The effect of forest management on endangered insects assessed by radio-tracking: the case of the ground beetle *Carabus olympiae* in European beech *Fagus sylvatica* stands

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Abstract

Beech forests are important for biodiversity conservation in Europe and studies to identify sustainable forest management practices are therefore required. ~~Several ground beetle species inhabiting European beech forests are endangered and potentially threatened by logging interventions.~~ The ground beetle *Carabus olympiae* Sella, 1855, is a large steno-endemic endangered alpine species with very restricted ranges. Its known range is only delimited in two beech forests in the western Italian Alps where beech wood is still harvested. Forty individuals were collected and radio-tracked in 2014-2015 in order to assess the effects of forest management on microclimatic conditions, microhabitat use and movements.

All management interventions changed microhabitat availability, with an increase of deadwood and bare ground. Thermo/hygro button loggers showed that temperature was higher and humidity lower in managed than in unmanaged stands, suggesting logging interventions may be detrimental to *C. olympiae*, either directly (inducing suboptimal climatic conditions) or indirectly (decreasing the availability of prey). Microhabitat selection analyses showed that in all scenarios, deadwood and tree bases were preferred, and were used as refuges during the daytime. Bare ground was never used. The length of the path travelled by individual insects was more variable and the tortuosity lower in managed than in unmanaged stands, suggesting that management induced more uncertain and constrained trajectories.

We concluded that logging may exert short-term negative effects on *C. olympiae* ground beetles (as suggested by the increase in bare ground, and changes in climatic conditions and movements). However, the preference for tree bases and deadwood suggests that forest management, concurrently, may also be beneficial, on the condition that: *i)* the coppice, which provides more suitable microhabitats, prevails over conversion to high forest, and *ii)* deadwood originating from cutting (branches and treetops) is properly accumulated.

Commento [EC1]: Abstract is way too long. Delete “several ground beetle…” sentence on L 23-25; clarify if the global distribution of C olympiae is indeed the two forests in Italy (L 27); results should focus on beetles not logging techniques; delete “suggesting logging… (…) …analyses showed that” (unnecessary text); “scenarios” (L 34) is misleading as it usually refers to modeling so rather say “Regarding microhabitat selection, deadwood…”; “never” (L 35) is too dramatic, say “not”; “more uncertain” (L 37) is unclear, rather clarify if you refer to movement directions and/or distances; L 39-40 delete the text in parentheses (unnecessary); L 45-47 while I do not disagree with this it is out of scope and should be omitted. It is better to end Abstract with a sentence about the importance of results concerning beetles themselves.

In methodological terms, this study indicates that radio-tracking may be successfully used as a tool to assess the effect of forest management on endangered and/or rare ground dwelling insects, and to identify forest management practices that are most compatible with their conservation.

Introduction

European beech (*Fagus sylvatica* L.) forests represent a unique ecosystem, stretching from the Mediterranean regions and southeastern Europe to the British Isles and Scandinavia, comprising vast areas in the Alps, Balkans and the Carpathians as well as in the northern European lowlands. The special history and ongoing ecological processes related to beech forests has been acknowledged by the establishment of the transnational UNESCO World Heritage site "Primeval Beech Forests of the Carpathians and the Ancient Beech Forests of Germany”, instigated in 2007 and 2011. Apart from old-growth remnants, even secondary or managed beech forests harbour relevant ecosystem processes, animal and plant species of conservation interest, and provide an immense array of ecosystem services to man. For these reasons, they feature prominently in the Habitats Directive of the European Commission, Annex I (EU Council 1992), which lists five different beech forest types that deserve conservation at the EU level~~ (9110 Luzulo-Fagetum beech forests, 9120 Atlantic acidophilous beech forests, 9130 Asperulo-Fagetum beech forests, 9140 Medio-European subalpine beech woods, 9150 Medio-European limestone beech forests of the Cephalanthero-Fagion)~~. Beech (*Fagus sylvatica* L.) forests are important for many autotrophic and heterotrophic organisms like soil macrofungi, ground dwelling arthropods, land snails, saproxylic fungi, hole nesting birds, saproxylic insects, epiphytic lichens and bryophytes and epixylic bryophytes (Brunet et al. 2010, Larrieu et al. 2014a; Larrieu et al. 2014b). European conservation policy also takes into account beech forests. The Annex 1 of the "Habitats Directive" (92/43/EEC~~),~~ ~~which aims to preserve biodiversity through the conservation of the environment,~~ lists eight beech habitat types as worthy of conservation. Current threats to these ecosystems comprise climate change (Gessler et al., 2007; Di Filippo et al., 2012), increased possibility of fire and drought damage (Piovesan et al., 2008; Ascoli et al., 2013), habitat loss and fragmentation (Kunstler et al., 2007), species invasion (Krumm and Vítková 2016) and grazing by domestic or wild ungulates (Vandenberghe et al., 2007; Olesen and Madsen, 2008). Forestry practices can also affect

Commento [EC2]: L 61-65, irrelevant lists, delete

Commento [EC3]: L70, irrelevant description of directive aim, delete biodiversity both positively and negatively, and studies focused on the impacts of beech forest management on animal diversity (e.g. Laiolo et al. 2004; Kappes 2005 and 2006; Müller et al. 2007; Moning and Müller, 2009; Floren et al. 2014; Chumak et al., 2015) are necessary to identify the practices which are compatible with animal conservation. A case in point are the beech forests of many mountain areas in Italy (Nocentini, 2009). Most of them were traditionally managed as coppice, i.e., by repeatedly cutting back sprouts to ground level to stimulate vegetative growth and provide firewood on a short rotation basis (20 to 40 years). High forests , i.e., stands where trees regenerate by seed, are rare. However, many coppices are now transitioning to a high-forest structure, due to either abandonment of regular management, or silvicultural conversion by thinning (Nocentini, 2009), yet the impacts of such management changes on animal biodiversity are not fully understood.

Ground beetles (Coleoptera: Carabidae) are typical inhabitants of European beech forests. Carabids show a wide range of life history traits and microhabitat requirements, and therefore they have been widely used as biological model of forest management (Rainio and Niemelä, 2003). They are relatively easy and cost-efficient to sample 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). Most studies on carabids in different forest habitats have focused on habitat fragmentation (Davies and Margules, 1998; Niemelä, 2001; Koivula and Vermeulen, 2005) and edge effects (Heliölä et al., 2001; Koivula et al., 2004; Negro et al., 2009). The consequences of forestry practices on ground beetle diversity have also been extensively studied in non-beech forests (Werner and Raffa, 2000; du Bus de Warnaffe and Lebrun, 2004; Pearce and Venier, 2006; Taboada et al., 2006, Baker et al., 2009; Lange et al., 2014; Skłodowski 2014; Macko, 2016). Habitat modification and destruction may be responsible for species decline, which affects particularly large-sized and brachypterous (short or reduced wings) ground beetles, because of their limited dispersal capacity (Kotze and O’Hara, 2003). A common trend in carabids is that populations of large, poorly dispersing species decrease with increasing

Commento [EC4]: L 87, only species and genus names are italicized

Formattato: Tipo di carattere: Non Corsivo

Commento [EC5]: L 96, the statement on “non-beech forests” appears strange as most of the other listed studies are non-beech studies too.

disturbance and forest management intensity (Raino and Niemela 2003, Kotze and O'Hara, 2003, Paillet et al. 2010). Since *C. olympiae* is a large, brachypterous species, we expected that forest management could exert some negative effect on individual microhabitat use and movements. Several ground beetle species are threatened (Assmann and Janssen 1999; Kotze and O'Hara, 2003, Brockerhoff et al., 2005; Matern et al. 2007; Pokluda et al., 2012), despite that, for most species, the status of populations is not known, and therefore field studies are needed in order to develop the most appropriate conservation measures.

Commento [EC6]: L 104, why would you expect only negative effects? Besides, I don't think there is much basis for linking these to management because of lack of replication.

The species *Carabus olympiae* Sella, 1855, is an endangered alpine species with a very restricted range, given that it inhabits only two neighboring beech forests (a few hectares each) in the western Italian Alps. After the alarming population decline suffered in the years 1930-42 (Malausa et al., 1983), *C. olympiae* has been declared a *priority species* (i.e. a species for the conservation of which the European Community has a particular responsibility) and included in Annexes II and IV of the EU Habitats Directive. It is listed in international agreements such as the Bern Convention, and is considered Vulnerable according to the IUCN red list of Threatened species (http://www.iucnredlist.org/). Despite this protection framework, *C. olympiae* still faces threats due to the construction of downhill skiing facilities (Negro et al. 2009, 2010, 2013) and to forestry practices. In addition to removing trees, logging usually alters the shrub, herbaceous, and litter layers. The period immediately after logging may therefore be dangerous for forest ground beetles, which are deprived of protection by the canopy and understory layers. Previous research focused on local ground beetle diversity, and tentatively indicated that the best option to protect this species was low-intensity or no management (Negro et al. 2007, 2013), particularly avoiding homogenous thinning in over-mature coppices (Negro et al., 2014).

