

Response of bat species to sylvo-pastoral abandonment

Martin K. Obrist^{a,*}, Emilie Rathey^{b,e}, Fabio Bontadina^c, Adriano Martinoli^d, Marco Conedera^e, Philippe Christe^{b,1}, Marco Moretti^{e,f,1}

^a Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Biodiversity and Conservation Biology Research Unit, Zuercherstrasse 111, CH-8903 Birmensdorf, ZH, Switzerland

^b Department of Ecology and Evolution, University of Lausanne, CH-1015 Lausanne, Switzerland

^c Institute of Ecology and Evolution, Division of Conservation Biology, University of Bern, CH-3012 Bern, Switzerland

^d Environment-Health-Safety Department, Insubria University, I-21100 Varese, Italy

^e Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Community Ecology Research Unit, CH-6500 Bellinzona, Switzerland

^f Bat Protection Centre Ticino, CH-6714 Semione, Switzerland

ARTICLE INFO

Article history:

Received 5 October 2010

Received in revised form 6 December 2010

Accepted 6 December 2010

Available online 28 December 2010

Keywords:

Castanea sativa
Chiroptera
Acoustic monitoring
Bat activity
Species richness
Forest management

ABSTRACT

We assessed the effect of abandonment of sylvo-pastoral practices in chestnut orchards (*Castanea sativa*) on bats in southern Switzerland to determine practical recommendations for bat conservation. We compared bat species richness and foraging activities between traditionally managed and unmanaged chestnut orchards, testing the hypothesis that managed orchards provide better foraging opportunities and harbour more bat species. Echolocation calls of foraging bats were sampled simultaneously at paired sites of managed and unmanaged orchards using custom made recorders. Vegetation structure and aerial insect availability were sampled at the recording sites and used as explanatory variables in the model. In a paired sampling design, we found twice the number of bat species (12) and five times higher total foraging activity in the managed chestnut orchards compared to the unmanaged ones. Bat species with low flight manoeuvrability were 14 times more common in managed orchards, whereas bats with medium to high manoeuvrability were only 5 times more common than in abandoned orchards. The vegetation structure was less dense in managed orchards. However, management did not affect relative insect abundance. Bats primarily visited the most open orchards, free of undergrowth. As a result of restricted access into the overgrown forests, the abandonment of chestnut orchards leads to a decline in bat species richness and foraging activities. Continued management of chestnut orchards to maintain an open structure is important for the conservation of endangered bat species in the southern Swiss Alps.

© 2010 Elsevier B.V. All rights reserved.

1. Introduction

Traditional forest clearing and agricultural practices in European landscapes have historically generated a mosaic of forests at different development stages, as well as permanent open stands and open agricultural areas. Although inadequate for forest specialists, this mosaic landscape favours species that prefer open habitats, and supports high species diversity (Blondel and Aronso, 1999). Recently, in the Swiss Alps, the combination of regional depopulation of rural areas and the abandonment of agriculture has led to major changes in the ecosystem (Dirnböck et al., 2003). The sub-

sequent renaturation of traditional landscape patterns into forests can lead to reduced biodiversity (Blondel and Aronso, 1999). However, although the effects of abandonment of traditional practices of cultivating and pasturing chestnut orchards are controversial, generally a mosaic of abandonment and active management seems favourable to biodiversity (e.g. McNeely, 1994; MacDonald et al., 2000; Benayas et al., 2007).

At present, chestnut orchards cover 0.4 million hectares in Europe or 17.7% of the total chestnut-growing area, with 80% concentrated in Italy and France (Conedera et al., 2004). In southern Switzerland, the area with chestnut orchard decreased from 9500 ha to 3000 ha in the last century (Stierlin and Ulmer, 1999). Since early medieval times traditionally managed sweet chestnut (*Castanea sativa* Mill.) orchards have formed a typical landscape element in the mountains of southern Europe (Conedera et al., 2004). The chestnut trees are grafted for fruit production and the orchards have a permanent open structure intercropped with cereals, hay or pasture (agro-sylvo-pastoral systems). With the rural depopulation of the last century and changes in human food consumption,

* Corresponding author. Tel.: +41 44 739 24 66; fax: +41 44 739 22 15.

E-mail addresses: martin.obrist@wsl.ch (M.K. Obrist), emilie.rathey@gmail.com (E. Rathey), fabio.bontadina@swild.ch (F. Bontadina), adriano.martinoli@uninsubria.it (A. Martinoli), marco.conedera@wsl.ch (M. Conedera), philippe.christe@unil.ch (P. Christe), marco.moretti@wsl.ch (M. Moretti).

