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

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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 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.

Keywords: *Carabus olympiae*, coppice, conversion to high forest, *Fagus sylvatica*, insect ecology, retention, ageing islands

1. Introduction

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

There are few studies concerning the effect of forest management on biodiversity in beech forests (e.g. Moning and Müller, 2009; Spiecker, 2003), and most of these focus on plant or mycorrhizal diversity (e.g. Van Calster et al., 2007; Bartha et al., 2008; Di Marino, 2008; Radtke et al., 2013). However, such information is a necessary pre-requisite for management of this habitat given the various environmental pressures to which it is subject. A case in point are the beech forests which characterize the landscape of many mountain areas in Italy (Nocentini, 2009). Most beech forests 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), yet the impacts of such management changes on biodiversity are not as yet fully understood.

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 of life histories and

microhabitat requirements, and therefore they have been widely recommended as bioindicators of forest management (Rainio and Niemelä, 2003). They are relatively easy and cost-efficient to assess with standardized methods (i.e., pitfall trapping), and are sensitive to environmental factors such as temperature, humidity and vegetation structure (Stork, 1990; Butterfield, 1996; Lövei and Sunderland, 1996). Furthermore, changes in carabid abundance and species richness can be useful tools to evaluate the effects of human disturbance in forest ecosystems (Brandmayr et al., 2009).

Most of the studies of carabid diversity in forest habitats have focused on the effects of habitat fragmentation (Davies and Margules, 1998; Niemelä, 2001; Koivula and Vermeulen, 2005), edge effects (Heliölä et al., 2001; Koivula et al., 2004; Negro et al., 2009), 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). Indeed, several authors have demonstrated that flight capability, and therefore dispersal ability, is a function of carabid wing form (Den Boer, 1970; Den Boer, 1990; Lovei and Sunderland, 1996; Gutierrez and Menendez, 1997). For example, radio-telemetry in the same beech forest stands considered in this study has shown that the endangered *Carabus olympiae* has very low dispersal (Negro et al., 2008).

We focused on a group of localized, medium and large-bodied brachypterous ground beetles inhabiting beech forests in the north western Italian Alps. The study site, located in the Sessera Valley, is part of Natura 2000 ecological network. In particular, the site houses *Carabus olympiae,* 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/) .

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

2. Methods

2.1 Study area

The study area was the Upper Sessera Valley (Fig. 1), about 108 km^2 wide, located in north-east Piedmont, Italy (45°40' N, 8°16' E). It includes the upper part of the River Sessera basin, a mountainous catchment, from the valley bottom up to an elevation of 2556 m a.s.l. (average elevation: 1350 m). Annual rainfall is 1700 mm with two equinoctial maxima, and mean annual temperature is 7°C. Snow cover lasts about 5 months (November to March).

Due to its position at the outer margins of the Alps, the Upper Sessera Valley provided a glacial refugium for many plant and animal genera, and is now a local hotspot for biodiversity. The most common land cover classes are pasture (dominated by graminaceous plants), shrubland (alpen

rose *Rhododendron ferrugineum* L. and blueberry *Vaccinium myrtillus* L.), secondary forest on former pastures (birch *Betula pendula* L. and common hazel *Corylus avellana* L.), and beech (*Fagus sylvatica* L.) forest (belonging to the association *Luzulo-Fagetum*). Moreover, large portions of the site were afforested by conifer plantations (Norway spruce *Picea abies* (L.) Karst) and other conifers before World War II.

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

2.2 Sampling design

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

We used baited pitfall traps to sample the carabid community in the study area. 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, relative 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).

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

Thermo/Hygro Button 23 loggers (Maxim Integrated Products, Inc., Sunnyvale, CA, U.S.A.) were used to record temperature and relative humidity in each sampling point. The buttons were

fixed to wooden poles (2 cm above the soil surface) and were sheltered from rain by means of a plastic roof. The data loggers measured the temperature and the relative humidity every 1 h and were run for the entire sampling period (about three months). In the lab, we computed mean, minimum, and maximum temperature and relative humidity for each of the 18 sampling periods.

Topography was characterized by extracting the elevation, slope, and 'southness' (i.e., a linearization of aspect: Chang et al., 2004) from a 10-m gridded digital terrain model. Elevation was not considered in statistical analysis because differences among sampling points were very small (ranging from 1090 to 1450 m a.s.l.).