Commento [EC7]: L 109, please clarify if these two forests are the whole population in this planet

Commento [EC8]: L 122, please clarify "homogeneous" – I suppose you refer to thinning that aims at rather even distribution of even-sized trees?

~~Here we tested different forest management techniques to identify those interventions that are compatible with and, possibly favourable to, the conservation of *C. olympiae*.~~

We radio tracked *C. olympiae* individuals in multiple stands that differed in terms of forest management and certain structural elements of forests in order to evaluate their effects on

Formattato: Tipo di carattere: Corsivo microhabitat use and movements of these beetles to identify those interventions that are compatible with and, possibly favourable to, the conservation of *C. olympiae*.

~~After logging, we collected and translocated tagged individuals into the managed stands and started to radio track them to assess individual ecological choices under different forest management scenarios. We hypothesized that logging would increase temperature and decrease humidity, change microhabitat use and affect movement parameters of the radio-tagged individuals.~~In particular we expected that bare soil should be avoided by this species, and many other studies provide more predictions regarding dead wood, dense field vegetation,

We assessed the short-term effects of different types of logging practices on: *i*) local microclimatic conditions, *ii*) habitat use and *iii*) movements of radio-tagged individuals. ~~In methodological terms, we aimed to test the effectiveness of the radio-tracking technique as a tool to assess the effect of forest management on endangered insects.~~

Study area

The study area was the upper Sessera Valley, in the North-western Italian Alps (45°40’ N; 8°16’E). The area is classified as Site of Community Importance (SCI, IT113002, Val Sessera) with the purpose of protecting ~~this ground beetle species~~*C. olympiae*. 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). The most common land cover classes are pasture, shrubland (Alpine rose *Rhododendron ferrugineum* L. and bilberry *Vaccinium myrtillus* L.), secondary forest on former pastures, coniferous plantation, and beech forest (belonging to the association *Luzulo-Fagetum*). In the study area, Alpine rose shrubland is characterized by sparse isolated patches as the result of historical forest cutting and

Commento [EC9]: Inserire citazioni

Commento [EC10]: 1.The study questions have been improved, but they are far from satisfactory. Microhabitat conditions per se should not be included here, as the focus was on beetles not on forest structures. These measurements and tests should definitely be presented in Results but they are used to explain some of beetle observations and are thus not in the focus. Delete. The same concerns the ending topic, the efficiency of your method, which cannot be assessed without comparing it with other methods (such as the use of radioactive powder in M.A. Baars’ studies in the 1970s, etc.). Delete that too. Also, there is no need to describe in such detail what you did in this part: it suffices to say that “We radio tracked C. olympiae individuals in multiple stands that differed in terms of forest management and certain structural elements of forests in order to evaluate their effects on microhabitat use and movements of these beetles” and then specify what you expected concerning microhabitats, based on earlier studies (your own research, for example, shows that bare soil should be avoided by this species, and many other studies provide more predictions regarding dead wood, dense field vegetation, etc.). These changes are necessary to put your study into a context of previous research.

Commento [EC11]: L 139, “this ground beetle species” => Carabus olympiae

Formattato: Tipo di carattere: Corsivo pastoral practices. Beech was traditionally managed as coppice-with-standards (i.e., trees retained to provide a seed source for stump replacement over time) to produce firewood and charcoal. Over recent decades, forest management has been progressively reduced. The last harvest in privately owned coppice stands was carried out in 1960; the density of standards is on average 100 trees per hectare, and they are now about 80 years old. On the other hand, most coppices on public properties have been actively converted to high forest in the 1980s. Conversion has been carried out by progressive thinning (3-4- entries) of sprouts (Giannini and Piussi, 1976), before reaching the final step of ‘‘temporary high forest’’, i.e., a forest that has the structure of a mono-layered high forest, but which originated from sprouting, to which the seeding cut will be eventually applied. Most of the coppices in conversion are currently between the second and the third thinning, and the trees are 70–75 years old, with some ~~standards~~ trees > 100 years old.

Commento [EC12]: L 157, “Standards” => trees

Methods

Experimental forest management

Experimental forest management was carried out in 2014 and 2015 in seven different stands, with the aim of reproducing “business as usual” as well as alternative management options for beech coppices and high forests (Fig. 1). Forest structure and ground cover were measured before and after logging across 30 sampling plots (details in Negro et al., 2014). In all logging practices adopted (interventions *ii*, *iii* and *iv*) the retention of coarse woody debris was prescribed and the following four treatments were applied:

i) no logging (control, C), only in over-mature coppices (two stands, one in 2014 and one in 2015, 3 hectares each). These had an average stem density of 2029 trees ha^{-1}, mean canopy cover of 89%, and mean living aboveground tree volume of 207 m^3 ha^{-1}. Ground cover by deadwood (downed logs and branches, either sparse or piled) was in the range of 0% to 10% (Negro et al., 2014);

Commento [EC13]: L173, please clarify "sparse or piled" – do you mean that the same amounts were distributed evenly all over the stands versus stacked in (how large?) piles?

ii) strip cuts in the high forest (one stand in 2015, 10 hectares) (management type 1, M1). This had an average stem density of 915 trees ha^{-1}, mean canopy cover of 89%, and mean living aboveground tree volume of 273 m^3 ha^{-1} before treatment. After the cut, which was carried out by removing all trees in 10 elongated openings (350-1250 m^2 each) and leaving a total of 30 m^3 of cut timber on the ground in the form of whole trees, ground cover by deadwood had increased on average from 2% to 6%;

iii) single-tree selection in over-mature coppices (two stands in 2015, 14 and 6 hectares respectively) (management type 2, M2). This was carried out by harvesting individual sprouts, trees, or small groups (tree diameter <25 cm) with the aim to promote the growth of better-quality beech stems, while retaining all other tree species and leaving all branches on the ground. Stem density and living tree volume were reduced on average by 26% and 30% respectively, while ground cover by deadwood increased on average from 2% to 8%;

iv) uniform thinning to convert over-mature coppices to high forest (two stands, one in 2014 and one in 2015, 3 hectares each) (management type 3, M3). This represents the "business as usual" scenario for beech coppices in the region, and was carried out by harvesting all but the best-quality sprouts from each stool, and leaving branches in small piles uniformly scattered on the ground. Stem density and living tree volume were reduced on average by 85% and 60%, respectively, while ground cover by deadwood increased on average from 2% to 5 %.

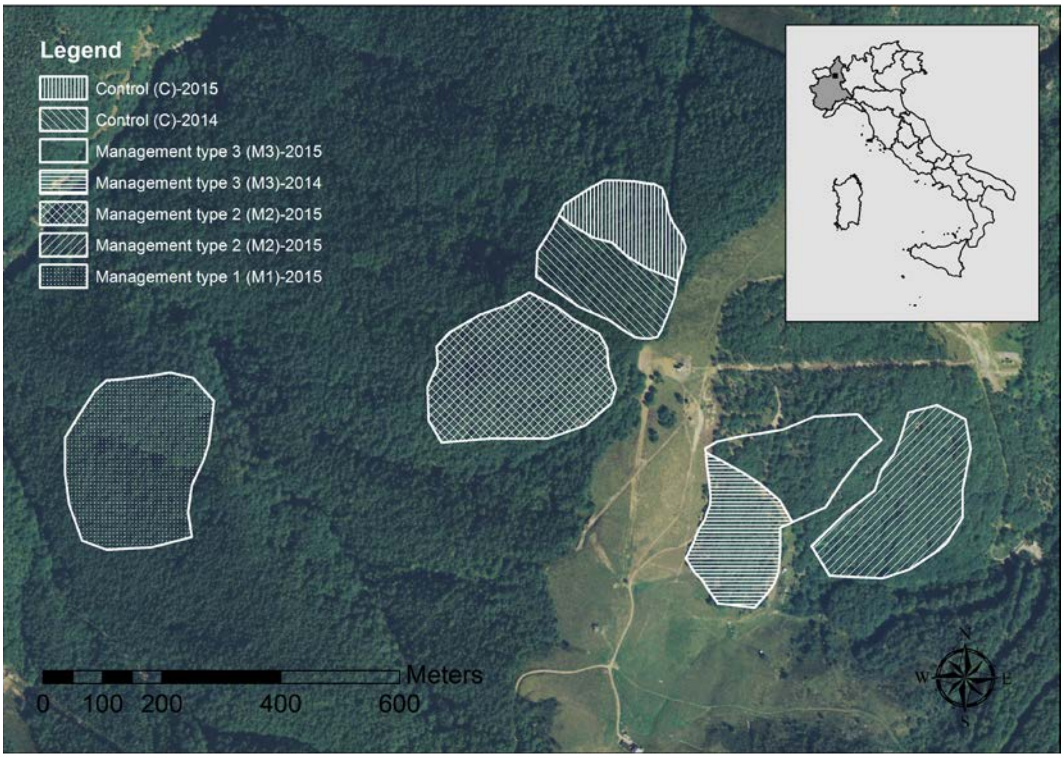

Figure 1. Experimental design. Seven different stands underwent four different forest management interventions: i) absence of management in over-mature coppices (control, C); ii) strip cuts in the temporary high forest (management type 1, M1); iii) single-tree selection in over-mature coppices (management type 2, M2); iv) uniform thinning to convert over-mature coppices to high forest (management type 3, M3).

