



Research Article

The effect of thinning on bat activity in Italian high forests: the LIFE+ “ManFor C.BD.” experience

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Abstract

Bats represent a major component of forest biodiversity. In forest, bats find many roosting and foraging opportunities. When foraging in forest, different bat species exploit a range of microhabitats according to their echolocation and flight style. When roosting, bats require sufficient numbers of suitable tree cavities. Overall, forest structure may influence both foraging and roosting behaviour, and in turn the number of bat species present and their population size. The exploitation of forests for commercial purposes may be a threat to biodiversity when logging leads to habitat loss, alteration or fragmentation. While some bat species may benefit from an increase in the amount of edge habitat determined by logging, others, more specialized to exploit forest interiors, may be potentially harmed. In this study we set out to assess the effect on foraging bats of different management approaches, comparing locally applied traditional approaches with innovative multifunctional management options and delayed logging. Within the framework of the LIFE+ ManFor C.BD. Project we surveyed the effects of thinning at four Italian forest sites, each representing a separate case study. We found that in logged plots bat activity either showed no difference from unlogged plots or resulted in an increase in foraging activity, suggesting that thinning, at least in the forest types we dealt with, has no adverse consequences on bat foraging. However, in our case the effects varied greatly across sites and were detected mostly when all bat species were pooled together for analysis. We conclude that forest exploitation may be sustainable and even favour foraging bats, but since our work neither covered direct mortality linked with forestry operations nor roost loss, further studies are needed to analyze these important aspects. We also highlight that total bat activity revealed by acoustic surveys carried out with automatic recorders may be used as an appropriate indicator of forestry effects on bats.

Introduction

Bats represent a major component of forest biodiversity. In forest, bats find plenty of roosting and foraging opportunities (Lacki et al., 2007a). Cavities such as spaces beneath loose bark, rot cavities, mechanical breaks (cracks or crevices) and woodpecker holes are typically used by tree-dwelling bat species worldwide in temperate forests (Kunz and Lumsden, 2003). Trees bearing such cavities are therefore of enormous importance for bats: many suitable trees are needed to support even small populations because forest bats frequently switch between tree roosts (Russo et al., 2005).

Forest also allows several bat species to forage, because different species exploit different microhabitats - closed forest, forest corridors, edges or clearings, ponds, streams, etc. (Lacki et al., 2007b) – according to their echolocation and flight style (Neuweiler, 1984). Because bats often hunt within limited distances from their roosts, ideally forest should provide feeding sites within the range they cover on their nightly movements. Moreover, many bats avoid flying in open spaces (Duvergé et al., 2000) so canopy continuity may be important to allow them to move between foraging or roosting sites (Russo et al., 2007). Migratory species often use forest sites as stopovers, wintering or reproductive quarters (Cryan and Veilleux, 2007).

Forest structure may affect both features needed for roosting and those important for foraging, so it may profoundly influence the num-

ber of species present and their population size. Characteristics such as tree age and structure, canopy closure, presence of gaps and more generally horizontal and vertical habitat heterogeneity may have significant consequences for bats (e.g. Jung et al., 2012).

Unmanaged high forests stand out as especially important because they comprise larger numbers of the specific tree types needed by many bat species such as large, decaying or dead trees, where suitable roost cavities are found (e.g. Russo et al., 2004). In those situations, natural disturbance factors generally promote sufficient heterogeneity to provide bats with a diverse choice of foraging habitats. However, apart from some forests in nature reserves, left untouched to preserve biodiversity, most forests worldwide are subjected to some form of logging. This is often seen as a threat to biodiversity because logging has many potentially adverse consequences such as habitat loss, alteration or fragmentation at various spatial scales (e.g. Dudley et al., 2004; Russo, 2012).

Logging may have different impacts on bats (Russo, 2012). First, it can decrease roost availability when trees bearing cavities suitable for bats are removed (Hayes and Loeb, 2007). Furthermore, when harvest rotations are short, the presence of standing dead trees is reduced by mitigating competition (i.e. trees that would not survive competition are removed) and/or cutting senescent or defective trees. This inevitably affects bat species roosting in snags (Russo et al., 2010).

Second, logging may reduce the amount of habitat available to roosting or foraging bats, fragment it, or open gaps, altering forest structure at multiple spatial scales with varying consequences depending on the

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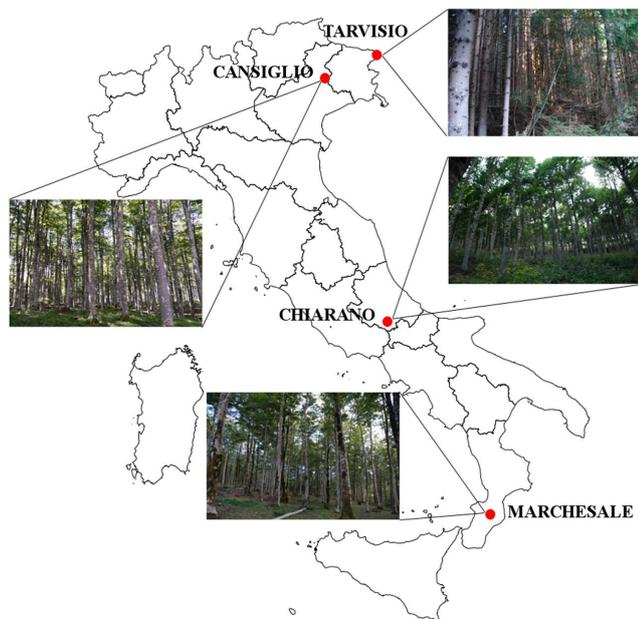


Figure 1 – Location of the four LIFE+ ManFor C.BD. study sites.

ecology of the bat species involved (Owen et al., 2004; Hayes and Loeb, 2007; Russo, 2012). Some species may benefit from an increase in the amount of edge habitat determined by logging, while other species that have specialized to exploit forest interiors may be harmed (Morris et al., 2010). Improvement cuttings and clearcuts often applied to intensively managed forest may also lead to a loss of structural heterogeneity reducing the variety of ecological niches available (Russo, 2012).