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

Additionally, the following variables were measured: percent cover of each plant species (Braun-Blanquet, 1932); percent cover of the regeneration layer, shrubs, herbs, bare soil, and litter; fine (branches, twigs, logs with diameter <5cm, FWD) and coarse woody debris (logs with DBH>5 cm, CWD); rocks in four size classes (<10 cm, 10-40 cm, 40-100 cm, and > 100 cm in mean diameter) within a concentric 5m radius circular plot; and, species and number of seedlings

(height < 10 cm) within four 1x1m square subplots, located at the outer edge of the regeneration plot along four orthogonal directions.

2.3 Data analysis

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

Characteristic carabid species in OC and CCHF were identified by means of the Indicator Value (IndVal) procedure (Dufrêne and Legendre, 1997). This method identifies quantitatively the characteristic species of each forest management system, and generates a significance value (p) for the strength of association using a randomized resampling technique. The IndVal of a species is expressed as a product of the specificity and fidelity measures. In our study, it reaches a maximum (100) when all individuals of a species are found within a single management system (high specificity), and when the species occurs at all plots of that type (high fidelity) (Dufrêne and Legendre, 1997). IndVal was calculated by means of the R package *labdsv* (Roberts, 2013).

2.3.1 Effect of macrohabitat variables

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

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

The optimal degree of smoothing was identified by cross-validation, and a gamma value of 1.4 was specified in order to minimise overfitting (Zuur et al., 2009) and provide a more conservative estimated degrees of freedom (edf). The higher the edf, the more non-linear is the smoothing spline (a GAMM with edf = 1 is a straight line). A log-transformed offset term was included to account for the variable number of hours in which the traps were active for each sampling period.

(1)

$$y = intercept + offset\,(log\,(hours\,sampling)) + management + TM + HM + slope + southness + f\,(period) + 1\,|\,plot$$

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

2.3.2 Effect of vegetation and structural variables

In order to identify which vegetation and/or structural variables were driving carabid relative abundance and diversity (and so which may have explained overall differences tested for above), we fitted a series of generalized linear models (GLM) to each of the response variables (N, S, CO_N and H'). Vegetation structure was measured only once for each sampling point, therefore GLMs were run on a matrix with 31 observations (i.e. the sampling 31 points), and response variables were calculated over the whole period. Predictors were selected by running a regression-based Random Forest, an ensemble machine learning method which extends classification and regression trees (Breiman, 2001). Random Forests have been successfully applied for variable reduction in datasets with high dimensionality and correlated predictors (Genuer et al., 2010). We used the *randomForest* package for R (Liaw and Wiener, 2002), with the following settings: number of trees to build = 999, minimum size of terminal nodes = 3, size of predictor subset = ⅓ (number of original predictors). For each dependent variable, we fitted a random forest and computed the permutation importance index (incMSE) associated with each predictor, i.e., the percent increase in mean square error of a tree in the random forest when the values of that predictor are randomly permuted. Predictors with incMSE >0 were retained and

entered in to GLMs; each GLM was fitted with a stepwise algorithm using 99 maximum iterations. We assessed a model's explanatory power by the percent deviance explained, and effect size and direction of each predictor by its standardized regression coefficient.

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

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

3. Results

3.1 Vegetation and structure of OC and CCHF

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

3.2 Ground beetle assemblage and effect of macrohabitat variables

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

Management system affected realtive abundance, species richness, relative abundance of *C.olympiae* and Shannon diversity: all dependent variables were significantly higher in OC

stands than in CCHF (Table 2, Fig. 2). Relative abundance and species richness responded positively to mean temperature and negatively to mean relative humidity, whereas relative abundance of *C.olympiae* was positively related to humidity. All response variables were negatively associated with slope, while southness had a negative effect only on relative abundance.

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

3.3 Effect of vegetation and structural variables

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

Relative abundance, Shannon diversity and relative abundance of *C.olympiae* were strongly influenced by several vegetation and forest structural variables; deviance explained was 44.8%, 55.7%, and 34.8%, respectively. Conversely, no variables could explain carabid species richness. Volume or cover of CWD played an important role in forest carabid diversity, having a strong positive effect on realtive abundance, Shannon diversity and relative abundance of *C.olympiae*

(Table 3). Relative carabid abundance was also associated with higher tree size variability and herb cover. *Carabus olympiae* relative abundance was negatively affected by bare soil cover and positively by canopy cover. Finally, Shannon diversity was negatively associated with QMD (Table 3).