¹ Both supervised the study.

this management scheme has become dramatically reduced. This trend has been further amended by the introduction and spread of chestnut diseases (Conedera and Krebs, 2008). Abandoned orchards are quickly invaded by other tree species, evolve into dense mixed forests and, within decades, disappear entirely (Conedera et al., 2000).

Since the late 1980s, an increasing interest in chestnut orchards as traditional landscape element has led to a revitalization of orchards for their aesthetic value (recreation), as fire-break areas, and for economic reasons (tourism) (Conedera et al., 2004). However, the costs of orchard restoration and maintenance are high, and the impacts on biodiversity and species of special conservation concern have not yet been assessed. Restoration of traditional, small to medium sized chestnut orchards conserves large, old trees thereby providing shelter for many species that use cavities. Such moderate management may positively affect biodiversity as a whole, including endangered species that depend on old trees. Among the species that may potentially benefit from such restoration, insectivorous bats (Microchiroptera) constitute one of the most endangered taxonomic groups worldwide (Arita, 1993; Ceballos and Brown, 1995; Mickleburgh et al., 2002; Safi and Kerth, 2004; Schaub et al., 2007; Weller et al., 2008), and particularly in Europe where, of the 25 species on the red-list for southern Switzerland only *Pipistrellus pipistrellus* and *Pipistrellus kuhlii* were classified as not vulnerable (Duelli, 1994).

Many studies have investigated the relationship between bats and the structure and composition of forested habitat (Crome and Richards, 1988; Lumsden and Bennett, 2005) and forest management (Menzel et al., 2002; Patriquin and Barclay, 2003; Clarke et al., 2005b; Castro-Arellano et al., 2007; Presley et al., 2008). Hayes and Loeb (2007) present a comprehensive review of work done on the influence of forest management on bats in North America. With few exceptions (e.g. Jaberg et al., 2007; Duchamp and Swihart, 2008), most of these studies show higher bat activity and diversity in openings and in less dense forest stands, which are comparable to managed chestnut orchards. Studies from tropical regions indicate that management of forested areas with e.g. reduced impact logging and even tropical agroforestry systems can maintain species richness of bat assemblages with only small effects on species composition (Castro-Arellano et al., 2007; Harvey and Villalobos, 2007; Presley et al., 2008). Finally, Davy et al. (2007) emphasize the value of agriculturally cultivated olive groves as possible buffer to deforestation. In a fine-scale forest mosaic landscapes, as encountered in Switzerland, bat presence may be most influenced by changes in habitat quality or hampered accessibility for foraging in densely overgrown stands.

For bats, accessibility to spatially cluttered foraging habitat is largely governed by their flight manoeuvrability. These flight abilities and the type of orientation have coevolved in bats in adaptation to their main foraging environment (Neuweiler, 1984). Long and narrow wings (high wing loading) are associated with fast flight and foraging at higher altitudes away from acoustic obstacles (clutter) (sensu Fenton, 1990). Species with broad wings (low wing loading) fly slowly and are highly manoeuvrable within, or very close to, clutter (Fenton, 1990). Bats must be able to avoid obstacles, which affect flight and foraging efficiency (Schnitzler and Kalko, 2001). They efficiently do so as experimentally shown by Brigham et al. (1997). Some bats avoid regions of high structural clutter by commuting and foraging along open structures as trails, gaps and edges (Lloyd et al., 2006; Caras and Korine, 2009; Hein et al., 2009). In traditionally managed chestnut orchards, the understory is reduced, thus improving the accessibility for bats with higher wing loading. Clutter tolerant species with low wing loading should be less affected by reduced accessibility and prevail in unmanaged forests, while less clutter tolerant species with high wing loading should be biased towards more open, managed forests.

The aims of this study were (i) to investigate the effect of managing abandoned chestnut orchards on bat species diversity and activity (foraging, commuting and searching), (ii) to test the significance of management-induced changes in vegetation structure and food availability (aerial insect abundance), and (iii) to provide recommendations that may improve bat conservation in chestnut orchards. As management reduces undergrowth vegetation and thus enhances accessibility of orchards, we expected a higher number of bat species and higher activity in managed chestnut orchards, but lower relative insect abundance due to less available organic matter. Furthermore, as wing morphology and body weight define the flight performance of bats (Norberg and Rayner, 1987), and thus their spatial foraging niches (Neuweiler, 1984), we expected management to have a more profound effect on less manoeuvrable species.

