaller bodies species actively select nearby open habitat areas dominated by grasses and shrubs. This has been demonstrated in a previous paper published in Biological Conservation (Negro et al 2013)

23. (Line 177) Identifications were carried out in the field, which may lead to misidentification of smaller-bodied species. There is no indication that sample specimens were removed for verification under laboratory conditions, which would be the recommended protocol.

We trapped all forest species (N = 13) inhabiting beech forests known from the area, and they are considered as medium/large species. The smallest one was *P. appenninus* with a length of 6-7.5 mm, but it is easily recognizable on sight. We have been studying this carabid assemblage for about ten years and we have developed considerable skill in the identification of the trapped species in the field. We therefore do not believe this presents a problem.

24. The authors do not say if beetles were released after identification or not - if they were, then this could bias the study yet again, as individuals are quite likely to be caught again in the same trap. The authors do not indicate that identified beetles were marked in any way, which would prevent re-counting of already-captured individuals.

If the unit of study had been the individual, or if each individual trap/visit had been considered as an independent data point, then there could have been statistical bias (i.e.

pseudoreplication). Furthermore, any measure of density, or an attempt to measure 'real' abundance would have been over-estimated given that we are likely sampling some of the same individuals on multiple occasions. This does not present a bias in the context of the paper for two reasons.

First, we consider a measure of relative abundance, i.e. we analyse the data using what is effectively an index of abundance (which we implicitly assume will be correlated with real abundance) which has been derived in the same way across all points, with an equal sampling effort. Relative comparisons are therefore valid. We now stress in the paper more strongly that we are using a measure of relative abundance which is in fact the sum of relative abundances of all species (which for brevity we still refer to as 'total abundance') rather than trying to estimate actual abundance. We explicitly define our terms in section 2.3.1, and stress that we are considering relative rather than absolute measures in section 2.3.2.

Second, for the visit-specific analysis, we have adopted a repeated measures design, which means we are taking repeated samples from the same subject (the beetle community around each plot in this case). This is taken into account statistically by including 'plot' as a random factor, hence we account for non-independence between plots. Removing individuals would have created a strict temporal autocorrelation which would have to have been statistically accounted for, but given the goal of the study, this complication was simply unnecessary. Use of marked individuals would have value, in particular if the goal of the study was to estimate actual population size. However, as stated above, our goal was to compare measures of relative abundance, using the same methods, between different management approaches. Our methods are sound for this purpose.

25. (Lines 233 - 245) Use of Generalized Additive Mixed Models appears to be correctly applied here, though it is a slightly unusual procedure for this particular investigation.

We are unsure if the referee is referring to the fact that these are mixed models or that they are additive, and hence used for the detection of highly non-linear trends. The use of Generalized Additive Mixed Models is supported in this ecological study by the fact that we have both fixed (mean temperature, mean humidity, southness, and aspect) and random (sampling plot) factors, and also as we took a repeated measures approach (see above). Moreover, visual inspection of scatter plots suggested highly non-linear seasonal trends, and AIC showed that a GAM provided a better fit than a linear model, and so sampling period was fitted with a smoother. For these reasons we used GAMMs.

26. AIC is used in the results (e.g. Table 2) but is not presented in the data analysis portion of the methods section.

We removed AIC values in the results and tables because they are usually used for comparative purposes. In our study no model comparison is presented, so they are not needed.

27. (Lines 310 - 314) Species listed are all large or medium-sized beetles, but there is no indication of their flight capabilities (some larger-bodied beetles are still capable of flight). Should also have some indication of their ecology (e.g. predatory), too

We added in the text: “All trapped species were medium and large-bodied predators and, except the macropterous *Platynus complanatus*, were brachypterous (Brandmayr et al., 2005)”.

28. The small diversity of species found (only 13 in the whole study) would suggest that a portion of the biota is missing here. Studies that have looked at carabid diversity in similar forests (see list at the end of this review) would suggest that this list is incomplete.

The carabid beetle community of the beech forest sites, which we have studied extensively, does not have a high species richness. In this study, we evaluated exclusively the species inhabiting beech forest stands. The low number of species is due to the lack of plant-eating species. Forest stands have very low coverage of herbaceous plants that could support these species. Indeed, in a previous paper (Negro et al, 2013) we showed that unforested habitats, in particular pastures, showed the highest values for all the diversity parameters, whereas forested habitats (artificial plantation and beech forest, as considered here) had the lowest ground beetle diversity.