4. Discussion

4.1 Vegetation and structure of OC and CCHF

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

4.2 Microclimate and topography

The occurrence of ground beetles may depend on microclimatic factors such as humidity (Epstein and Kulman, 1990, Niemelä et al, 1992) and air temperature (Thiele, 1997). Usually, forest species prefer cooler and moister sites, characterized by small fluctuations over time

(Pearce and Venier, 2006). These conditions occur in stands characterized by limited natural or anthropogenic disturbance, where a closed canopy moderates ground surface conditions. Within this microclimatic framework, we have unexpectedly found that relative abundance and species richness responded positively to mean temperature and negatively to mean relative humidity. Conversely, *Carabus olympiae* relative abundance increased with mean humidity.

Mean humidity and temperature could be used as indirect measures of habitat complexity. Lower percentages of canopy cover cause an increase in mean temperature and a decrease in mean humidity, but can also promote the growth of grasses and shrubs that are important for providing hunting and foraging niches and protection from predator and disseccation.

The occurrence of ground beetles may also depend on topographic features (Negro et al., 2007). In particular, carabid diversity was negatively associated with slope, as found by Thiele (1977) and Lövei and Sunderland (1996). In our study area, beech forests characterized by steep slopes had low structural variability, due to the lower amount of coarse wood debris and leaf litter that are removed by gravity and surface runoff water (Johnson and Lewis, 1995). Therefore, we believe a lack of shelters and the reduced presence of favorable microhabitats reduces the diversity of carabids.

4.3 Management systems

Much research has found that ground beetles respond to different forest management systems (Werner and Raffa, 2000; du Bus de Warnaffe and Lebrun, 2004; Pearce and Venier, 2006). In this study, the diversity of forest specialist carabids was higher in OC. The last harvest of coppice stands in our study site was carried out more than 50 years ago, whereas conversion to high forests occurred about 20 years ago. It may therefore appear that, irrespective of the

management type, the long period of absence of forest management has enhanced ground beetle diversity. The five species (*C. olympiae*, *C. depressus*, *P. flavofemoratus*, *P. spinolae* and *P. appeninus*) that significantly selected OC stands (IndVal analysis) are wingless with low dispersal power which may prevent them from quickly recolonizing recently harvested stands (Niemela et al., 1993; Spence et al., 1996).

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

4.4 Structural Variables

Carabids are strongly sensitive to changes in forest heterogeneity and respond to structural variables (Taboada et al., 2010). Microhabitat complexity was a powerful predictor of the total abundance of pitfall-trapped beetles. We detected a positive response of several diversity variables to CWD cover or volume, herb cover, and standard deviation of tree diameter distribution. In a similar study, coarse woody debris, snag volume, gap area, understory

vegetation and forest floor depth were all critical in structuring beetle communities (Latty et al., 2006).

Volume or cover of coarse woody debris had a strong positive effect on N, CO_N and H'. CWD volume ha^{-1}, in particular, was about twice as large in OC stands (11 m^3 on average) than in CCHF stands (6.8 m^3), although the difference was not significant after correcting for multiple comparisons. Woody debris, such as branches, logs, and twigs, is a major habitat feature on forest floors (Jonsson et al., 2005). In mature or restored forests, it provides a set of microsites that offer food and habitat resources to several arthropods, such as saproxylic organisms (Siitonen, 2001; Komonen et al., 2014), soil mites (Johnston and Crossley, 1993) and carabids (Hanula et al., 2009). In particular, it is an important resource for many ground beetle species as an overwintering site, and for ovipositioning and larval development (Larochelle and Lariviere, 2003; Bousquet, 2010). In fact, in sampling points characterized by higher levels of CWD, we also trapped seven *Carabus olympiae* in the third instar larval stage.

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

Carabus olympiae relative abundance was negatively related to bare soil cover. Bare ground, defined as exposed soil deprived of vegetation, is not considered a suitable habitat (Fry and Lonsdale, 1991; Key, 2000) for many insect groups. Often, it is the result of the erosive action of

rainwater, which is particularly strong on steeper slopes, that leads to a reduction of vegetation and microhabitat complexity (Fayt et al., 2006).

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

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

More research needs to be carried out to elucidate the tradeoffs between positive and negative impacts of silvicultural interventions on carabid diversity, i.e., mechanical disturbance as opposed to the opportunity of regulating the mosaic of patches and producing woody debris of multiple decay classes.