Microclimate monitoring

Five *Thermo/Hygro Button* loggers (Maxim Integrated Products, Inc., Sunnyvale, CA, U.S.A.) were used to record temperature and relative humidity every 1 h in each stand in 2015. The data loggers, ~~fixed~~ attached to wooden poles (2 cm above the soil surface) and sheltered from rain by means of a plastic roof, were located in areas that were representative of the treatment applied in that stand. Recorded data were used to compute daily mean, minimum, and maximum temperature and relative humidity.

Commento [EC14]: L 209, “fixed” => attached

Commento [EC15]: L 201, werelocated => were located

Pitfall trapping

We captured ground beetles by pitfall trapping in un-managed areas. In each sampling area, five baited 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. Each trap (7.5 cm diameter and 9 cm deep), filled with 150 ml of vinegar as an attractant (van den Berghe, 1992), was assembled with a double bottom in order to keep animals alive. A flat stone was placed above each trap to prevent flooding. The exact location of traps was determined by means of a Global Positioning System (GPS) Garmin eTrexR Navigator. A total of 23 sampling areas in 2014 (early July-mid August) and 24 in 2015 (mid June-early August) were set and traps emptied at three-day intervals.

Commento [EC16]: L 220, what are these “areas”? Do you refer to traps?

Radio-tracking

Individuals were radio tagged with Micro-Pip radio-tag transmitters (about 0.3 g, 15 × 5 × 4 mm) developed by Biotrack Ltd, (Wareham, England, www.biotrack.co.uk). Transmitters were attached with cyanoacrylate on top of the elytrae, with the short antenna (2.5 cm) directed backwards, in keeping with Negro et al. (2008). After radio-tagging, individuals were kept for some hours in a dark terrariurm before releasing them back to the wild. In the field, radio-signals could be detected from about 300 m, with a battery life span of about three weeks. Tagged carabids were relocated once a day, in the morning, using a receiver and a hand-held Yagi directional antenna. The exact radio-telemetry location (fix) was determined in the field by a GPS, where a coloured peg was also driven into the soil. At the end of the experiment period, radio tagged individuals were caught to retrieve transmitters before being released.

C. olympiae are more active at night than by day. During the day, they do not move or move only ~~very short distances (typically < 2.5 m)~~up to few meters, whilst ~~long distance~~ movements of several tens of meters ~~(the maximum linear dispersal range was 77.7 m)~~ were almost exclusively at night (Negro et al. 2008). The fixes collected in the present study reflect therefore the microhabitat used by individuals as a refuge or shelter during the day time.

Commento [EC17]: L 236-237, too precise values for any practical use. Rather say “up to a few meters” and “of several tens of meters”

Microhabitat assessment

Microhabitat availability for ground beetles was assessed in October 2015 by transect sampling. We set six linear transects (60 m long) per stand in the same areas used by radio-tracked individuals (a total of 42 transects, i.e. 6 transects x 7 stands). Quadrats (60 x 60 cm) along transects were set at two metres one from another (i.e. 30 quadrats for each transect) for a total of 1260 quadrats (30 quadrats x 42 transects). We took a picture of ground cover in each quadrat and the dominant microhabitat was later classified into one of the following categories: shrubs (SH), tree bases (ST), deadwood (DW, i.e. coarse woody debris such as pieces of branches or trunks), grass (G), bare ground (BG), rocks (R) and litter (L).

Individual microhabitat use was assessed by recording the microhabitat used by radio-tagged individuals as shelter during the day (i.e. the dominant microhabitat category at the fix).

Data analysis

Microhabitat use

We used a binomial Generalized Linear Mixed Model to model microhabitat use (i.e. 1 used, 0 unused) as a function of management (i.e. C, M1, M2 and M3), year of study (2014 and 2015), sex, and microclimate (average humidity and temperature), specifying the identity of radio tagged individuals as a random effect. We modelled the use of three microhabitat types, i.e. litter, deadwood and tree bases, for which the sample size was statistically adequate not to have convergence problems of the model.

In our study design, microhabitat use was measured for each individual, whilst microhabitat availability was measured at the population scale (i.e. inside each managed stand), assuming that microhabitat types were equally available to all monitored animals (Thomas & Taylor 1990). To compare use and availability in this kind of study design (i.e. to study microhabitat selection), we used Compositional Analysis, calculating the significance of Wilk's Λ and t statistics by randomization tests (Aebischer et al. 1993). Analyses were performed using the function *compana* in the package adehabitatHS for R (Calenge, 2011; R Core team, 2016). We also calculated the selection ratio: $w_j = u_j/a_j$ where u_j is the proportion of use of the habitat class j and a_j is the proportion of availability (relative frequency) of habitat class j (Manly et al., 2002). If individuals use all habitats in relation to their availability, the ratio is 1, if they use a certain habitat proportionally less than its availability, the ratio is a value between 1 and 0, while if they use the habitat proportionally more than its availability, the ratio is > 1 (i.e., the higher the value, the higher the preference for that habitat).

Since the selection ratio showed that microhabitat selection was different from one animal to another, we investigated these differences by means of eigenanalysis of selection ratios (Calenge, 2006). If W is the table containing the selection ratios for each animal (rows) and each microhabitat type (columns), the eigenanalysis consists of a non-centred and non-scaled principal component analysis of the table W − 1, using the proportion of availability of each microhabitat type as column weights and the number of relocations of each animal as row weights. This analysis partitions the statistics:

$$S = \sum_{i=1}^{P} \sum_{j=1}^{K} \frac{\left(u_{ij} - p_i u{+}j\right)^2}{p_i u{+}j}$$

where u_{ij} is the number of relocations of animal j in microhabitat i, p_i is the proportion of available resource units in microhabitat i, and u+j is the total number of relocations of animal j. This statistic was proposed by White and Garrott (1990) to test microhabitat selection~~. What is interesting is that this analysis connects two widely used approaches for microhabitat selection studies into a unified framework [selection ratios and the White and Garrott (1990) statistic]~~.

Commento [EC18]: L 283, the journal may want you to number this formula

Commento [EC19]: L 287, delete the unnecessary "What is interesting is that"

Commento [EC20]: L 288-289, please clarify (rewrite) this sentence; also, (connects => combines

Movements

Movements were studied by measuring the linear distances (with a telemeter) and the turning angles between consecutive fixes (Cain, 1989). Vagility indices were computed for each individual, consistent with Negro et al., 2008. Independence among successive angles was tested by the non-parametric Runs Test above and below the median, which is used to test the randomness of a sequence of a series of observations (turning angles, in our case) (Sokal & Rohlf, 1995). To approach normality (checked by using normal probability plots), distance data were square-root transformed (Sokal & Rohlf, 1995).

To test the agreement among turning angles, we computed an index of angular concordance, or angular concentration (Zar, 1999; Fortin & Dale, 2005), converting angles in a circular system using Batschelet’s (1981) protocol. ~~For any sets of data the angles (θ_i) are represented in a circular system by vectors of unit length and coordinates (x_i, y_i) by means of the following equations: $x_i = \cos(\theta_i)$ and $y_i = \sin(\theta_i)$. The coordinates of the mean vector are $(\bar{x}, \bar{y})$, while its length is equal to $r_a = \sqrt{x^{-2} + y^{-2}}$). The circular equivalent of the standard deviation is $s = \sqrt{2(1 - r_a)}$, which can be converted to degrees by multiplying by 180°/π (Batschelet, 1981).~~ The mean vector length ~~(r_a)~~ takes a value of 1 when all the angles are the same and a value of 0 when the vectors cancel each other out (Upton & Fingleton, 1989; Fortin & Dale, 2005).

To check the compactness of the paths travelled by each radio-tagged individual, we calculated the Index of Tortuosity (T) that considers both distances and angles. This index is based on the convex hull, which is the smallest convex polygon that fully contains the path. T is equal to the L/M ratio, where L is the total distance covered and M is the major diameter of the convex hull (Claussen et al., 1997). The coefficient of variation (CV = standard deviation/mean × 100) of distance was used to test the variability of daily distance between fixes among different forest management types.

Commento [EC21]: L 300-304, unnecessary jargon; just say that you used Batschelet’s (1981) protocol for these

Movement data were merged with those of 21 individuals radio-tracked in Alpine rose shrubberies and over-mature beech coppices in years 2005 and 2006 (Negro et al., 2008). This merger significantly increased the size of the data set and gave us the opportunity to study movements in a gradient of increasing human impact (from undisturbed forest to managed forest to shrubs resulting from past forest harvesting).