Moreover the forest stands sampled had a relatively narrow altitudinal range (see Materials and Methods), which is a further factor limiting the number of species. Therefore, the specific habitat type considered and the low altitudinal range lead to a relatively species-poor community. Many of the references referred to by the referee in fact looked at a much greater range of conditions (see responses below). In conclusion, we are certain that the low species richness is due to ecological rather than sampling factors.

29. (Line 319) Paragraph describing management system uses symbols for results (e.g. N = total abundance), which obscures the point of the results. Would be much better to actually state abundance, richness, etc.

In the results paragraph, we replaced N, R, N_CO, H' with total abundance, species richness, abundance of *C.olympiae* and Shannon diversity respectively.

30. (Lines 320 - 322) Correlation to temperature not really surprising, given the likelihood of seasonality in carabid activity. Humidity is more of an interesting result, given that dry forests appear to have more beetles and more species of beetles. Results in this paragraph are not indicated as statistically significant.

Finding that abundance and richness were negatively correlated to moisture is surprising, given that moisture is a key determinant for activity levels in all other forests and across arthropod taxa. This finding is counter-intuitive and not discussed by the authors at all (in discussion).

For reasons of clarity all the significant values are shown in Table 2 and 3 and not in the text. In the discussion, we explained that humidity and temperature could be used as indirect measures of habitat complexity. In fact, lower levels of canopy cover cause the increase in temperature and the decrease in humidity on the ground, but at the same time can promote the growth of grasses and shrubs that are important for providing hunting and foraging niches and protection from predators and from dessication.

31. (Figure 3) Total abundance, richness, and diversity results would suggest that the peak period for activity of the beetles was missed (i.e. happened before May sampling), which means that this is an incomplete description of these forests' diversities

This is very unlikely: we could not start the sampling season before the end of May because the study area was for the most part still covered by snow. It is unlikely that there was a steady increase in beetle abundance with snow on the ground, with a peak at the beginning of our sampling period (as implied by the referee). Instead, there is a rapid emergence of beetles after snow melt and then a steady decline over the season. For this reason we think that the description of forest carabid diversity is complete.

32. (Line 374) Implication of reasons why habitat shifts might be important are not substantiated with another study or with any of their data. Can't really make this inference.

This comment does not seem relevant to the line cited (L374). We are therefore not able to address this comment.

33. (Line 396) Comments on wingless, large-bodied species. Asserts that they have 'low dispersal power', but I would want to see something that evidences this. This context to the species ecology could possibly have been discussed in the introduction.

Several authors demonstrate that flight capability, and therefore dispersal ability, is a function of carabid wing form (Den Boer 1970; Den Boer 1990; Lovei and Sunderland 1996; Kotze and O'Hara, 2003). Moreover, in a previous paper (Negro et al., 2008) we pointed out, by means of radiotelemetry, the low dispersal power of the endemic species *Carabus olympiae* in the same beech forest stands considered in this study. We have now added these points to the introduction.

34. (Lines 430 - 435) The authors do not mention any diversity studies that are new, when there have been several publications in the past 10 years (see selection provided in lit review at end of this review.)

Müller et al., 2005 is within the last ten years. The other papers are especially relevant (including the classic work coordinated by MacArthur), although not very up-to-date. Given the requirement to shorten the paper, we have decided not to add further references here.

35. (Line 445) Typo ('hass') should be 'has'

OK

36. (Line 441) Implied goal of maintaining larger diversity of carabid beetle community is finally stated quite plainly here, but this is not really obvious in the introduction. It's also a questionable goal, given that larger diversity habitats tend to have more disturbance than self-sustaining ecosystems (e.g. old-growth forest). I would strongly question the recommendation for additional action to manage these forests, based on this study, which does not necessarily provide evidence for all carabid diversity in these forests, nor does it provide a synthetic focus on forest-preferring beetles, though they are included in the analysis. It's possible that the analysis could be re-tooled fairly easily to be a more focused comment on forest-preferring species.