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Table captions

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

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

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

Figure captions

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

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

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

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

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Table 1

			CCHF		OC		
Variable	**Description**	**units**	**mean**	**std.err.**	**mean**	**std.err.**	**p**
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^2ha^{-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^3ha^{-1}	243.11	17.04	217.29	10.73	0.29
CWD volume	comulative volume of coarse woody debris	m^3ha^{-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

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
AIC = 2637			

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
AIC = 1279			

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
AIC = 1008			

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
AIC = 779			

Table 3

***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%	**AIC = 130.9**		
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%	**AIC = 310.8**		
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%	**AIC = 81.3**		

Fig. 1

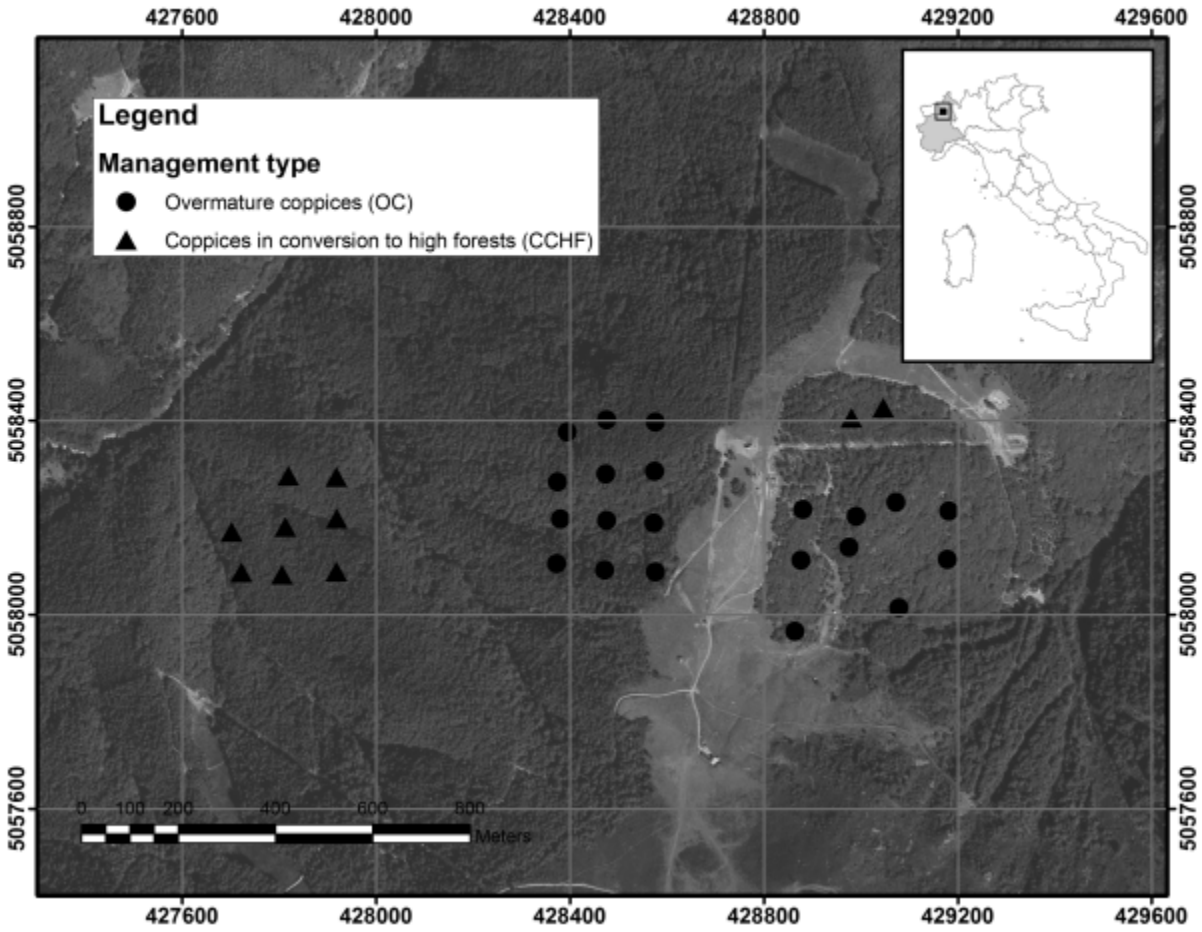

427600
428000
428400
428800
429200
429600
5058800
5058400
5058000
5057600
Legend
Management type
Overmature coppices (OC)
Coppices in conversion to high forests (CCHF)
0 100 200 400 600 800
Meters