Third, although the effects of forest harvesting on insect communities are not fully understood, some types of logging, such as clear-cut, may be detrimental to the survival of insects important for bat foraging such as moths (Summerville and Crist, 2002).

Finally, direct mortality linked to logging operations is likely to occur in bats as found for other mammal species (Escobar et al., 2015) but unfortunately this is extremely difficult to assess, so practically no information is available (Hayes and Loeb, 2007; Russo et al., 2010).

However, management that takes into account the requirements of bats may also favour them by improving forest structure and generate new habitat conditions for foraging or roosting (Humes et al., 1999). A full understanding of the effect of forest management on bats is thus essential to mitigate potentially harmful effects or even increase population size and improve the diversity of forest bat assemblages.

Much of the work carried out so far on the impact of forest exploitation on bats in temperate regions has focused on North America (see e.g. Lacki et al., 2007a and papers therein), while far less information is available for Europe. Management practices are deeply influenced by many factors, including forest type, local economy, administrative procedures, legal requirements, cultural aspects and traditions. Therefore, it is sometimes difficult to apply the same management strategies to different geographical areas. The scant information regarding bats and forestry in Europe is therefore a serious obstacle towards the development of sustainable forms of forest exploitation in the continent and the urgency of increasing research efforts in this field has been repeatedly stated in international contexts such as the Agreement on the Conservation of Populations of European Bats (EUROBATS).

In this study we set out to assess the effect of different management practices on foraging bats in high forest stands. Specifically, we compared bat activity recorded in different forest plots that were respectively a) managed by traditional approaches, b) managed by applying innovative multipurpose options and c) not yet logged at the time of the survey (hereafter such plots are referred to as “unlogged” for brevity). Our work was carried out within the framework of the LIFE+ project called “ManFor C.BD.” (Managing Forests for multiple purposes:

Carbon, BioDiversity and socio-economic wellbeing). The latter project aimed to test in the field the effectiveness of forest management options in meeting multiple objectives (production, protection, biodiversity, etc.), providing data, guidance and indications of best practice. Our activities were conducted as part of the “ForBD” project’s action (Assessment of indicators related to forest biodiversity).

We surveyed the effects of thinning at four forest sites located along a latitudinal gradient on the Italian peninsula. As the four sites differed in terms of geography, type of forest and silvicultural treatments applied, they were considered as separate case studies.

Methods

Description of study sites

We carried out our study at four ManFor C.BD. sites (Fig. 1): the Cansiglio State Forest (Veneto, Northern Italy), the Tarvisio State Forest (Friuli Venezia Giulia, Northern Italy), the Chiarano Sparvera Regional Forest (Abruzzo, Central Italy) and the Marchesale State Forest (Calabria, Southern Italy). Forests differed across sites mainly in terms of structure and historical management and, in one case (Tarvisio), also by the presence of different dominant tree species.

All sites were characterized by the presence of natural forest managed traditionally. The “unmanaged” plots we refer to hereafter are forest plots that by the time of the study had not been logged for at least ca. 20 years.

The Tarvisio site (UTM 33T 392871 5149302), situated at 850 m a.s.l., was a ca. 25 ha parcel of a young, even-aged Norway spruce (*Picea abies*) stand in the pole stage, characterized by abundant regeneration. In the stand there were few and sparse deciduous tree species (mainly beech, *Fagus sylvatica*).

The Cansiglio Forest (UTM 33T 297096 5102174), at 1200 m a.s.l., is part of the Pian Parrocchia-Campo di Mezzo Natural Biogenetic Re-

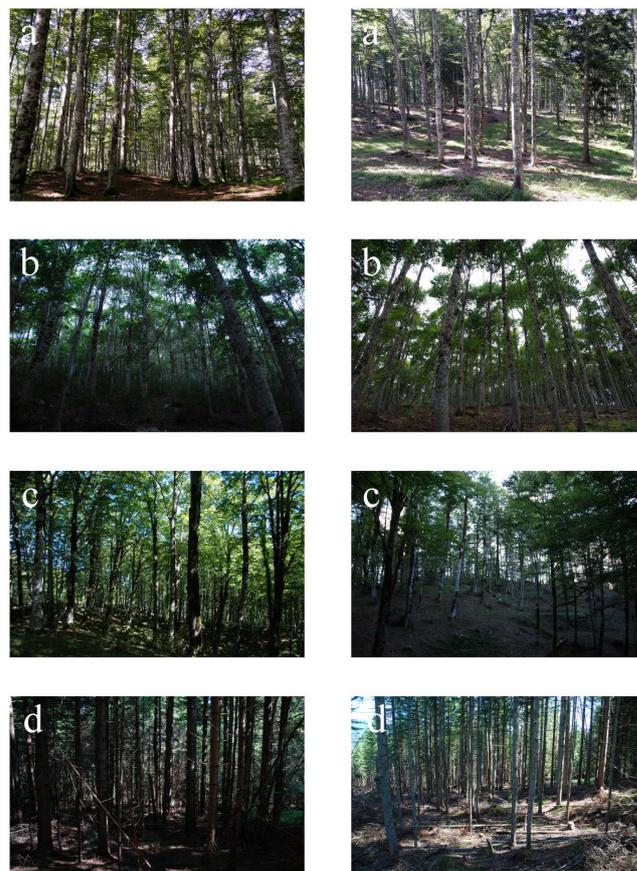


Figure 2 – Comparison between unthinned (left) and thinned (right) plots at different sites: a) Cansiglio, b) Chiarano Sparvera, c) Marchesale, d) Tarvisio.

serve. The 40 ha study area was characterized by high forest, traditionally logged by shelterwood cutting. The site was dominated by a pure mature and mainly even-aged beech (*F. sylvatica*) forest with rare silver fir (*Abies alba*) and Norway spruce (*P. abies*) trees in the lower and western portions of the site.