First, we feel that the general goals in relation to the importance of the habitat, and the conservation interest of *C. olympiae*, are clearer with the re-structuring and editing of the introduction. Second, the referee's concerns about the maintenance of diversity being a questionable goal seem largely based on the assumption that the research does not provide a sufficient sample of the carabid community. We have already responded to this point, but to re-iterate, we consider the effects of different management strategies for the same general type of forest which we know (through our long-term experience of working at the site) is relatively species-poor. The methods provide a good sample of the community of carabids (which are mostly specialised forest species). It is true that disturbance may increase diversity, but that is usually due to the creation of 'new' habitats which allow (often generalist) species to colonize. Here, we are interested in maximising the diversity of the existing carabid community of beech forests, rather than creating new habitats to allow new species to colonise (in fact, there was not really any evidence for colonization by generalist species).

37. Lost story? The findings on the endangered species in this ecosystem receive very little attention in the discussion - only in the 'wash' of information on habitat and structural variables. This element should have been drawn out in a more synthetic discussion of *Carabus olympiae*, its needs and how forest ecosystem management can contribute to the retention of this species in managed landscapes. One of the main assertions in the conclusion is that conversion to high forests is going to be damaging to *Carabus olympiae*, but I'm not sure that this received enough attention or discussion to be supported here (e.g. increased with mean humidity - would this be higher or lower in the CCHF?).

We do not feel that a separate section on *C. olympiae* is warranted, given that the main focus of the paper is on the beech forest carabid community. However, we have now highlighted where necessary the specific results relating to this species, including specific management recommendations for its conservation.

38. Post-review literature search (related papers): there are many relevant papers on carabid beetle diversity in managed beech and related forests that are not used in this manuscript. In general, all of them suggest that the current manuscript has underestimated diversity of the carabid beetle community.

We have not underestimated the diversity of the carabid beetle community (see above). Simply, we considered only the species inhabiting a single habitat type (beech forest) with a narrow altitudinal range, because of this is the *locus typicus* of the endemic species *Carabus olympiae*.

In a previous paper, we pointed out that the Valsessera carabid community as a whole is constituted of 46 species, but in that study we sampled several habitat types: pasture, shrub, pioneer forest, beech forest and artificial plantations. The author is presumably referring to these kinds of studies which consider a much greater range of habitat types and often at greater spatial and temporal scales, and therefore they inevitably consider a much greater range of species, whereas our study is much more focussed on a particular habitat type and therefore a particular carabid community. We have nevertheless cited some of the references given below when relevant.

Brandmayr et al 2009 did work in managed oak forests in Italy - compare these findings to this manuscript. Journal of Insect Conservation

Taboda et al 2010 Plant and beetle diversity in a number of different European forest types (note: authors use another paper by Taboda et al (2006) but this is an older paper)

Taboda et al 2004 did another study that's pretty close to this one, looking at oak and beech forests.

Wiezik et al 2007 worked in oak forests that were having conifers introduced. Species richness was substantially higher (over 100 species)

Andorko and Kadar (2006) presented findings in Entomologica Fennica (conference?) that found 39 species in samples from Spain

Mathe 2006 looked at species assemblages in beech forests of Romania and found that high diversity in open habitats was because of edge-preferring species.

deWanaffe and Lebrun 2004 looked at VERY similar question for variety of managed forests and basically found the same things, but possibly with greater insight?

HIGHLIGHTS

- 1) we examine the influence of beech forest management on ground beetle diversity
- 2) the diversity of forest specialist carabids was higher in over-mature coppices
- 3) we detected a positive response of several diversity variables to coarse wood debris
- 4) in beech forest stands is essential to promote structural and microhabitat diversity