2. Methods

2.1. Study area and orchard stands

The study was carried out along the sweet chestnut belt between 200 and 1000 m above sea level, on the southern slope of the Swiss Alps (45.9–46.5°N, 8.1°E and 9.2°E; Fig. 1), in the Canton Ticino. In this region, most of the formerly managed chestnut orchards are now abandoned and invaded by shrubs and trees.

Candidate orchards were evaluated by comparing chestnut distribution maps of 1959 and 2000, field assessment of management state, and interviews with orchard owners. Orchards were classed as unmanaged when management had ceased ≥ 30 years ago, while managed orchards were defined as those currently, or within the past 15 years, maintained by pruning, mowing, or grazing. The final set of paired sample sites consisted of 30 managed and 30 unmanaged chestnut orchards. Paired sites were of similar geography (average Euclidian distance between paired treatments: 916 m, range 110–3451 m), slope, exposition and elevation, and covered the major distribution area of chestnut orchards in the region (Fig. 1). Distance between sampling pairs was an average 23.2 km and distance to closest pairs an average 1.6 km with only two pairs being closer than 500 m to a second. Management area varied between orchards from less than 5 ha ($n = 17$) to more than 20 ha ($n = 5$) with 7 intermediate sites. Landscape characteristics around the sites were analysed for forested, open and built areas within ranges of 1, 2 and 5 km radius with GIS. Land use did not differ significantly between treatments within these ranges, with forested areas covering an average 50–60%, open areas 30–40% and built areas contributing with 8–10%. Forest canopy and undergrowth were generally more open and the grass more lush in managed chestnut stands, while unmanaged stands showed more closed canopies and were often invaded by other tree species and shrubs.

2.2. Bat recording and call identification

Bat activity was recorded from 02-June-2005 to 05-September-2005 during 30 full nights, one night per treatment pair. Two equivalent sets of recording equipment (Obrist et al., 2004b) were simultaneously placed in each paired site.

For optimal site-coverage, five custom-built microphones (frequency response ± 3 dB from 20 to 120 kHz; Ultrasound Advice, London, UK) connected to a central recording unit were dispersed around the centre of each orchard, and ≥ 20 m away from its edge. Microphones were set 1 m above ground pointing 45° upwards, 20–150 m away from the recording unit and ≥ 20 m from each other. Obstruction by close leaves or branches in the recording direction was avoided. Bat echolocation was digitally recorded with PCMCIA data acquisition cards (PCCARD-DAS16/330, Measurement