The ca. 35 ha study area enclosed in the Chiarano Sparvera Forest (UTM 33T 412023 4633705) was managed until mid-70's as "coppice with standards" i.e. entire forest plots reproducing agamically were logged except selected trees saved to protect soil and favour forest regeneration. The whole forest area is currently under conversion to high forest management (in which case trees reproduce by seeds and are typically single-stemmed, older and larger). At that site, we surveyed bat activity in a pure beech forest stand part of a mainly even-aged beech forest situated at 1700 m a.s.l.

The Marchesale site (UTM 33T 608270 4261775) is included in the Marchesale Biogenetic Reserve and is characterized by an even-aged high forest. We worked in a beech forest stand at 1120 m a.s.l. scattered with sporadic silver fir trees.

Silvicultural treatments

All treatments applied for the project (both traditional and innovative) may be broadly categorized as selective logging, i.e. "the removal of selected trees within a forest based on criteria such as diameter, height or species. Remaining trees are left in the stand" (Berthinussen et al., 2014). Specifically, in most stands, traditional logging was "selective thinning" (Fig. 2) as it aimed to reduce forest density by removing selected trees without opening significant gaps, i.e. maintaining a homogeneous cover ("thinning from below"). In the innovative approaches proposed within the ManFor C.BD. project, specific ("candidate") trees were selected according to their dominance, shape, position in the canopy and technological quality; all adjacent trees were cut, opening up gaps in the forest. The treatments were slightly different in the Tarvisio stand, due to its pole-stage structure.

At all sites, each management option was randomly assigned to a group of three plots (Fig. 3). Unlogged plots were selected as controls. Plots had the following size (mean \pm S.D.): Tarvisio, 2.22 \pm 0.36 ha; Cansiglio, 4.34 \pm 1.33 ha; Chiarano Sparvera, 4.36 \pm 1.48 ha; Marchesale, 3.69 \pm 1.13 ha. At each site, plots had similar water availability, topography, tree age, understory and presence of rocks so no variables other than treatment were assumed to potentially influence bat activity.

All the innovative options proposed within the project were designed to take into account multipurpose compromises among timber production, biodiversity conservation and enhancement and the forest's carbon sink/stock role. As an example, in all the innovative treatments proposed, dead wood was increased compared to traditional approaches, both as standing and laying dead trees. As for bat activity, in all sites

unlogged plots were also surveyed and used as controls. A site-by-site description of the specific treatments applied is provided below.

Tarvisio

Traditional logging: thinning from below, selecting only understory trees (i.e. those beneath the canopy) to reduce inter-tree competition (tending, pre-commercial thinning).

Innovative logging Type 1: to reduce the density of the canopy and encourage forest regrowth within the understory layer, selected well-shaped trees in the dominant canopy level were saved and adjacent competitors removed. This treatment often opens up gaps in the canopy cover. Dead wood from cutting was spread on the ground to increase debris.

Innovative logging Type 2: similar to "Innovative Type 1" but dead-wood was stacked. In both innovative types, trees of other species were retained to increase the canopy's overall diversity.

Cansiglio

Traditional logging: moderate thinning from below, felling understory trees with a 20-year rotation. This treatment usually tends to preserve canopy closure.

Innovative logging: selected well-shaped trees usually in the canopy layer were saved and adjacent competitor trees were cut, leading to openings in the canopy. In Cansiglio, the structure of the forest allowed one of the treatments to be assigned to the "delayed thinning" option.

Chiarano Sparvera

Traditional logging: thinning from below in which understory trees are removed every 20–30 years.

Innovative "40" logging: 40 "well-shaped" trees/ha were saved (chosen according to stem form, crown development, position in the canopy) and the adjacent competitor trees were cut.

Innovative "80" logging: same as innovative 40 but 80 trees/ha were saved from logging.

Marchesale

Traditional logging: periodical thinning from below, cutting off only understory trees.

Innovative logging: 45–50 trees/ha were saved from logging and the adjacent trees were cut.

Surveys of bat activity

Bat activity was surveyed in June–September 2014. Each site was visited three times (June, July, August–September). Each time, with the sole exception of Tarvisio, we surveyed each plot once and all plots were surveyed over two consecutive nights. The maximum number of plots sampled on one night was limited by the availability of bat detectors (in all, 6 units). Therefore, on each night we randomly selected 4–6 plots and in their centre we set a Pettersson D500X automatic detector (Pettersson Elektronik AB, Uppsala, Sweden) recording for 8 hours beginning 30 minutes after sunset. Sampling rate was set at 500 kHz. At most sites, control and treatment plots were not necessarily surveyed simultaneously as the sampling order was established randomly.

In Tarvisio, logging operations had not been completed when we surveyed bats; consequently, only one plot per treatment was available so we had to adopt a different design. Based on the similarities between traditional and innovative treatments we lumped together the plots that had been already cut and simply compared 3 logged vs. 3 unlogged (i.e. control) plots. In this case each plot was sampled twice over two consecutive days.