All vagility parameters (i.e. tortuosity index, angular concordance and CV of distance) were modelled by means of GLMs, in relation to the sex of the individual and forest management.

Results

A total of 40 *C. olympiae* individuals were collected and radio-tracked within stands: 15 in 2014 (in two stands i.e. C and M3) and 25 in 2015 (in four stands i.e. C, M1, M2 and M3) (Table 1). Forest management increased deadwood (M1: from 2 to 6%; M2: from 2 to 8%; M3: from 2 to 5%) and bare ground cover (M1: from 4 to 9%, M2: from 3 to 9%; M3: from 3 to 29%) in all managed stands. Cover by litter decreased greatly (M1: from 80 to 60%, M2: from 75 to 63%; M3: from 75 to 32%), while grass cover exhibited only little change (M1: from 0 to 3%, M2: from 5 to 1%; M3: from 5 to 4%). The harvest did not affect ground cover by tree bases, shrubs and rocks.

Table 1. Number of fixes, daily mean ± SE and total distances covered by radio-tagged ground beetles in 2014-2015.

No.	Management	Sex	Year	Fix No.	Total distances (m)	Mean (m) ± SE
1	Control	F	2014	31	151.10	5.04 ± 0.76
2	Control	M	2014	6	12.91	2.58 ± 1.25
3	Control	M	2014	14	130.05	10.00 ± 2.65
4	Control	M	2014	4	97.10	32.37 ± 6.93
5	Control	F	2014	20	88.90	5.56 ± 0.84
6	Control	F	2014	9	134.80	19.26 ± 4.44
7	Control	M	2014	3	8.65	4.33 ± 2.98
8	M3	F	2014	6	76.91	15.38 ± 11.78
9	M3	M	2014	6	57.99	11.60 ± 6.74
10	M3	M	2014	6	130.47	26.09 ± 11.05
11	M3	M	2014	31	310.72	11.10 ± 3.23
12	M3	F	2014	11	125.00	15.63 ± 6.03

13	M3	M	2014	11	195.30	19.53 ± 5.65
14	M3	F	2014	4	3.40	1.13 ± 0.34
15	M3	F	2014	22	319.40	15.21 ± 3.54
16	M3	M	2014	16	73.40	4.89 ± 1.36
17	Control	M	2015	37	806.50	22.40 ± 3.09
18	Control	M	2015	38	388.60	10.50 ± 1.40
19	Control	M	2015	6	7.00	1.40 ± 0.44
20	Control	F	2015	13	67.65	5.64 ± 1.91
21	Control	M	2015	29	654.15	23.36 ± 3.79
22	Control	F	2015	4	71.80	23.93 ± 3.14
23	Control	F	2015	15	95.80	6.84 ± 2.50
24	M2	F	2015	24	259.00	11.26 ± 2.73
25	M2	F	2015	24	27.28	1.19 ± 0.55
26	M2	M	2015	19	135.50	7.53 ± 2.65
27	M2	M	2015	24	63.30	2.75 ± 1.27
28	M1	M	2015	14	91.20	7.02 ± 2.16
29	M1	M	2015	11	66.80	6.68 ± 3.35
30	M1	M	2015	6	110.00	22 ± 11.49
31	M1	M	2015	6	155.10	15.51 ± 4.74
32	M1	F	2015	26	306.85	12.27 ± 2.38
33	M1	F	2015	15	102.73	7.34 ± 2.98
34	M2	M	2015	11	201.85	20.19 ± 4.77
35	M2	F	2015	17	289.35	18.08 ± 4.75
36	M2	F	2015	15	109.13	7.80 ± 2.48
37	M2	M	2015	14	54.75	4.21 ± 1.74
38	M3	F	2015	20	343.30	18.07 ± 5.10
39	M3	F	2015	13	162.20	13.52 ± 4.66
40	M3	M	2015	7	88.50	14.75 ± 6.68
41	M3	M	2015	26	453.55	17.44 ± 6.28

Microclimatic conditions

A complete series of climate data was only available for C and M3 stands in 2015, where data loggers ran without interruption from 18 June to 5 August. Microclimatic conditions in these control and managed stands were significantly different. No significance differences were found between control and M1 and M2 stands, likely because the incompleteness of the data collected; the maximum temperature was on average significantly higher in M3 than in C (Gaussian GLM: beta 5.0297, SE 0.4861, t value 10.35, p <2e-16), whilst the minimum and average humidity were lower (minimum humidity: Gaussian GLM: beta -3.27, SE 0.86, t value -3.77, $p < 0.000185$; average humidity: Gaussian GLM: beta -18.74, SE 1.53, t value -12.2, $p < 0.000185$).

Microhabitat use

Five microhabitats were available for radio-tagged ground beetles in all managed and control areas. The most available microhabitat was litter (min= 48% of quadrats in M1, max= 63% in C), followed by deadwood (min = 6% in C, max=27% in M2), bare soil (min = 1% in C, max=34% in M1), tree bases (min = 4% in M3, max=12% in C) and rocks (min= 1% in M3, max=5% in M2). Shrubs were absent from M1 and grass cover from M1 and M2. Overall, control areas used by radio-tagged individuals had more litter, shrubs and tree bases, while managed areas had more deadwood and bare soil (Fig. 2, on top).

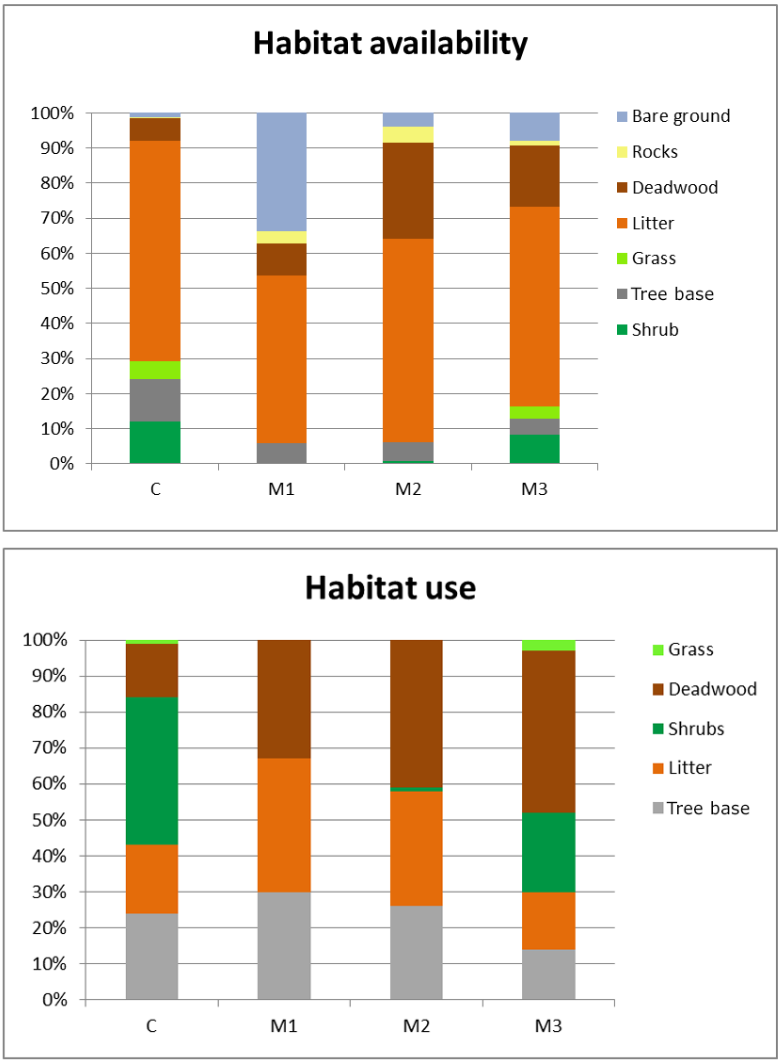

Fig 2. Available (top) vs used (bottom) microhabitat types in managed and control areas used by radio-tracked individuals.

Radio-tagged individuals used five microhabitat types, i.e. litter, tree bases, deadwood, shrubs and grass (Fig. 2, on bottom). Bare ground and rocks were ~~never~~ not used. Microhabitat use modelling did not show any significant differences in the use of litter, deadwood or tree bases due to year of sampling, sex, mean temperature or humidity. The use of these microhabitat types significantly changed according to management type only. In particular, litter was used more frequently in M1

Commento [EC22]: L 357, "never" => not than in control stands, and deadwood was used more frequently in all managed than in control stands (Table 2).

Table 2. Binomial Generalized Linear Mixed Models of the frequency of the use of Litter, Tree bases and Deadwood diurnal shelter in the different forest management stands. Control was set as reference category. Significance codes: ‘***’ p < 0.001; ‘**’ p<0.01; ‘*’ p<0.05; ‘.’ p<0.1.