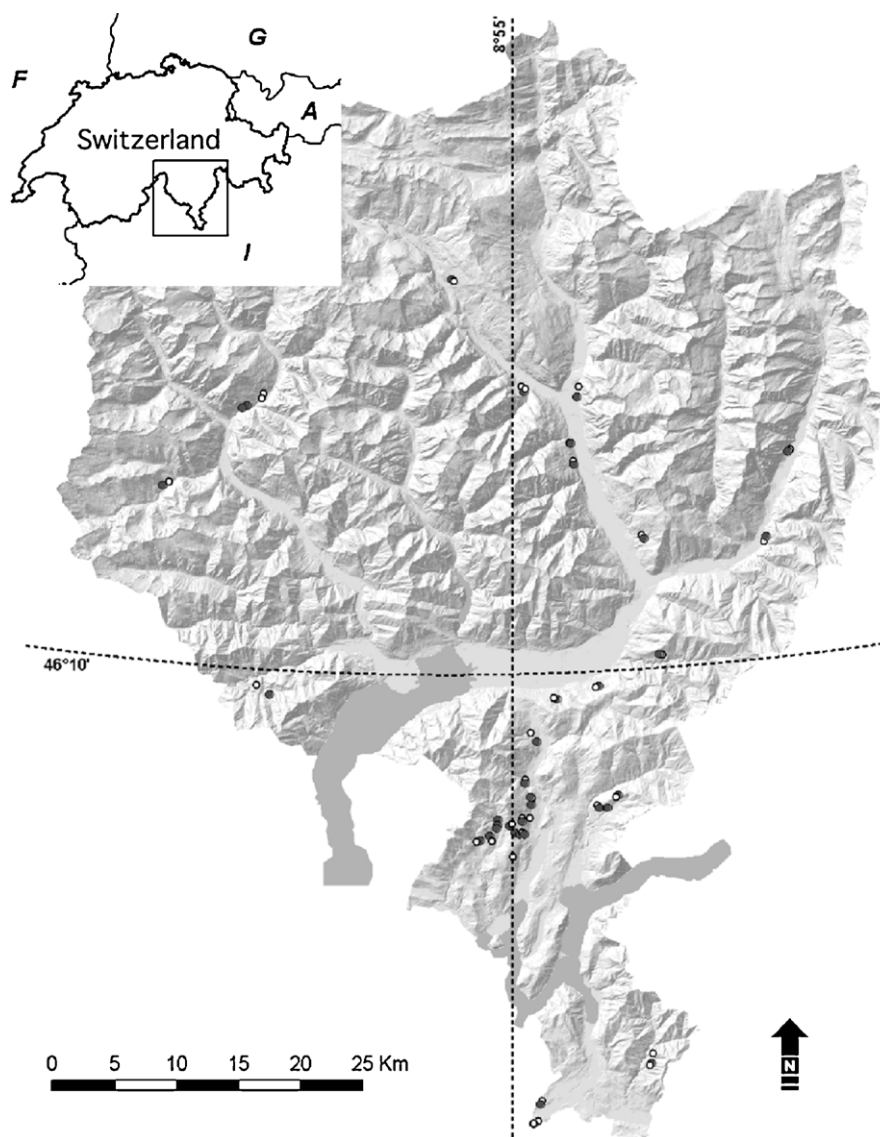


Fig. 1. Distribution map of recording locations. Maps of Switzerland, Canton of Ticino and Moesa Valley (Canton of Grison) showing the locations of the managed (white circles) and unmanaged (dark circles) orchards sampled.

Map: K606-01 © 2004 Swisstopo.

Computing Corporation, Middleboro, MA, USA) in Apple Power-Book computers. Looped recordings of 10 s duration were driven by custom-made software (Obrist et al., 2004b). If a peak-detection algorithm, that scanned the recorded sequences after high-pass filtering at 7.5 kHz, found ≥ 4 peaks, sequences were stored and logged. This processing took 20 s, thus every 30 s the computer switched between the five recording channels, even when no signals were detected. Saved sequences were analysed offline in the lab. We used custom written software (Obrist et al., 2004b) to automatically identify echolocation calls to bat species. The program cut every sequence into single echolocation calls and processed them to spectrograms, which were synergetically compared against five sets of averaged spectrograms of known species and thus classified to species. These five sets had previously been identified to optimally recognize 26 Swiss bat species (Obrist et al., 2004b) with an average correct classification rate of 86%. In a probabilistic approach, of the five classifications at least four had to pass a given quality standard and of these at least three classifications had to point to the same species. Spectral (highest frequency, lowest frequency, frequency of peak energy) and temporal (duration)

parameters of a classified signal were then validated against a parametric database of the classified species. A signal was only considered as recognized if pattern recognition and call parameter control passed all tests for the species in question. After automatic recognition, all sequences of questionable probability (e.g. multiple species and/or only few calls recognized) were visually screened for errors and manually classified to species, after comparing spectral and temporal parameters with published data (Zingg, 1990; Obrist et al., 2004b). Additionally, classification certainty was marked as either high (e.g. obvious species affiliation but masked for the automatism by noise) or low (e.g. signal characteristics in overlapping range of species). Only nightly total number of sequences assigned to a species with high classification certainty was used to quantify bat activity in terms of echolocation sequences recorded.

2.3. Food availability

During recording sessions, potential prey abundance (mainly aerial insects) available for bats was sampled at each orchard with a non-directional light trap (11 W neon bulb, superactinic blue

Philips TL 20 W/05; 365 nm peak energy; 12 V DC-powered). The trap was placed 1.5 m above ground and ≥ 30 m away from the nearest microphone to avoid any interaction between the two techniques. Simultaneous light-trapping at both treatments (managed and unmanaged) further minimized any bat attracting bias. In the dense vegetation of the unmanaged orchards, the traps were set in small vegetation gaps for functionally similar placement across treatments. The insects were collected in 70% alcohol and sorted in the lab into 12 taxonomic groups (Blattaria, Coleoptera, Diptera, Ephemeroptera, Heteroptera, Homoptera, Hymenoptera, Lepidoptera, Neuroptera, Plecoptera, Thysanoptera, Trichoptera) and individuals were counted. After drying the insects (12 h, 60 °C), each taxonomic group in each sample was weighted to the nearest 0.001 g.