For each recording session the minimum night temperature was also recorded and a mean value calculated for subsequent analysis. No recordings were carried out in heavy rain or on windy nights.

Data analysis

All echolocation sequences were manually screened with BatSound 4.14 (Pettersson Elektronik AB, Uppsala, Sweden).

One call per bat pass with a good signal-to-noise ratio was selected for analysis. For echolocation call analysis we applied a 512-point

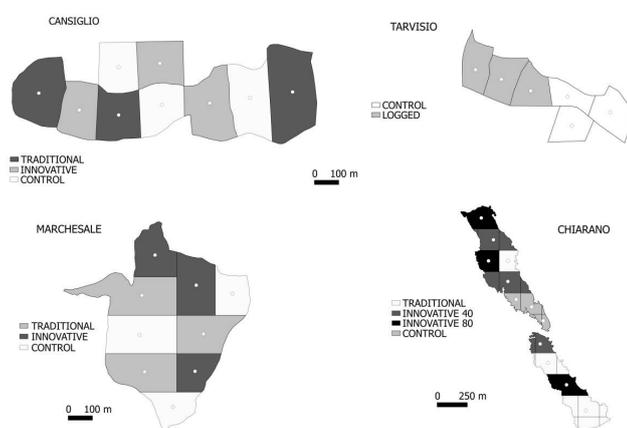


Figure 3 – Map showing the position of plots in the four study sites and the corresponding treatments applied (see text for treatment details). White circles show the approximate location of bat detectors.

Table 1 – Mean numbers of bat passes and corresponding standard deviations recorded in differently managed plots in the Tarvisio Forest (June–September 2014). Control = unlogged plots; see text for definitions of innovative treatments.

| Species | Mean N passes (s.d.) | | | |
|----------------------------------|----------------------|--------|--------|----------|
| | Control | | Logged | |
| <i>Hypsugo savii</i> | 0.00 | (0.00) | 0.33 | (0.58) |
| <i>Myotis mystacinus</i> | 0.00 | (0.00) | 21.00 | (22.54) |
| <i>Myotis nattereri</i> | 0.00 | (0.00) | 2.33 | (1.53) |
| <i>Myotis</i> sp. | 0.33 | (0.58) | 3.33 | (4.04) |
| <i>Nyctalus leisleri</i> | 0.00 | (0.00) | 1.00 | (1.73) |
| <i>Pipistrellus pipistrellus</i> | 0.00 | (0.00) | 0.33 | (0.58) |
| <i>Rhinolophus ferrumequinum</i> | 0.00 | (0.00) | 330.67 | (379.03) |
| <i>Tadarida teniotis</i> | 0.67 | (1.15) | 2.67 | (4.62) |
| All species | 1.00 | (1.00) | 361.67 | (374.93) |

Hamming window (98% overlap). Call temporal variables were taken from oscillograms and frequency variables from spectrograms (end, start and centre frequencies) or power spectra (frequency of maximum energy). Echolocation call identification was carried out following Russo and Jones (2002). When the response was associated with a low likelihood of correct classification (<80%) calls were classified to the genus level. To assess the effect of thinning on bat activity we carried out GLM (General Linear Model) ANOVAs and entered treatment (traditional / innovative logging / control), month and plot (nested within treatment) as main effects and minimum night temperature as a covariate. Normality of the dataset residuals was checked with a Ryan-Joiner test and when needed we normalized data by log- and square-root transformations. Since for Tarvisio all plots were compared simultaneously and the influence of sampling day was not controlled by randomization, we also entered the recording day as a further model variable. For data exploration we also used Pearson correlation analysis.

At all sites, we tested the effects of the above factors on the total bat activity, i.e. the total number of passes recorded over an entire night. At each site, we also selected one or more focal species / guild (see below) for separate analysis, which we assumed to be those for which >200 passes over the entire study period had been recorded. Due to the identification difficulties posed by *Myotis* species, their passes were pooled together: this choice was ecologically meaningful since in forests these bats tend to forage in cluttered habitat so they represent a specific guild. Based on their foraging ecology, *Pipistrellus* spp. and *Hypsugo savii* were also pooled together for analysis as a guild of their own as they are all edge habitat specialists. All analyses were done with MINITAB rel. 13.1. The statistical significance threshold was set at $p=0.05$.

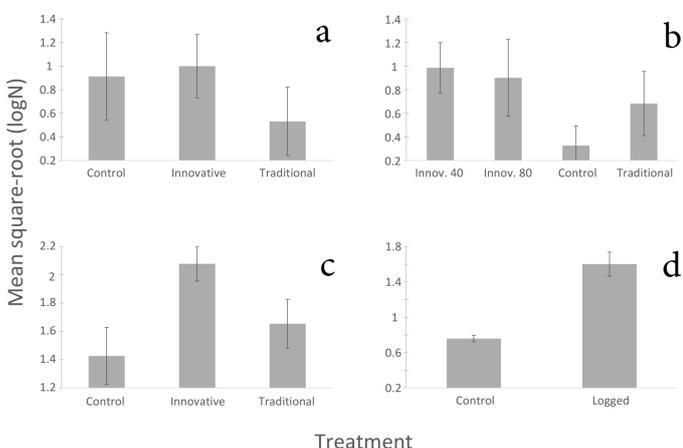


Figure 4 – Bat activity corresponding to different treatments at the four study sites: a) Cansiglio, b) Chiarano Sparvera, c) Marchesale, d) Tarvisio. Error bars show standard deviations. N = number of bat passes. For statistical comparisons see Tables 2, 4, 6, 8.