Commento [EC23]: L 364, “diurnal shelter” is an interpretation and should be omitted

Litter				
	Estimate	St. Error	z values	Code
(Intercept)	-1.61	0.28	-5.75	***
M1	1.02	0.48	2.13	*
M2	0.69	0.43	1.61	NS
M3	-0.06	0.40	-0.14	NS
Deadwood				
	Estimate	St. Error	z values	
(Intercept)	-1.83	0.27	-6.87	***
M1	1.10	0.45	2.45	*
M2	1.49	0.39	3.78	***
M3	1.67	0.35	4.76	***
Tree bases				
	Estimate	St. Error	z values	
(Intercept)	-1.15	0.22	-5.14	***
M1	0.26	0.42	0.63	NS
M2	0.03	0.37	0.09	NS
M3	-0.68	0.35	-1.95	.

The ranking of microhabitats obtained through Compositional Analysis showed that deadwood and tree bases were the most preferred microhabitats both in managed and control stands, whilst litter and grass were the least preferred ones. Shrubs was a high ranking microhabitat in control stands, but a low ranking one in M2 and M3 stands (Table 3 and Appendix I).

Table 3. Microhabitat selection as revealed by Compositional Analysis. Microhabitats are ranked in ascending order of preference.

	C	M1	M2	M3
Shrub	5	-	2	2
Tree base	6	4	4	5

Grass	2	-	-	4
Litter	3	2	3	3
Deadwood	4	3	5	6
Rocks	0	1	0	1
Bare ground	1	0	1	0
Lambda	0.068	0.088	0.021	0.134
p-value	0.002	0.040	0.018	0.002

Manly’s selection ratio W_i for deadwood, tree bases and shrubs was higher than 1 (i.e. positive selection) and ranged between 0 and 1 for litter and grass (negative selection) both in the managed and control stands. The selection ratio for tree bases was higher in M1 and M2 stands (4.74 and 4.40, respectively), suggesting a high preference for that microhabitat, and close to 1 for shrubs in M2 stand (1.06), suggesting a weak positive selection or a random use for that microhabitat (Fig. 3).

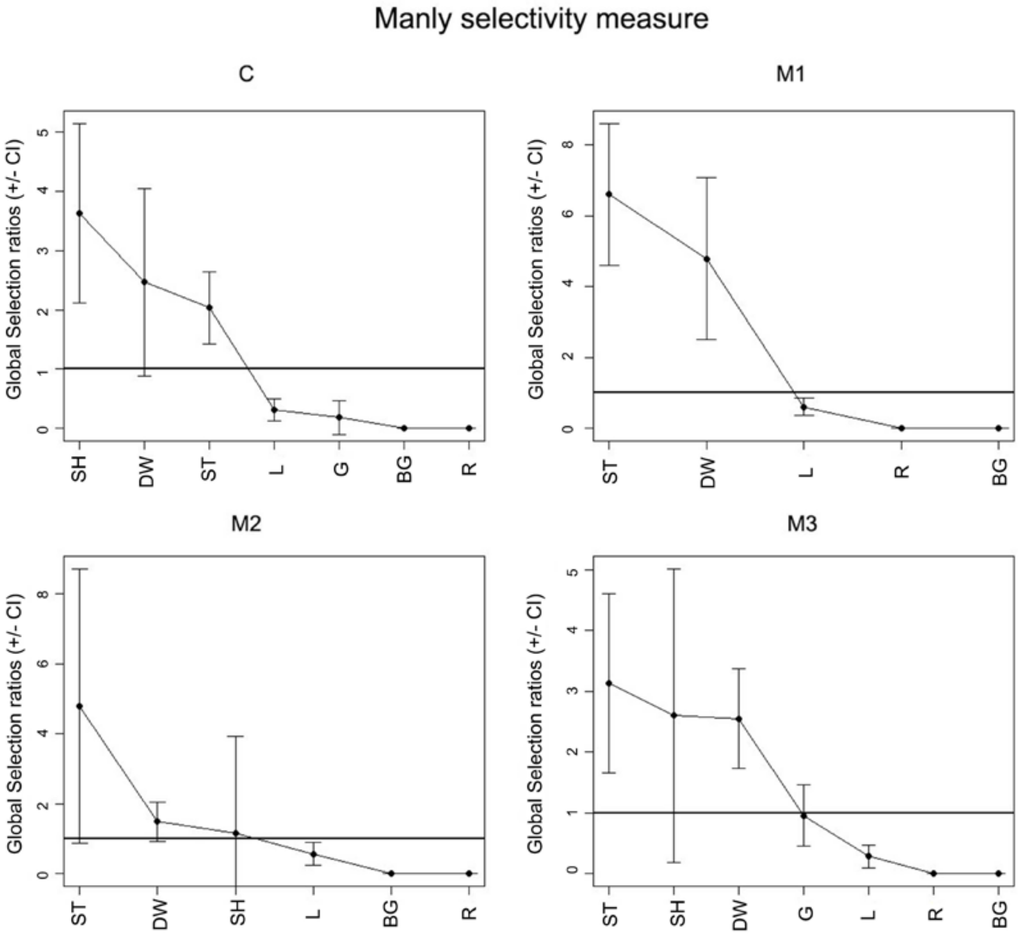

Figure 3. Microhabitat selection in control (C), and managed stands t (M1, M2 and M3) as revealed by Manly selection ratio Wi (± SE). Microhabitat codes as follows: shrubs (SH), tree bases (ST), deadwood (DW), grass (G), bare ground (BG), rocks (R) and litter (L).

The eigenanalysis of selection ratios (Calenge and Dufour, 2006) graphically showed that all individuals avoided bare ground, grass and rocks and showed variable preference in the use of tree bases, shrubs and deadwood (Appendix II). The radiotracked individuals selected shrubs, deadwood and tree bases in C, in M1 they selected deadwood and tree bases, in M2 some individuals selected shrubs and deadwood and some selected tree bases, while in M3 most individuals selected tree bases and deadwood.

Movements

By pooling old (2005 and 2006) and new (2014 and 2015) fixes together, a four-year integrated data set of 1161 fixes (527 + 634) relative to 61 (21 + 40) ground beetles was obtained. All individuals displayed zig-zag trajectories (Fig 4).

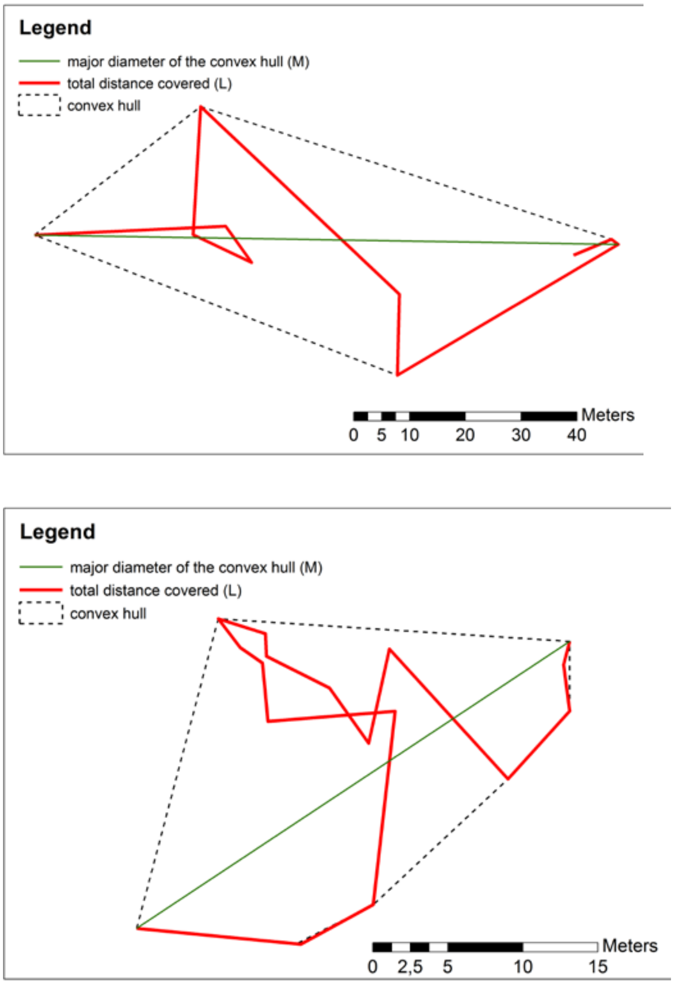

Fig 4. Trajectories of two randomly selected *Carabus olympiae* individuals (i.e. male No. 13, top and female No. 5, bottom) radio-tracked in 2014. The individual’s path (red line) and the major diagonal of the Minimum Convex Polygon (green line) that includes the entire path are shown.

The total distances covered by radio-tracked individuals varied between 3.40 and 806.50 metres, with mean daily distances ranging from 1.13 to 32.37 metres (Table 1). Angles were evenly distributed in all stands (shrubberies, control and in managed stands), indicating the lack of a prevailing walking direction (Appendix III).