Fig. 2

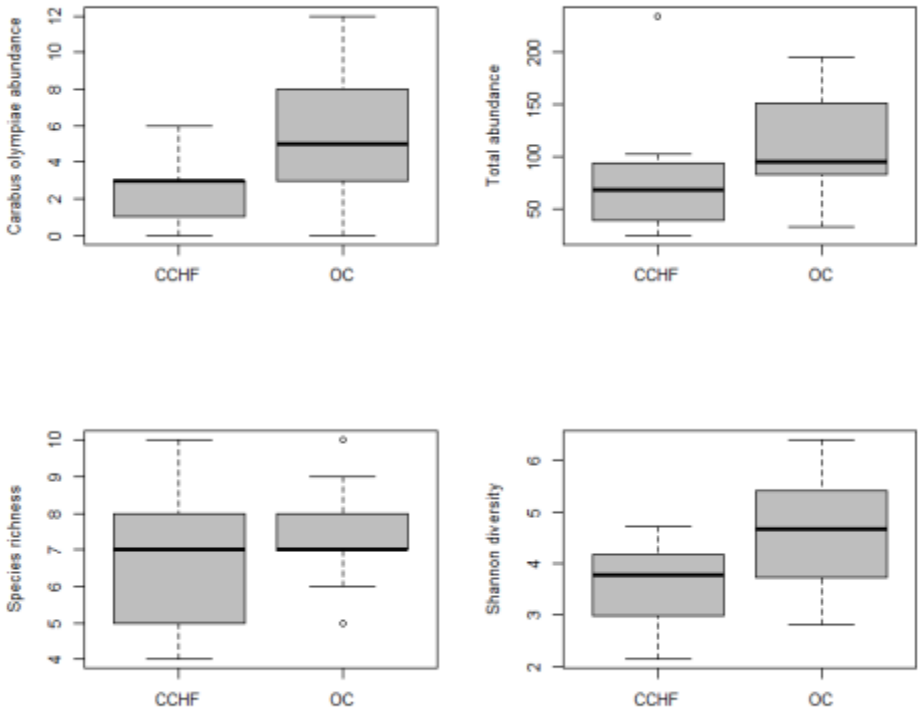

Carabus olympiae abundance
0
2
4
6
8
10
12
CCHF
OC
Total abundance
50
100
150
200
CCHF
OC
Species richness
4
5
6
7
8
9
10
CCHF
OC
Shannon diversity
2
3
4
5
6
CCHF
OC