Table 2 – Outcome of GLM analysis of bat activity at Tarvisio on log-transformed squared values of bat passes. Treatment = Traditional, Innovative 1, Innovative 2, Control (see text for details). Adjms = Adjusted mean square values, d.f. = degrees of freedom, min. temp. = minimum nightly temperature.

| Variable | Source | d.f. | Adjms | F | p |
|-------------------------|------------------|------|-------|--------|-------|
| All passes | Min. temp. | 1 | 0.06 | 1.20 | n.s. |
| | Day | 1 | 0.09 | 1.74 | n.s. |
| | Month | 2 | 0.11 | 2.25 | n.s. |
| | Treatment | 1 | 6.38 | 129.49 | <0.05 |
| | Plot (Treatment) | 4 | 1.12 | 22.82 | <0.05 |
| <i>Myotis</i> sp. | Min. temp. | 1 | 0.03 | 0.84 | n.s. |
| | Day | 1 | 0.02 | 0.59 | n.s. |
| | Month | 2 | 0.04 | 1.00 | n.s. |
| | Treatment | 1 | 2.36 | 57.22 | <0.05 |
| | Plot (Treatment) | 4 | 0.29 | 7.03 | <0.05 |
| <i>R. ferrumequinum</i> | Min. temp. | 1 | 0.00 | 0.17 | n.s. |
| | Day | 1 | 0.00 | 0.09 | n.s. |
| | Month | 2 | 0.02 | 1.28 | n.s. |
| | Treatment | 1 | 2.31 | 170.24 | <0.05 |
| | Plot (Treatment) | 4 | 2.31 | 170.24 | <0.05 |

Table 3 – Mean numbers of bat passes and corresponding standard deviations recorded in differently managed plots in the Cansiglio Forest (June–September 2014). Control = unlogged plots; see text for definitions of innovative treatments.

| Species | Mean N passes (s.d.) | | | | | |
|---------------------------|----------------------|----------|------------|---------|-------------|---------|
| | Control | | Innovative | | Traditional | |
| <i>H. savii</i> | 0.33 | (0.58) | 0.33 | (0.58) | 1.67 | (2.89) |
| <i>M. mystacinus</i> | 20.00 | (34.64) | 5.33 | (9.24) | 2.00 | (3.46) |
| <i>M. nattereri</i> | 1.33 | (2.31) | 0.00 | (0.00) | 0.00 | (0.00) |
| <i>Myotis</i> sp. | 8.67 | (15.01) | 0.33 | (0.58) | 0.00 | (0.00) |
| <i>nd</i> (social calls) | 0.00 | (0.00) | 0.33 | (0.58) | 1.33 | (2.31) |
| <i>N. leisleri</i> | 0.00 | (0.00) | 2.33 | (2.52) | 0.00 | (0.00) |
| <i>P. kuhlii/nathusii</i> | 1.33 | (2.31) | 1.67 | (1.53) | 0.33 | (0.58) |
| <i>P. nathusii</i> | 0.00 | (0.00) | 4.00 | (6.93) | 0.00 | (0.00) |
| <i>P. pipistrellus</i> | 9.00 | (15.59) | 10.67 | (18.48) | 16.00 | (27.71) |
| <i>R. ferrumequinum</i> | 171.00 | (158.15) | 4.67 | (8.08) | 21.67 | (37.53) |
| <i>T. teniotis</i> | 1.00 | (1.73) | 0.00 | (0.00) | 1.00 | (1.00) |
| All species | 212.67 | (218.73) | 29.67 | (35.73) | 44.00 | (75.35) |

Table 4 – Outcome of GLM analysis of bat activity at Cansiglio on log-transformed squared values of bat passes. Treatment = Traditional, Innovative, Control (see text for details). Adjms = Adjusted mean square values, d.f. = degrees of freedom, min. temp. = minimum nightly temperature. Edge habitat guild correspond to passes of *Pipistrellus pipistrellus*, *P. nathusii* and *Hypsugo savii* pooled together.

| Variable | Source | d.f. | Adjms | F | p |
|--------------------|-------------------------|------------|-------|-------|-------|
| All passes | Min. temp. | 1 | 2.70 | 9.68 | <0.05 |
| | Month | 2 | 5.08 | 18.19 | <0.05 |
| | Treatment | 2 | 1.13 | 4.05 | <0.05 |
| | Plot (Treatment) | 6 | 0.91 | 3.28 | <0.05 |
| | <i>Myotis</i> sp. | Min. temp. | 1 | 0.77 | 3.65 |
| <i>Myotis</i> sp. | Month | 2 | 2.15 | 10.19 | <0.05 |
| | Treatment | 2 | 0.17 | 0.80 | n.s. |
| | Plot (Treatment) | 6 | 0.18 | 0.87 | n.s. |
| | <i>R. ferrumequinum</i> | Min. temp. | 1 | 0.62 | 1.46 |
| Month | | 2 | 0.96 | 2.26 | n.s. |
| Treatment | | 2 | 0.00 | 0.01 | n.s. |
| Plot (Treatment) | | 6 | 1.17 | 2.77 | n.s. |
| Edge habitat guild | Min. temp. | 1 | 0.42 | 3.59 | n.s. |
| | Month | 2 | 2.30 | 19.59 | <0.05 |
| | Treatment | 2 | 0.33 | 2.83 | n.s. |
| | Plot (Treatment) | 6 | 0.22 | 1.89 | n.s. |

Table 5 – Mean numbers of bat passes and corresponding standard deviations recorded in differently managed plots in the Chiarano-Sparvera Forest (June–September 2014). Control = unlogged plots; see text for definitions of innovative treatments.