GLMs showed that the coefficient of variation of the distances and the tortuosity index varied according to the management; the length of the paths of individuals in M2 and M3 stands was more variable than in control stands and the tortuosity index was significantly lower in shrubbery and in M2 stands than in control, and significantly higher in males than in females (Table 4 and Fig. 5).

CV Distance				
	Estimate	St..Error	t values	P
(Intercept)	0.86	0.07	11.88	<2E-16
M1	0.31	0.16	1.93	5.80E-02
M2	0.50	0.14	3.49	9.52E-04
M3	0.33	0.12	2.70	9.25E-03
Shrubbery	0.18	0.13	1.41	0.16
Tortuosity				
	Estimate	St..Error	t values	P
(Intercept)	0.83	0.08	9.76	<2.96E-12
M1	-0.18	0.16	-1.11	0.27
M2	-0.39	0.15	-2.60	0.01
M3	-0.16	0.13	-1.30	0.20
Shrubbery	-0,47	0.11	-4.22	1.31E-04
Sex	0.29	0.09	3.34	1.80E-03

Table 4. Generalized Linear Mixed Models of CV of distances and tortuosity in the different forest management and shrubland stands. Control was set as reference category.

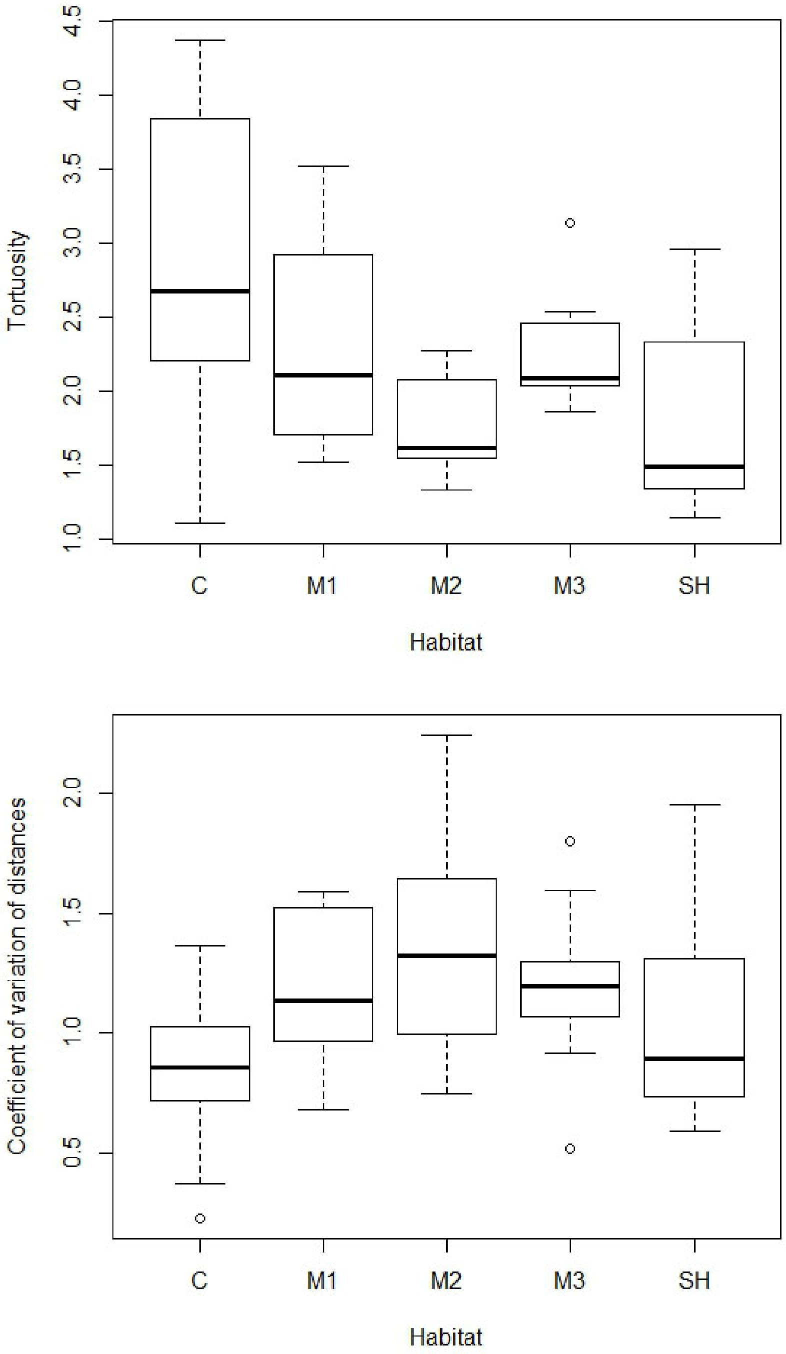

Fig.5 Box plots of the tortuosity index (top) and of the coefficient of variation of the distances (bottom) between management types (Control C, Management M1, Management M2, Management M3 and Shrubs SH)

Discussion

Logging may ~~have negative impacts f~~affects or forest wildlife and insect fauna because of the induced changes in microclimatic conditions and microhabitat availability. Ground beetles strongly depend on particular humidity and temperature requirements (Skłodowski 2014). Data loggers showed that temperature was higher and humidity lower in M3 than in control stands, suggesting that uniform logging may induce significant short term climatic changes. Warmer and drier microclimates may negatively affect *C. olympiae* both directly (this species likes fresh and humid beech forests, Negro et al. 2014) and indirectly, reducing the local availability of snails and slugs (*Arianta arbustorum*, *Arion* and *Limas* spp.), which are the preferred prey (Negro ~~et al., 2008~~pers. comm.). Canopy and shrub cover usually take several years to recover after a cut, depending on the intensity of the removal. Montagnoli et al. (2012) compared canopy cover and soil temperature between May and October at 5 cm depth in over-mature beech coppices (not cut for 40 years) against those following uniform conversion to high forest (75% of trees removed). Even 14 years after the cut, canopy cover was on average 22% lower and soil temperature 1 °C warmer than in the uncut forest.

The low-intensity interventions (M1 and M2) may have resulted in only negligible changes in micro-climate, shadiness and shrub cover ~~M1 and M2 forest management interventions, conversely, might have produced negligible climatic changes. Such lower-intensity cuts may mitigate the changes in shading, shrub cover, and soil microclimate~~ by preserving patches or corridors of trees throughout the stands. Small canopy gaps (20 to 30 m diameter) ~~were found~~have been found to increase maximum soil temperature by +0.2 - +1.9 °C relative to an uncut control, but the effect was already cancelled out at the edge of the gap (Prévost and Raymond, 2012). Gap cutting may be even more conservative in terms of soil moisture, which has been found to be unchanged, or even increased, in small (300-400 m^2) and large (500-700 m^2) gaps compared to below fully closed canopy (Bilek et al., 2014).

Commento [EC24]: 9. Discussion is exhaustingly long. It would benefit from 2-3 subtitles which would bring about clearer structure, for example based on your research questions.

Commento [EC25]: 8. Discussion begins rather weaklyby stating general logging impacts, but it should begin with one of your results (concretely, the sentence on lines 441-443). The rest of the paragraph would then clarify and present other studies. Also, logging has also positive effects so L 439 should perhaps say “”logging may affect forest wildlife…”.

Commento [EC26]: L 446, the cited study does not present data on prey so this “preferred prey” is unwarranted or at least the reference is incorrect. There may not be any study that would show this for this species, but generally slugs and snails are used as part of the diet of many large carabids. Cite, for example, Rob Hengeveld’s studies from 1980s, or some general papers about carabids (Thiele’s 1977 book, or more recent papers such as Kotze et al. 2011/ZooKeys or Lövei & Sunderland 1996/Annu.Rev. Ent.).

MATTEO

Commento [EC27]: L 453-456, very wordy text, compress, for example “The low-intensity interventions (M1 and M2) may have resulted in only negligible changes in micro-climate, shadiness and shrub cover.”

Commento [EC28]: L 456, you did not show anything about canopy gaps. If you intend to refer to Prevost et al., then rather say “have been found”

Compared to other broadleaves, beech has a strong ability to fill canopy gaps by crown extension (Brunet et al. 2010). If the regeneration strategy is successful, a new beech layer will establish in recently opened gaps within a few years, resulting in moderate microclimatic changes with a new canopy (Dovciak and Brown, 2014). Finally, the release of deadwood on the ground may provide shadier microsites that mitigate the absence of a more uniform canopy or shrub cover as a consequence of the cut (Marzano et al., 2013) and contribute to preserving soil moisture (Ritter and Vesterdal, 2006).