Fig. 3

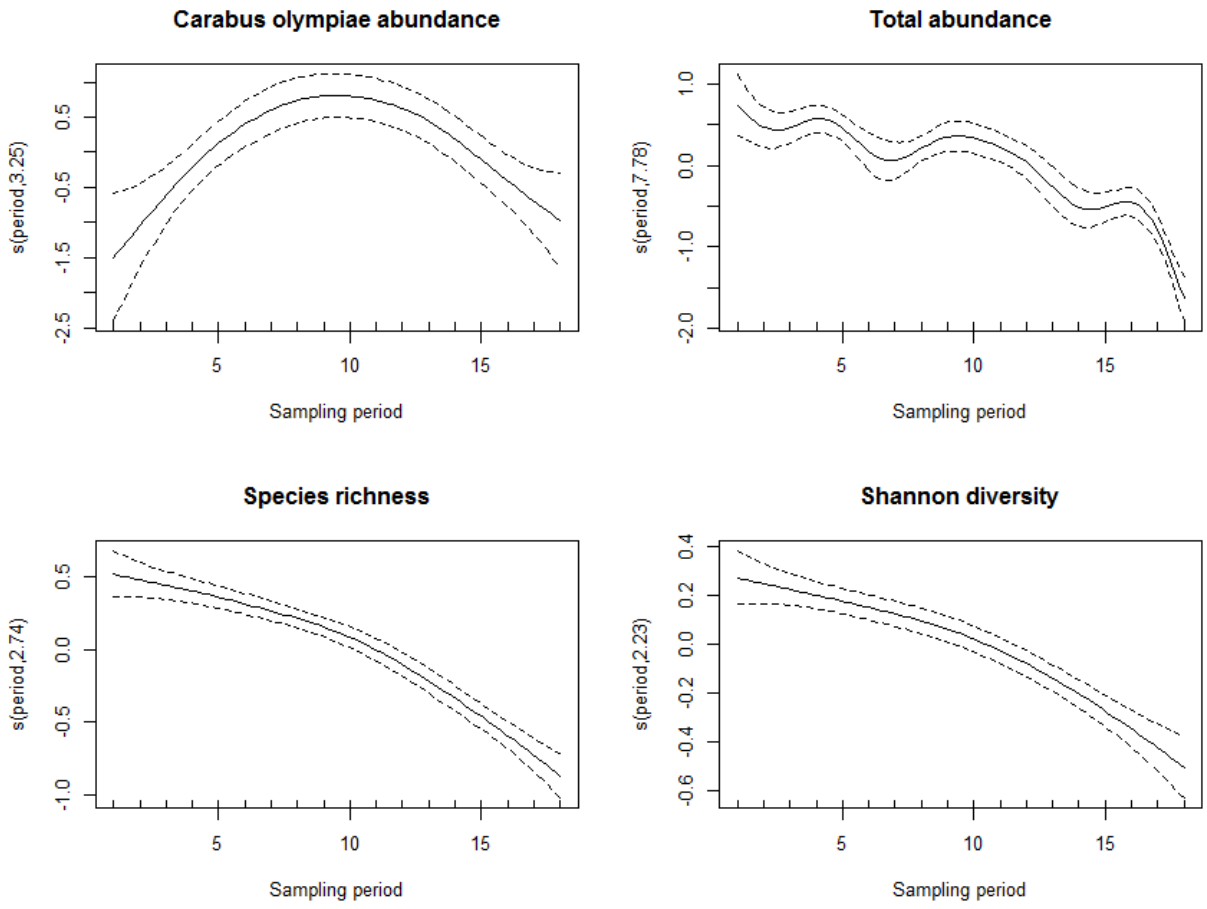
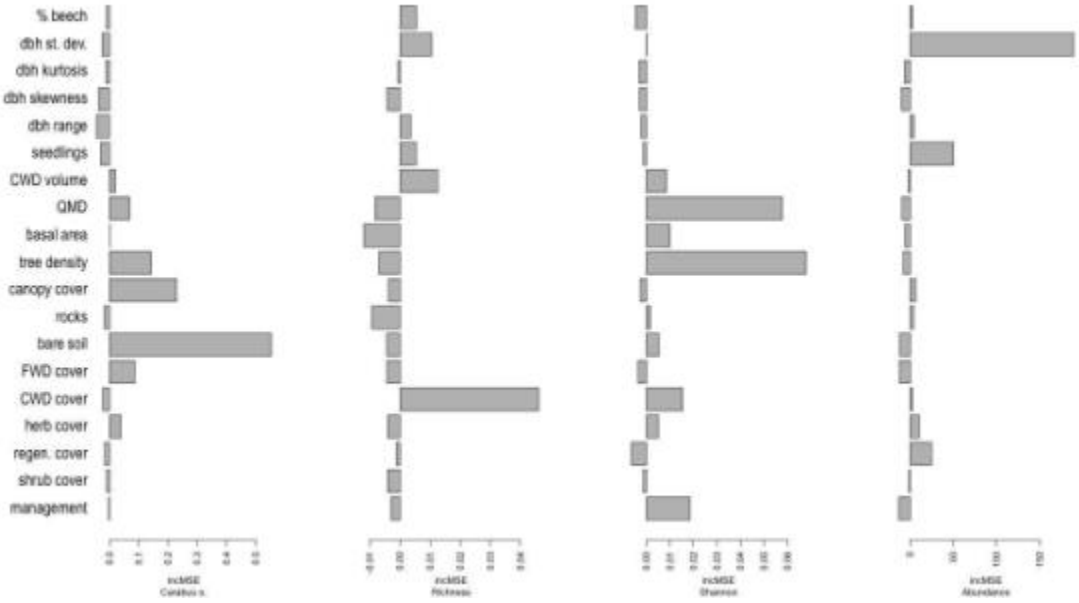

Carabus olympiae abundance
s(period,3.25)
-2.5
-1.5
-0.5
0.5
5
10
15
Sampling period
Total abundance
s(period,7.78)
-2.0
-1.0
0.0
1.0
5
10
15
Sampling period
Species richness
s(period,2.74)
-1.0
-0.5
0.0
0.5
5
10
15
Sampling period
Shannon diversity
s(period,2.23)
-0.6
-0.4
-0.2
0.0
0.2
0.4
5
10
15
Sampling period

Fig. 4


% beech
dbh st. dev.
dbh kurtosis
dbh skewness
dbh range
seedlings
CWD volume
QMD
basal area
tree density
canopy cover
rocks
bare soil
FWD cover
CWD cover
herb cover
regen. cover
shrub cover
management