Table 1

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Variable	Description	units	CCHF		OC		p
			mean	std.err.	mean	std.err.	
canopy	% canopy cover by hemispherical photography	%	89.29	0.62	90.29	0.7	0.662
regeneration	% soil covered by regeneration	0-1	0.01	0	0	0	0.662
shrubs	% soil covered by shrubs	0-1	0.03	0.03	0.05	0.03	0.878
herbs	% soil covered by herbaceous vegetation	0-1	0.02	0.01	0.04	0.03	0.878
litter	% soil covered by litter	0-1	0.78	0.05	0.77	0.04	0.878
CWD	% soil covered by coarse woody debris	0-1	0.02	0	0.02	0	0.966
FWD	% soil covered by fine woody debris	0-1	0.04	0.01	0.03	0	0.29
bare soil	% soil covered by bare soil	0-1	0.04	0.01	0.03	0.02	0.29
rocks	% soil covered by rocks (all sizes)	0-1	0.07	0.03	0.04	0.01	0.897
tree density	trees per hectare	ha ⁻¹	894.92	59.97	2182.08	180.12	0.001*
seedlings	seedlings per hectare	ha ⁻¹	519.35	305.45	517.07	170.8	0.662
basal area	cumulative tree basal area	m ² ha ⁻¹	28.3	1.52	31.08	1.6	0.426
QMD	quadratic mean diameter	cm	20.36	0.77	13.79	0.45	0.001*
tree volume	comulative aboveground tree volume	m ³ ha ⁻¹	243.11	17.04	217.29	10.73	0.29
CWD volume	comulative volume of coarse woody debris	m ³ ha ⁻¹	6.84	1.18	11.13	1.72	0.29
dbh range	range of tree diameters	cm	31.77	1.63	34.88	2.26	0.662
dbh skewness	skewness of tree diameter distribution	-	0.8	0.1	1.3	0.1	0.101
dbh kurtosis	kurtosis of tree diameter distribution	-	3.8	0.3	5.4	0.7	0.29
dbh st. dev.	standard deviation of tree diameter distribution	cm	7	0.48	6.62	0.3	0.878
% beech	percent beech by basal area	0-1	0.97	0.01	0.95	0.01	0.29

Table 2

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<i>Carabus olympiae</i> abundance			
Family: Negative binomial			
Link: log			
	Estimate	SE	P
intercept	-7.02	0.24	<0.001
management : OC	0.62	0.26	<0.05
mean humidity	0.33	0.14	<0.05
slope	-0.35	0.12	<0.01
smooth term	edf	F	P
period	3.25	11.12	<0.001
<i>Total abundance</i>			
Family: Negative binomial			
Link: log			
	Estimate	SE	P
intercept	-3.69	0.17	<0.001
management : OC	0.58	0.20	<0.01
mean temperature	0.14	0.07	<0.05
mean humidity	-0.14	0.05	<0.01
slope	-0.21	0.09	<0.05
southness	-0.20	0.09	<0.05
smooth term	edf	F	P
period	7.78	32.45	<0.001
<i>Species richness</i>			
Family: Poisson			
Link: log			
	Estimate	SE	P
intercept	-4.30	0.10	<0.001
management : OC	0.40	0.12	<0.001
mean temperature	0.14	0.04	<0.001
mean humidity	-0.06	0.02	<0.01
slope	-0.14	0.05	<0.05
smooth term	edf	F	P
period	2.74	66.20	<0.001
<i>Shannon Diversity</i>			
Family: Gamma			
Link: log			
	Estimate	SE	P
intercept	-4.28	0.06	<0.001
management : OC	0.23	0.07	<0.01
slope	-0.10	0.03	<0.01
smooth term	edf	F	P
period	2.23	42.6	<0.001

Table 3

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***Carabus olympiae* abundance**

Family: negative binomial

Link: log

	Estimate	SE	P
intercept	1.24	0.11	< 0.001
bare soil	-0.73	0.18	< 0.001
canopy	0.27	0.09	< 0.01
CWD volume	0.19	0.08	< 0.05

Deviance explained = 55.7%

Total abundance

Family: negative binomial

Link: log

	Estimate	SE	P
intercept	4.55	0.07	< 0.001
herbs	0.17	0.07	< 0.05
CWD cover	0.21	0.08	< 0.01
seedlings	0.12	0.07	N.S.
dbh st. dev.	0.28	0.07	< 0.001

Deviance explained = 44.8%

Shannon diversity

Family: Gamma

Link: log

	Estimate	SE	P
intercept	1.44	0.04	< 0.001
CWD cover	0.10	0.04	< 0.05
QMD	-0.10	0.04	< 0.05