In addition to microclimatic conditions, forest management may change ground cover and understory, and induce a different microhabitat use. Even though we were able to consider only 1-2 stands per management, we nonetheless described in details and by means of several sampling points the variance within each treatments. This allowed us to identify that the use of microhabitat types by radio-tagged *C. olympiae* individuals indeed changed significantly according to the management. The increase in bare ground after logging is obviously a negative effect, given that individuals cannot hide in such a microhabitat ~~(which was never used)~~ (Niemelä et al., 1996, Skłodowski 2008). This finding is consistent with previous analyses that showed that *C. olympiae* abundance was negatively related to bare ground cover (Negro et al., 2014). However, the increase in deadwood availability may be beneficial. Microhabitat selection analyses (i.e. Compositional Analysis and Manly ratio) showed that deadwood and tree bases were ~~positively selected~~preferred and litter ~~negatively selected~~ ~~(i.e.~~was avoided ~~avoided)~~ in all managed and control stands, suggesting that microhabitat preferences did not significantly change with forest interventions. At the same time, univariate models showed that deadwood was used more frequently in all managed stands than in control stands. This major use, given the consistency of microhabitat preferences, may be easily explained by the greater deadwood availability in managed stands. The abundance of deadwood in managed stands was a consequence of experimental logging that aimed at a high level of retention of coarse woody debris (Negro et al. 2014).

Commento [EC29]: L 471-472, this is what you did indeed, but it brings pseudoreplication regarding the treatments. Much caution must be added. Besides, the less intense (M1, M2) were not that different from the more intensive (M3) management, and results comparing these were often not systematic (Tables).

Commento [EC30]: L 475, delete "(which was never used)" (unnecessary text)

Commento [EC31]: L 479-480, use biological terms: were preferred, were avoided

Commento [EC32]: L 485, what is "high level of retention"? Retention should also be clarified in Mat & Met: how much dead wood per hectare, were it all dead before logging, etc.

~~It should be emphasised that d~~Deadwood is crucial for hundreds of rare and threatened species in Europe alone (cit?!)

~~decomposition plays a key role in the recycling of nutrients and organic matter, as well as in providing a wide variety of microhabitats for plants and invertebrates, particularly insect species and other organisms (Stevens 1997, Floren et al. 2014, Chumak et al. 2015). Insects, in turn, may be beneficial to forest bird specialists, whose diversity increases with increasing amounts of deadwood, both in breeding and in wintering seasons (Laiolo et al. 2004; Caprio et al. 2009).~~

The quantity of deadwood in Europe's forests has decreased significantly since the middle of the 19th century due to intense forest exploitation. Since 2000, however, a small overall increase in deadwood has been observed (Forest Europe 2011). This may be due to management practices that deliberately increase the amount of woody debris in managed forests (as in our case), either thanks to legal or policy prescriptions, or as a measure to comply with forest certification requirements (European Environment Agency 2015). The increases in forest cover and stem density in many European forests, following extensification of forest use, have also led to a increased natural disturbance levels (Seidl et al. 2014). Wind storms and bark beetle disturbance events may have influenced the production of dead wood in some areas (Kulakowski et al. 2017), although this should not be relevant for the area studied here (no evidence for large disturbances in the managed beech forest was found). Finally, climate change may also contribute to increased disturbance frequency and severity, and increased deadwood input (Seidl et al. 2017).

All the above confirms that the retention of deadwood is thus crucial in conservation of forest organisms, and specific attention should be paid for securing its spatio-temporal continuity in managed forests ~~a method that produces results that are superior to those achieved by other means and should therefore be recommended as best practice in forest management~~ devoted to animal diversity conservation.

Commento [EC33]: L 487-492, too wordy text. The message is that deadwood is crucial for hundreds of rare and threatened species in Europe alone (add references). Then, this simple statement could/should be added as a beginning sentence for the next paragraph, discussing deadwood role.

Lassauce, A., Paillet, Y., Jactel, H., Bouget, C., 2011. Deadwood as a surrogate for forest biodiversity: Meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. Ecological Indicators 11, 1027–1039. doi:10.1016/j.ecolind.2011.02.004

Gossner, M.M., Wende, B., Levick, S., Schall, P., Floren, A., Linsenmair, K.E., Steffan-Dewenter, I., Schulze, E.-D., Weisser, W.W., 2016. Deadwood enrichment in European forests – Which tree species should be used to promote saproxylic beetle diversity? Biological Conservation 201, 92–102. doi:10.1016/j.biocon.2016.06.032

Commento [EC34]: L 505-507 Add caution by just saying, for example, that "Retention of deadwood is thus crucial in conservation of forest organisms, and specific attention should be paid for securing its spatio-temporal continuity in managed forests." It is dangerous to say that deadwood would be superior: it is one important thing, but there will not be much dead wood if e.g. all large trees are harvested as it would interrupt the continuity of this resource.

Formattato: Colore carattere: Automatico

Very large bases of living and dead trees were clearly preferred by C. olympiae individuals that probably used this resource as shelter for daytime rest or against micro-climatic variation~~Enlarged tree bases, especially those with decaying wood, were also greatly appreciated by radio-tagged *C. olympiae* (Manly ratio was well above 1 and scored the highest values in M1 and M2 stands), which took advantages of splits and cavities as shelters~~. Coppices may provide more of this habitat than high forests, since the tree base tends to expand if it must support a larger number of sprouts. Interventions aimed at maintaining over mature coppices are therefore preferable to those aimed at converting over-mature coppices to high forest, consistent with previous analyses (Negro et al., 2014, Seidle et al. 2017).

The eigenanalysis of selection ratios showed that microhabitat preferences changed from one individual to another.

The present research also indicates that forest management may affect *C. olympiae* movements. Both the coefficient of variation of the distances and the tortuosity index varied according to the management. The length of the paths of individuals in managed stands was more variable than in control stands, suggesting that movements of individuals were ~~more uncertain and unpredictable~~random in terms of direction and length ~~(sometimes they moved a lot, sometimes they did not move)~~ when relocated in forest stands subjected to logging. Trajectories were rather tortuous, fitting the ~~requirements~~ hunting behaviour of a typical "olfactory-tactile" predator that looks for prey by systematically exploring its territory. The high tortuosity is also in keeping with the use of decaying fruits and vegetables (as shown by multiple choice tests carried out in the lab by Negro and Palestrini, unpublished). We did not track individuals in between two successive telemetric locations. This means that true paths were likely longer and trajectories more tortuous than those measured. The tortuosity index was significantly lower in Alpine rose shrubland and in M2 stands than in control. Negro et al. (2008) found that most individuals located in shrubland were hidden under Alpine rose shrubs, which probably were used as shelter from extreme temperatures

Commento [EC35]: L 508-510, rewrite as "Very large bases of living and dead trees were clearly preferred by C. olympiae individuals that probably used this resource as shelter for daytime rest or against micro-climatic variation."

Commento [EC36]: L 521, "uncertain and unpredictable" sounds strange, perhaps say "random in terms of direction and length

Commento [EC37]: L 522-523, delete the text in parentheses (not needed)

Commento [EC38]: L 523, "requirements" is not the correct word here, perhaps say behavior?

and protection from predators. We believe the low availability of shrubs (which were isolated and sparse) may have constrained trajectories (individuals were compelled to move from shrub to shrub) and reduced their tortuosity. Analogously, changes in microhabitat and/or resource availability in some managed forest stands may have significantly reduced tortuosity in comparison with controls. Tortuosity index was significantly higher in males than in females. Males of insects are able to detect pheromones produced and emitted by females (Gullan & Cranston 1994). We therefore hypothesize the paths of males were more tortuous in order to diminish the time allocated for the searching for females (in keeping with Negro et al. 2008).

We assumed that microhabitat use and movements of radio-tracked individuals were unaffected by radio-tags. Although their weight and dimensional impediment were low, concerns about the effects of tagging on animal behaviour may arise and a reduction in dispersal ability cannot be excluded. In fact, the weight of the tag (0.3 g) is about 40% of the average weight of individuals, and the tag fixed on top of the elytra may be a hindrance to the movements across narrow passages (leaf-litter, thick grass, etc.). In a previous paper on movements of the common ground beetle species *C. coriaceus*, Riecken & Raths (1996) stated that foraging success was not substantially reduced by radiotags. During the present research, radio-tagged individuals were observed on many occasions to feed on molluscs and to copulate with untagged individuals~~ (in keeping with Negro et al., 2008)~~, suggesting radio-tagging did not significantly affect feeding and mating behaviour. If a reduction in dispersal existed, however, this would have affected both individuals in control and in managed stands to the same degree. Our results, focused on the comparative analyses between managed and un-managed forest patches are therefore ~~highly~~ reliable.

Commento [EC39]: Sono stati osservati anche durante questo studio? Quante volte?

Commento [EC40]: L 548-549, these are not from present data, plus unclear “many occasions”, so delete.