| Species | Mean N passes (s.d.) | | | | | | | |
|---------------------------|----------------------|--------|-------------|--------|---------------|--------|---------------|----------|
| | Control | | Traditional | | Innovative 40 | | Innovative 80 | |
| <i>H. savii</i> | 0.00 | (0.00) | 0.33 | (0.58) | 0.00 | (0.00) | 0.00 | (0.00) |
| <i>M. myotis</i> | 0.00 | (0.00) | 0.00 | (0.00) | 0.33 | (0.58) | 0.00 | (0.00) |
| <i>M. mystacinus</i> | 0.00 | (0.00) | 2.00 | (1.73) | 3.00 | (4.36) | 10.33 | (13.80) |
| <i>M. nattereri</i> | 1.67 | (2.08) | 1.00 | (1.00) | 4.33 | (4.04) | 0.33 | (0.58) |
| <i>Myotis</i> sp. | 0.00 | (0.00) | 0.00 | (0.00) | 2.33 | (4.04) | 2.67 | (4.62) |
| <i>P. kuhlii/nathusii</i> | 0.00 | (0.00) | 0.33 | (0.58) | 0.00 | (0.00) | 0.00 | (0.00) |
| <i>P. pipistrellus</i> | 0.33 | (0.58) | 5.00 | (4.36) | 5.00 | (6.08) | 93.67 | (161.37) |
| <i>R. ferrumequinum</i> | 0.00 | (0.00) | 5.67 | (9.81) | 0.67 | (1.15) | 4.67 | (8.08) |
| <i>T. teniotis</i> | 0.00 | (0.00) | 0.00 | (0.00) | 0.00 | (0.00) | 0.33 | (0.58) |
| All species | 2.00 | (2.65) | 14.33 | (6.03) | 15.67 | (8.74) | 112.00 | (176.06) |

Results

We observed different responses of bat activity to management depending on site, treatment and other environmental factors, as follows.

Tarvisio

Rhinolophus ferrumequinum passes accounted for most of the activity (all in traditionally logged plots) recorded during the entire study period so this bat was selected as a focal species (Tab. 1). *Myotis* sp. passes were also commonly recorded.

Total bat activity, as well as that of *R. ferrumequinum* and *Myotis* sp., were significantly higher in logged plots than in the corresponding control plots (Tab. 2, Fig. 4). Neither minimum temperature nor sampling month influenced bat activity.

Cansiglio

Total bat activity was significantly influenced by minimum temperature, sampling month, treatment and plot (Tab. 4, Fig. 4). Temperature had a moderate positive effect on bat activity ($r=0.38$, $p<0.05$, test done on log-transformed squared values of activity). Tukey's post hoc tests showed that August activity was significantly higher than activity recorded in July and September, which did not differ significantly between each other. Total activity was comparably low across treatments in July while it peaked at unlogged plots in August–September. Although a simple comparison of mean bat activity across treatment suggested that this was higher in control plots than in logged ones (Tab. 3), after adjusting for the other factors mentioned above, the ANOVA and post-hoc tests showed a different pattern, i.e. that activity at unlogged and innovatively treated plots was in fact higher than in the traditionally managed plots. The edge habitat guild comprised *Pipistrellus pipistrellus*, *P. nathusii* and *Hypsugo savii*. The analysis conducted for focal species (*Rhinolophus ferrumequinum*) or guilds (*Myotis* sp., edge habitat guild) showed no significant effects except for month, corresponding to an August peak of activity.

Chiarano Sparvera

Overall, at this site bat activity was higher in logged plots than in the control (Tab. 5). Only treatment had a significant influence on the total bat activity (Tab. 6, Fig. 4) which was higher in both Innovative “40” and Innovative “80” plots than in plots managed traditionally and control plots. No significant effect of treatment, temperature or sampling month was detected for the focal species / guilds selected for this site (*Pipistrellus pipistrellus* and *Myotis* sp.; Tab. 6).

Marchesale

Activity at innovatively logged plots was much higher than that in both traditional and unlogged plots (Tab. 7).

Treatment, month and temperature all had a significant effect on the total bat activity (Tab. 8, Fig. 4). According to the Tukey's post hoc test the innovative treatment differed significantly from the control but not from the traditional treatment.

The activity of the edge habitat guild (in this case comprising *Pipistrellus pipistrellus*, *P. pygmaeus*, *P. kuhlii* and *Hypsugo savii*) was affected by treatment and month. It was higher in the innovatively logged plots than in plots managed traditionally or left unlogged. Activity was also higher in August than in June and July.

Myotis sp. activity was only affected by the minimum temperature, as the former increased on warmer nights ($r=0.57$, $p<0.05$). No effect was detected on the activity of *Rhinolophus ferrumequinum* at this site.

Discussion

Generally speaking, we found that bat activity in logged plots was either higher than or equal to that recorded in unlogged plots, suggesting that thinning at least in the forest types we dealt with has no adverse consequences on bat foraging and may have positive effects. This result is in agreement with studies done in North America which also showed that thinning may increase bat foraging activity (Erickson and West, 1996; Humes et al., 1999; Loeb and Weldrop, 2008). However, the effects we observed largely varied among sites especially at species/species group level, while they tended to be fairly similar for the total bat activity.