Deviance explained = 34.8%

Figure 1
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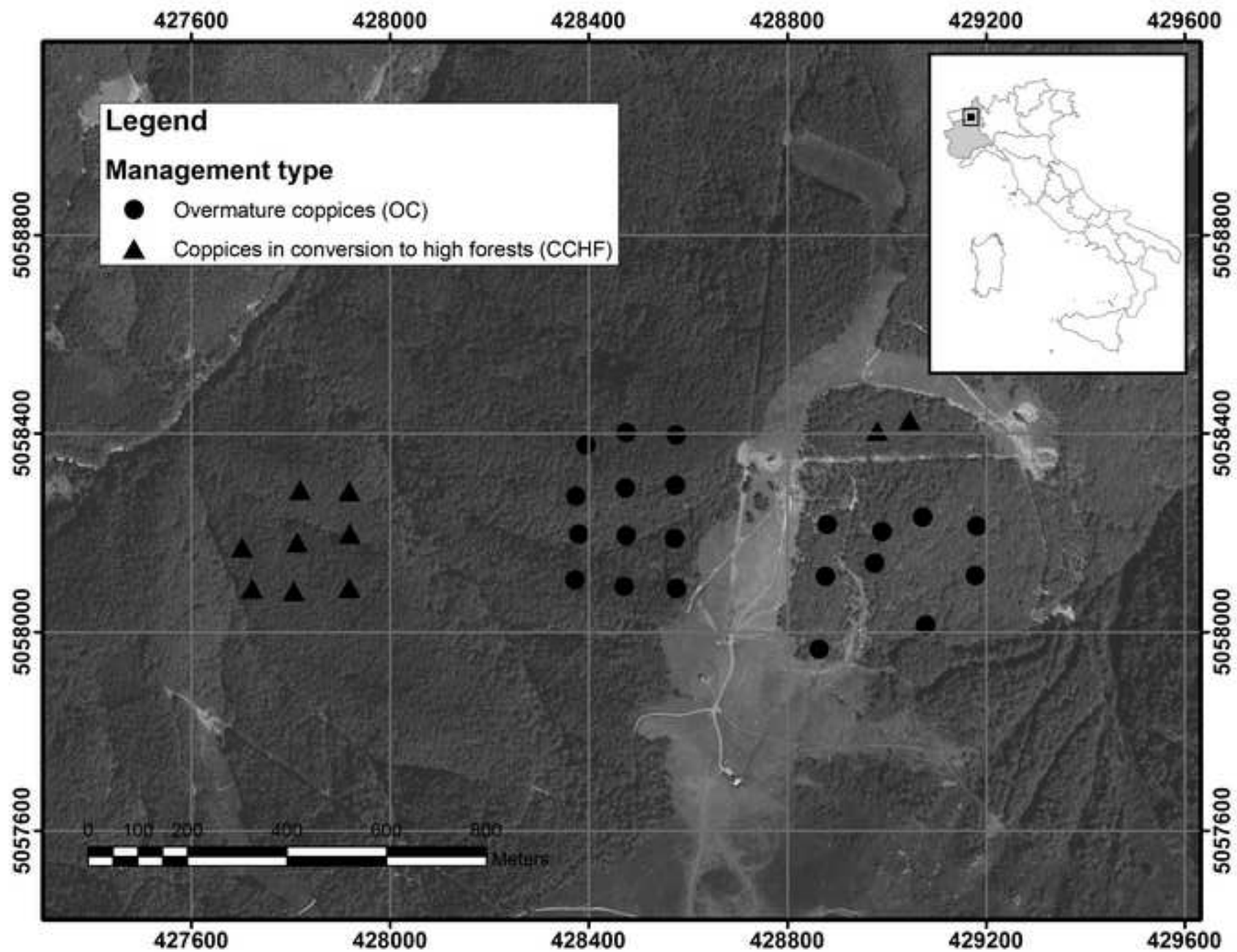