Commento [EC41]: L 553, I disagree with this statement (poor replication) so delete “highly”

Conclusions

Our results support the evidence that logging may exert short-term negative effects on *C. olympiae* ground beetles (as suggested by the increase in bare ground, and changes in climatic conditions and movements). However, the preference for tree bases and deadwood suggests that forest management, concurrently, may also be beneficial, on the condition that: *i)* the coppice, which provides more suitable microhabitats, prevails over conversion to high forest, and *ii)* deadwood originating from cutting (branches and treetops) is properly accumulated.

To our knowledge, this is the first time that radio-telemetry has been used as a tool to assess the effect of forest management on ground dwelling insects. In methodological terms, this study indicates therefore that radio-tracking may be successfully used as a tool to assess the effect of forest management on relatively large ground dwelling insects, and to identify the logging practices that are more compatible with their conservation.

Commento [EC42]: 10. Discussion ends with suspicious statements about logging being beneficial (L 558-561) and about an off-topic (and mostly unwarranted) statement about radio telemetry use (L 562-566). Regarding the former, clearly say that if these beetles are to be maintained in managed forests, deadwood continuity and high abundance must be secured while harvesting, and that very large clearings probably make the microclimate too warm and dry for this species, suggesting that only thinning or gap harvesting, if any, should be used in these habitats. Regarding the latter, this is a poor way to end a paper; rather end with a clear management statement, such as the one I suggest above. This is not a methodological paper, and the usefulness of telemetry has been shown over 20 years ago already (Riecken & Raths 1996/Ann.Zool. Fennici, etc.).

Acknowledgements

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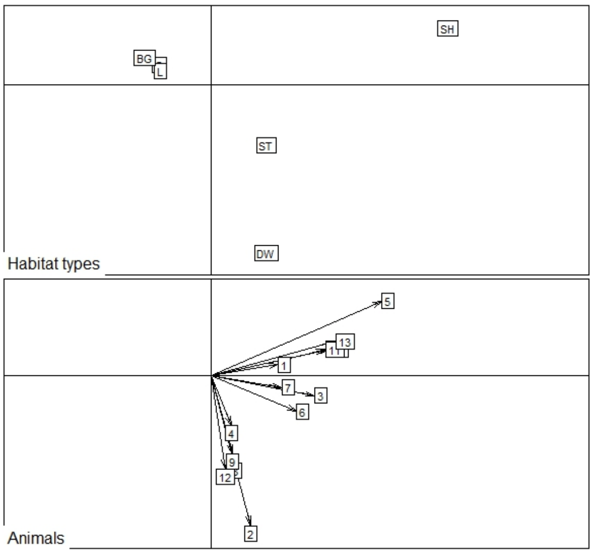
Appendix I. Ranking matrices of Compositional Analysis for ground beetles based on comparing proportional microhabitat use of fixes with proportions of total available microhabitat types in Control (C) and Managed (M1, M2, M3) stands. Microhabitat codes as follows: shrubs (SH), stumps (ST), deadwood (DW), grass (G), bare ground (BG), rocks (R) and litter (L). Each mean element in the matrix was replaced by its sign; a triple sign represents significant deviation from random at $P < 0.05$.

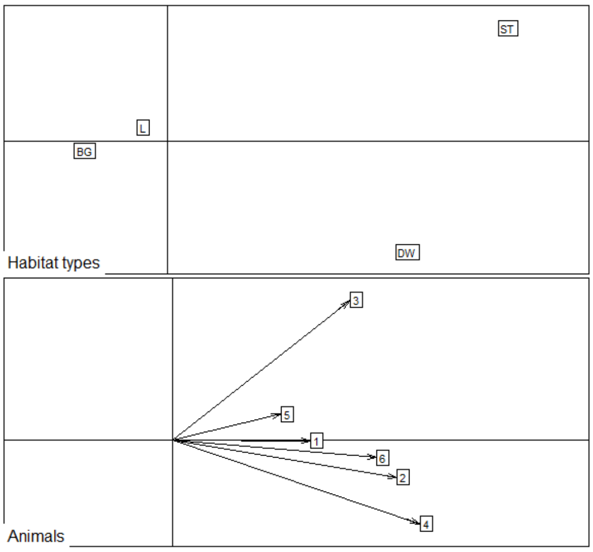
Habitat type																
C									**M1**							
	SH	**ST**	**G**	**L**	**DW**	**R**	**BG**			**ST**	**L**	**DW**	**R**	**BG**		
SH	0	-	+++	+++	+	+++	+++		ST	0	+++	+	+++	+++		
ST	+	0	+++	+++	+	+++	+++		L	---	0	---	+++	+++		
G	---	---	0	---	---	+++	+++		DW	-	+++	0	+++	+++		
L	---	---	+++	0	---	+++	+++		R	---	---	---	0	+++		
DW	-	-	+++	+++	0	+++	+++		BG	---	---	---	---	0		
R	---	---	---	---	---	0	---									
BG	---	---	---	---	---	+++	0									
M2									**M3**							
	SH	**ST**	**L**	**DW**	**R**	**BG**				**SH**	**ST**	**G**	**L**	**DW**	**R**	**BG**
SH	0	-	-	---	+++	+++			A	0	---	-	-	---	+++	+++
ST	+	0	+	-	+++	+++			C	+++	0	+++	+++	-	+++	+++
L	+	-	0	---	+++	+++			E	+	---	0	+	---	+++	+++
DW	+++	+	+++	0	+++	+++			L	+	---	-	0	---	+++	+++
R	---	---	---	---	0	---			N	+++	+	+++	+++	0	+++	+++
BG	---	---	---	---	+++	0			P	---	---	---	---	---	0	+++
									SN	---	---	---	---	---	---	0

Appendix II. Results of the eigenanalysis of selection ratio carried out to highlight microhabitat selection by *Carabus olympiae* individuals radiotracked in Control (C) and Managed (M1, M2 and M3) stands. Top panel: microhabitat type loadings on the first two factorial axes. Bottom panel: animal scores on the first factorial plane (see Calenge & Dufour 2006 for further details). Microhabitat codes as follows: shrubs (SH), stumps (ST), deadwood (DW), grass (G), bare soil (BG), rocks (R) and litter (L). Numbers indicate animals in each treatment (i.e. 13 individuals in controls, 6 in M1, 8 in M2 and 13 in M3). The distance of the label from the center of the graph in the top panel indicates microhabitat preference (those close to the origin not being selected), the length and direction of the arrows in the bottom panel indicates the preferred selection for each individual.

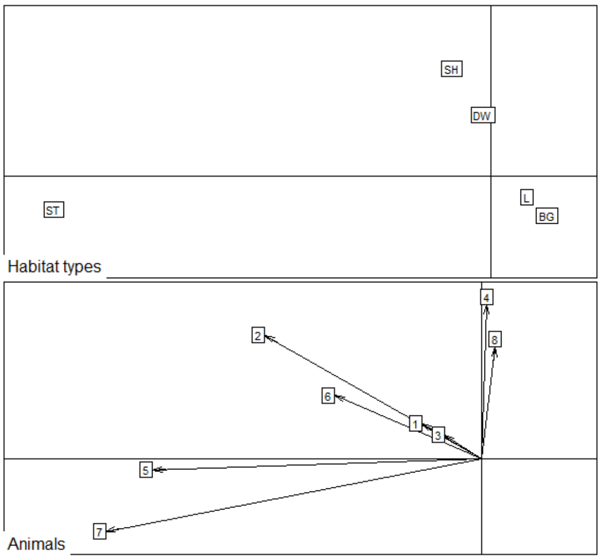
Control



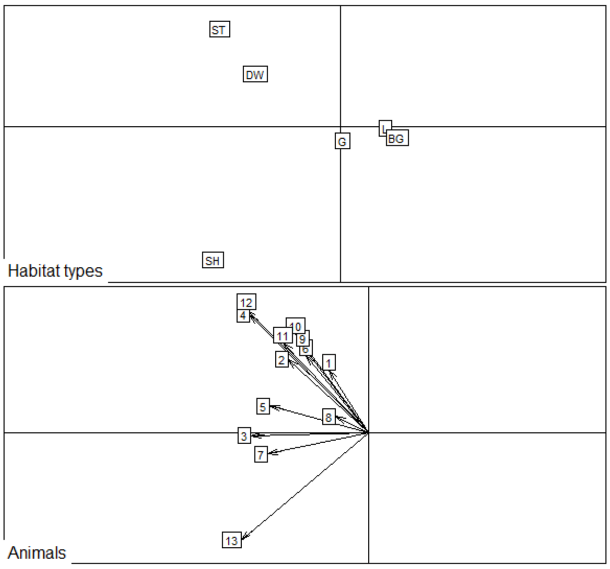
M1


ST
L
BG
DW
Habitat types
3
5
1
6
2
4
Animals

M2


SH
DW
ST
L
BG
Habitat types
4
2
8
6
1
3
5
7
Animals

M3


ST
DW
L
BG
G
SH
Habitat types
12
4
10
11
9
6
2
1
5
8
3
7
13
Animals

Appendix III. Even distribution of angles in shrubbery, control and managed stands.