In Tarvisio, where different types of logging treatment were pooled together for analysis, opening gaps in an otherwise very cluttered forest led to clear positive responses in bats, especially *R. ferrumequinum*, that was absent in the control. This species typically hunts by perch feeding, i.e. it hangs to small branches particularly along edges and scans for prey in the surrounding open space (Jones, 1990). However, in Cansiglio *R. ferrumequinum* was most frequently recorded in the control. Tarvisio and Cansiglio greatly differed from each other in forest composition and structure: the former was a dense conifer stand with no space available for perch feeding, while the latter was a mature high

Table 6 – Outcome of GLM analysis of bat activity at Chiarano-Sparvera on log-transformed squared values of bat passes. Treatment = Traditional, Innovative 40, Innovative 80, Control (see text for details). Adjms = Adjusted mean square values, d.f. = degrees of freedom, min. temp. = minimum nightly temperature.

| Variable | Source | d.f. | Adjms | F | p |
|------------------------|------------------|------|-------|------|-------|
| All passes | Min. temp. | 1 | 0.10 | 0.18 | n.s. |
| | Month | 2 | 0.90 | 1.59 | n.s. |
| | Treatment | 3 | 0.80 | 4.14 | <0.05 |
| | Plot (Treatment) | 8 | 0.19 | 0.34 | n.s. |
| <i>Myotis</i> sp. | Min. temp. | 1 | 0.01 | 0.09 | n.s. |
| | Month | 2 | 0.21 | 1.43 | n.s. |
| | Treatment | 3 | 0.14 | 1.84 | n.s. |
| | Plot (Treatment) | 8 | 0.07 | 0.51 | n.s. |
| <i>P. pipistrellus</i> | Min. temp. | 1 | 0.02 | 0.10 | n.s. |
| | Month | 2 | 0.26 | 1.54 | n.s. |
| | Treatment | 3 | 0.19 | 2.64 | n.s. |
| | Plot (Treatment) | 8 | 0.07 | 0.42 | n.s. |

Table 7 – Mean numbers of bat passes and corresponding standard deviations recorded in differently managed plots in the Marchesale Forest (June–September 2014). Control = unlogged plots; see text for definitions of innovative treatments.

| Species | Mean N passes (s.d.) | | | | | |
|-------------------------|----------------------|---------|------------|----------|-------------|---------|
| | Control | | Innovative | | Traditional | |
| <i>B. barbastellus</i> | 0.33 | (0.58) | 1.33 | (1.53) | 1.00 | (1.00) |
| <i>H. savii</i> | 2.33 | (3.21) | 13.33 | (1.53) | 7.33 | (12.70) |
| <i>M. mystacinus</i> | 1.00 | (1.00) | 0.33 | (0.58) | 0.00 | (0.00) |
| <i>M. nattereri</i> | 0.33 | (0.58) | 1.33 | (1.53) | 1.33 | (0.58) |
| <i>Myotis</i> sp. | 3.33 | (2.08) | 32.00 | (46.86) | 0.67 | (0.58) |
| <i>N. leisleri</i> | 0.33 | (0.58) | 1.00 | (1.00) | 2.00 | (2.00) |
| <i>P. kuhlii</i> | 5.67 | (8.14) | 31.00 | (53.69) | 5.33 | (7.57) |
| <i>P. pipistrellus</i> | 0.33 | (0.58) | 0.67 | (1.15) | 17.67 | (22.50) |
| <i>P. pygmaeus</i> | 26.33 | (42.15) | 150.67 | (54.60) | 42.67 | (38.53) |
| <i>R. ferrumequinum</i> | 15.00 | (25.98) | 58.00 | (100.46) | 0.00 | (0.00) |
| <i>R. hipposideros</i> | 0.67 | (1.15) | 0.67 | (1.15) | 0.00 | (0.00) |
| <i>T. teniotis</i> | 0.67 | (0.58) | 1.00 | (1.00) | 1.33 | (1.15) |
| All species | 56.33 | (50.54) | 291.33 | (191.17) | 79.33 | (77.67) |

beech forest where control plots had gaps and corridors suitable for this hunting style. It is worth noting that forest in Tarvisio was so dense that even clutter-foragers such as *Myotis* bats benefited from thinning.

In Cansiglio, innovatively logged sites showed no difference from control (unlogged) sites: in both cases total activity was greater than in traditionally logged plots. In Chiarano Sparvera, both innovative treatments had higher numbers of bat passes than traditionally thinned or unlogged plots. Finally, in Marchesale, the number of bat passes recorded in both traditionally and innovatively logged plots was greater than that recorded in unlogged plots.

Total bat activity was the most sensitive variable to both the treatment adopted and the other environmental factors considered, perhaps due to the higher statistical power of a greater sample size and/or the synergistic responses of bats foraging in different microhabitats whose activity was favoured by opening gaps and / or increasing edges. Although little evidence is available for controlled, replicated surveys in Europe, similar positive effects of logging on bat foraging have been recorded in North America where bat activity increased in (larger) gaps opened by group-selection (Menzel et al., 2002) or shelterwood (Titchenell et al., 2011) harvesting. In case studies in rainforest in Brazil (Castro-Arellano et al., 2007; Presley et al., 2008) where abundance and activity of bat species were tested respectively, control (un-

logged) forest sites and reduced-impact logging sites did not differ from one another.

The positive effect of increasing open spaces was not always restricted to the innovative treatments applied, as in some sites it was also observed in traditionally thinned plots. The innovative treatments were beneficial to bats in Chiarano Sparvera, Cansiglio and Marchesale. In these cases, we found no specific differences between innovative treatments. For example, opening gaps around 40 or 80 trees/ha in Chiarano Sparvera both favoured bat foraging more than traditional thinning: unlike the latter, both innovative treatments thin the forest, opening canopy gaps. Similarly to our study, Menzel et al. (2002) found no difference in bat activity between small and large gaps opened by forest practices.