Figure 2
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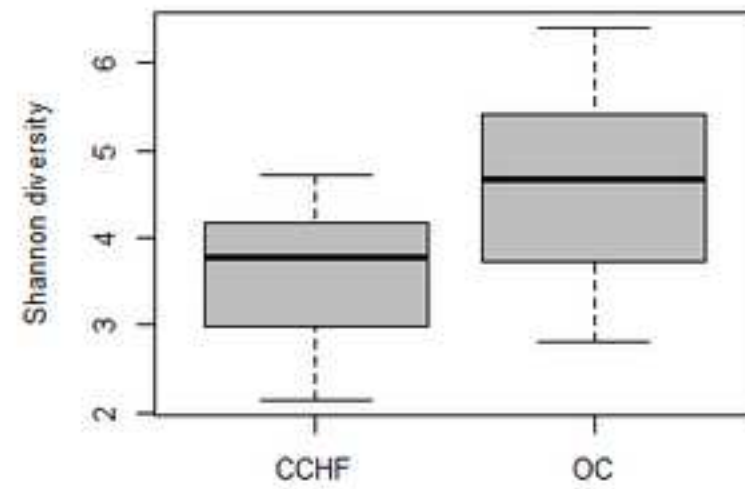
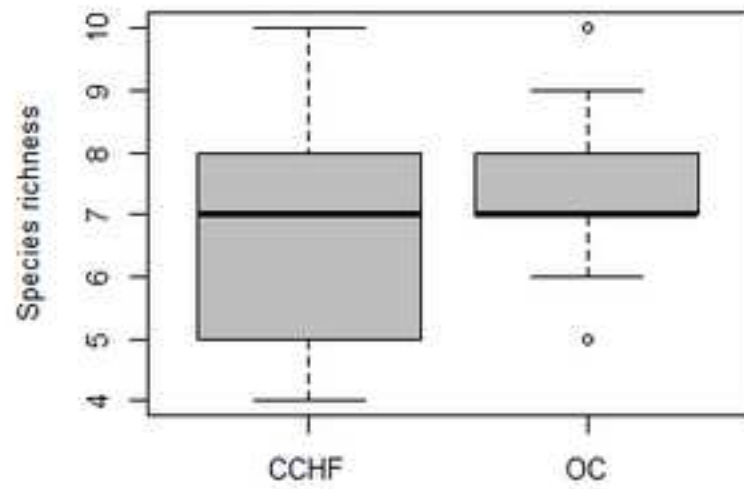
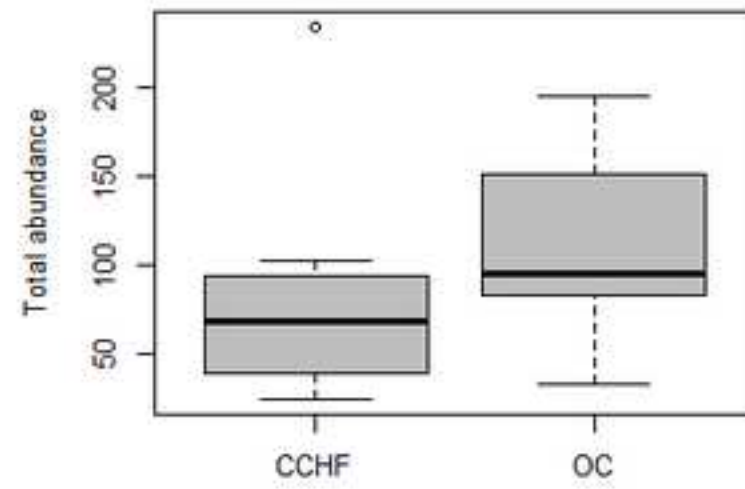
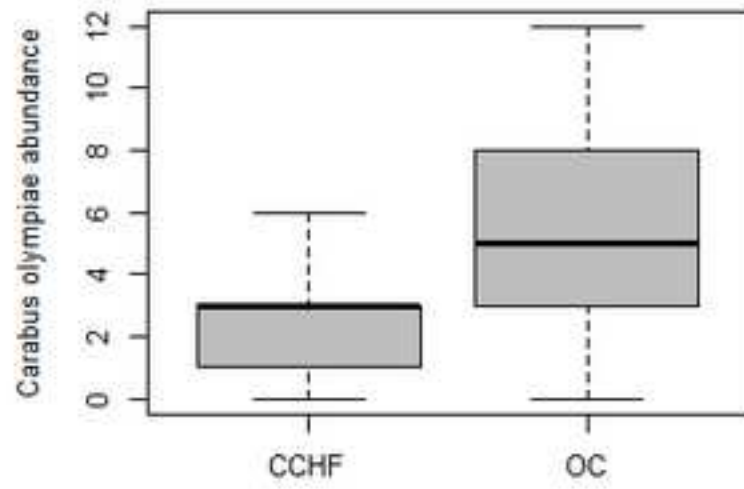