We also highlighted that other factors besides the type of thinning strategy applied may affect bat activity, including temperature, survey month and the individual plots considered (whose effect was significant in all cases), yet no generalization can be made since such influences differed across sites. We highlight that these factors must not be overlooked when designing bat monitoring in forests subject to different forestry practices, otherwise their influence may possibly either mask or mimic the effect of thinning. Within summer, different months may lead to critically different levels of bat activity, most likely corresponding to various life-cycle stages, such as pregnancy or lactation, fledging of juveniles, or mating behaviour (Altringham, 2011). The seasonal presence of migratory bats in forests may be a further source of variation in species composition, abundance and activity (Giavi et al., 2014).

Temperature is a critical factor influencing foraging as it has direct effects on insect prey abundance. In general, temperatures less than 10 °C correspond to reduced insect availability and, in turn, decreased bat foraging activity (Vaughan et al., 1997; Russo and Jones, 2003).

Furthermore, although some common traits in the responses of foraging bat assemblages were noticed across sites, specific site differences also emerged. This could be due to the different treatments applied within the framework of the LIFE+ ManFor C.BD. project, but the influence of topographical features, forest type, age and structure cannot be ruled out. In our study sites real-world operations, rather than academic simulations, took place necessitating a pragmatic approach for bat surveys. From a practical point of view, this may give our results greater credence with forestry professionals, and illustrates effectively the variation in response to different locations, emphasising the importance of replicating studies in different regions.

The sensitivity of total bat activity offers a robust way of monitoring the effects of forestry practices on bats, acting as a promising bioindicator (Russo and Jones, 2015), because it overcomes the difficulty of identifying bat calls to species. Identifying bats to species from their echolocation calls remains challenging and despite the advances in this field several species are still difficult to distinguish.

Table 8 – Outcome of GLM analysis of bat activity at Marchesale on log-transformed squared values of bat passes. Treatment = Traditional, Innovative, Control (see text for details). Adjms = Adjusted mean square values, d.f. = degrees of freedom, min. temp. = minimum nightly temperature. Edge habitat guild correspond to passes of *Pipistrellus pipistrellus*, *P. pygmaeus*, *P. kuhlii* and *Hypsugo savii* pooled together.

| Variable | Source | d.f. | Adjms | F | p |
|-------------------------|------------------|------|--------|-------|-------|
| All passes | Min. temp. | 1 | 1.16 | 4.95 | <0.05 |
| | Month | 2 | 0.87 | 3.73 | <0.05 |
| | Treatment | 2 | 0.69 | 14.12 | <0.05 |
| | Plot (Treatment) | 6 | 0.04 | 0.19 | n.s. |
| <i>Myotis</i> sp. | Min. temp. | 1 | 1.60 | 12.69 | <0.05 |
| | Month | 2 | 0.07 | 0.57 | n.s. |
| | Treatment | 2 | 0.02 | 0.21 | n.s. |
| | Plot (Treatment) | 6 | 0.11 | 0.88 | n.s. |
| <i>R. ferrumequinum</i> | Min. temp. | 1 | 139.90 | 0.20 | n.s. |
| | Month | 2 | 957.80 | 1.38 | n.s. |
| | Treatment | 2 | 622.90 | 1.59 | n.s. |
| | Plot (Treatment) | 6 | 408.10 | 0.59 | n.s. |
| Edge habitat guild | Min. temp. | 1 | 0.39 | 1.93 | n.s. |
| | Month | 2 | 1.15 | 5.32 | <0.05 |
| | Treatment | 2 | 1.23 | 10.77 | <0.05 |
| | Plot (Treatment) | 6 | 0.11 | 0.52 | n.s. |

More investigations in a variety of forest types under different management regimes are needed before generalizing our findings. Besides the local environmental effects discussed above, locally different bat assemblages may have dissimilar responses based on their structure, the relative abundance of edge vs. interior species and other factors (e.g. Patriquin and Barclay, 2003).

Our study could only look at the effects of thinning on bat activity (i.e. foraging) but did not assess those on roosting behaviour — a crucial component of forest bat biology. Although the innovative treatments also aimed to increase the amount of dead wood, for example by girdling trees (as done at Marchesale and Chiarano Sparvera), the time scale available for our work did not allow us to assess the effects of such actions on roost availability, because this is only testable a few years after treatment. Likewise, thinning may have potentially decreased the number of available roosts or caused direct mortality, but these aspects were not surveyed. Bats with specialized roosting behaviour may be affected by logging. For example, a study carried out in the beech forests of central Italy (Russo et al., 2010) showed that *Barbastella barbastellus* was rarer in logged forests than in unlogged ones and only roosted sporadically in the former.

Future work, also employing radiotracking to identify roosts in trees and follow bat behaviour during logging, should be carried out to gain a more comprehensive picture of the multifaceted effects of logging on bats in forest. Borkin and Parsons (2014) radiotracked *Chalinolobus tuberculatus* in New Zealand and found that the bats use of smaller home ranges post-harvest probably reflected smaller colony sizes and lower roost availability. Ideally, future studies should also determine the minimum number of suitable tree roosts to be left in place to sustain viable bat populations. Moreover, direct mortality — so far unstudied — may be locally important and is presumably highly dependent on the time of year when logging is scheduled. Research should try to estimate mortality in order to tailor logging schedules to the temporally variable presence of bats in forest. Logging when bats occur less frequently in the forest or when their use of the forest is less critical, e.g. outside the reproductive season, would avoid turning sustainably managed sites (which despite being logged still host considerable numbers of roosting bats) into ecological traps (Russo et al., 2010). ☞

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