Figure 3
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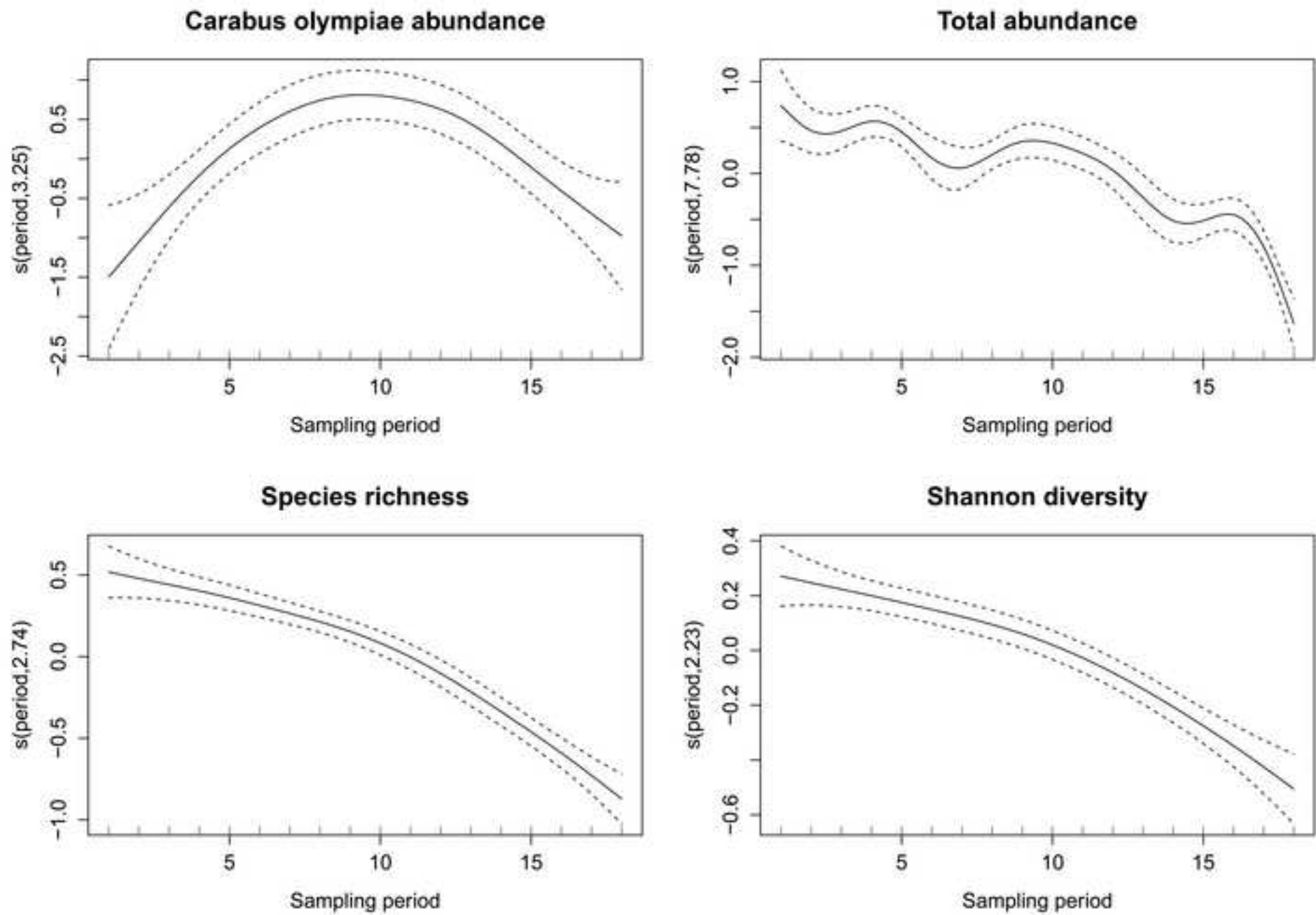
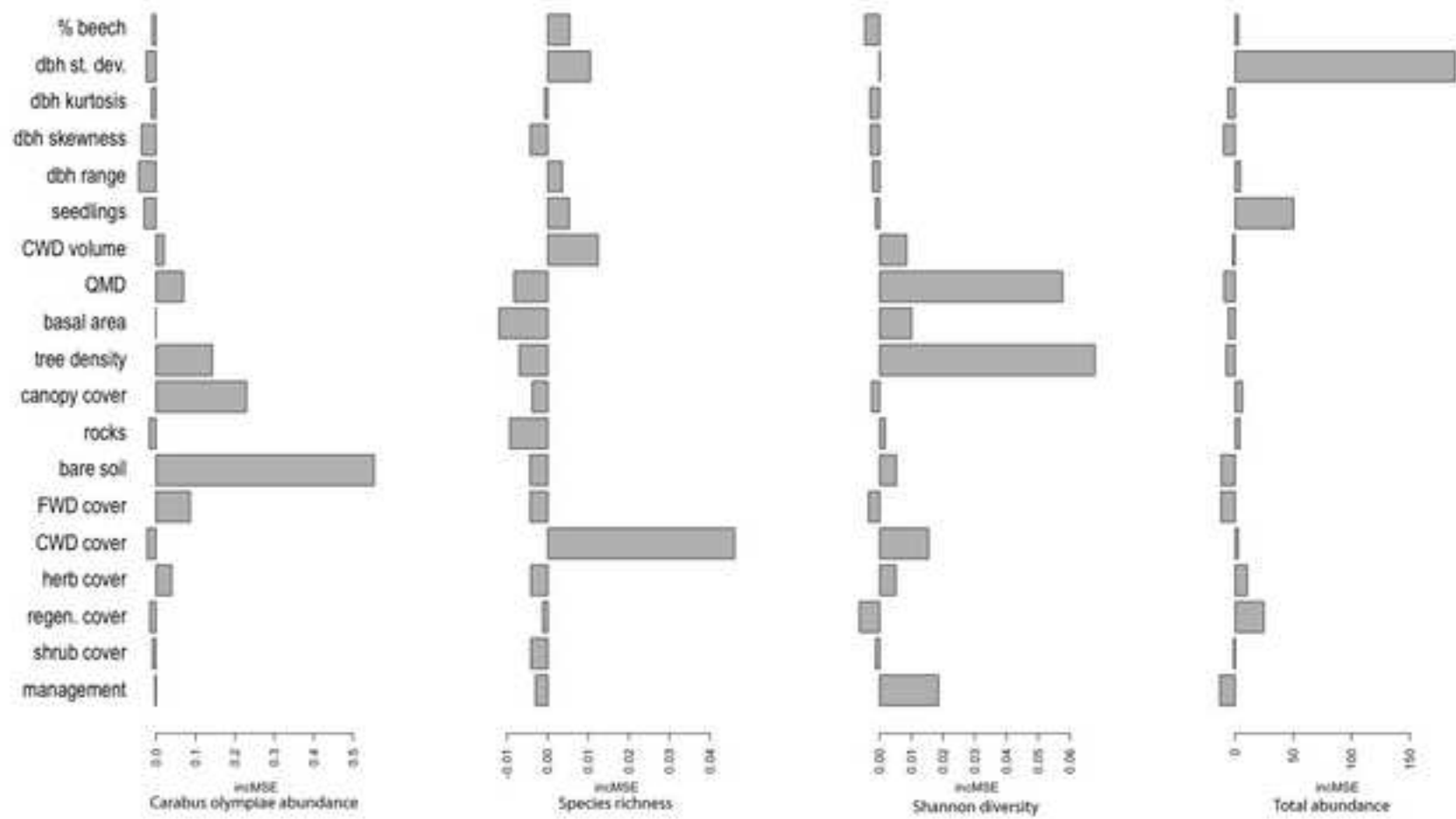


Figure 4
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