2.4. Environmental factors

Eighteen environmental variables were assessed within two 20 m \times 20 m quadrats at each sampling site (see Appendix A, Table 1). Treatment (managed versus unmanaged) was derived from the Forest Service maps. Nine of the environmental variables collected were considered directly related to the management effect: cover of stones, cover of litter, cover of herb layer, height of herb layer, cover of shrub layer, height of shrub layer, cover of tree layer, height of tree layer, number of trees (which we differentiated in diameter classes; Table 1, Appendix A). In August, herbs, shrubs, trees and litter on the ground were separately recorded using a five-point species cover-abundance scale following the methodology of the Swiss National Forest Inventory (Keller, 2005). Trees and shrubs were counted and assigned to one of nine categories of trunk diameter measured at breast height (DBH). In very dense orchards shrub and tree densities with DBH <8 cm were assessed within two smaller quadrats of 10 m \times 10 m. Numbers were extrapolated and expressed as stems per hectare. The herb height was measured with a measuring stick, shrub and tree heights with a laser device (Leica, model DISTO classic 5). Additional site variables not related to management were recorded (see Appendix A, Table 1). Latitude and longitude, elevation, slope and aspect were calculated from raster (25 m \times 25 m) or vector maps or from digital elevation models (DEM25 and Vector25, Swisstopo, 2005). We calculated area of buildings, length of streets and water streams, within a buffer of 150 m radius around each orchard's GPS-measured centroid with ArcMap 9.1 (ESRI, Environmental Systems Research Institute 1992–99, Redlands, USA).

2.5. Data analyses

We calculated the effects of management, local site factors and food availability on number of bat species and bat activity level. All analyses were conducted treating the 60 orchards as independent replicates (Hurlbert, 1984), after checking for non-significant spatial autocorrelation of species numbers using Mantel tests (Mantel statistic $r = 0.036$, $P = 0.277$, with 999 permutations) (Legendre and Legendre, 1998). No statistical influences were found for recording channels and computers (locations alternated between treatments) on the number of sequences (ANOVA; channel: $F_{4,137} = 0.283$; $P = 0.888$, computer: $F_{1,137} = 0.476$; $P = 0.491$, interaction: $F_{4,137} = 0.844$; $P = 0.499$), indicating no methodological bias (e.g. temporary equipment failure) in the data.

To test for differences in species numbers and activity of bats (number of identified recording sequences) between managed and unmanaged chestnut orchards we included 22 pairwise comparisons for sites in which we obtained in both treatments uninterrupted recordings throughout the night. In six nights, equipment failed in one treatment, making pairwise comparison impossible. However, as overall equipment failure was not

depending on treatment, 28 nights could be taken into account for the summary analyses, thereby only dropping two nights with complete equipment failures. Differences in activity between bat species and treatments were investigated (the 22 pairwise comparable nights) with two ANOVAs after checking the restrictions regarding normality by using Shapiro test (Legendre and Legendre, 1998). We compared bat species numbers registered in the 22 paired nights with a paired t -test. Total bat activity and invertebrate dry mass (all 28 night) was compared between treatments using Wilcoxon tests, as neither of these parameters fulfilled ANOVA assumptions.

A discriminant analysis using a Monte Carlo permutation test ($P < 0.05$; 999 randomisations) was applied with all habitat descriptors to find significant differences in forest structures between treatments. Depending on data distribution, environmental differences between treatments were tested with a t -test or Wilcoxon test. Ecological similarity between all pairs of managed orchard stands was calculated using the Bray–Curtis similarity coefficient (Bray and Curtis, 1957). With the resulting resemblance matrix, we clustered the managed orchards with the complete linkage method. Based on branch lengths, we identified subgroups of the managed orchards. The number of identified recording sequences was tested between these subgroups with Mann–Whitney U -tests.

Finally, a classification and regression tree (De'ath and Fabricius, 2000), with a categorical response variable, was used to quantify forest factors which determined the difference within and between the groups of managed and unmanaged chestnut orchards (see Appendix A, Table 1). We used the library 'tree' (Ripley, 2010) in the software 'R' (R Development Core Team, 2010) to identify these variables and the values, which separate groups in the classification tree, an information that is very important for conservation management.

We estimated flight performance of bats into manoeuvrability classes in order to relate them to forest factors possibly affecting species activity. Corresponding calculations for turning diameters (Aldridge, 1987), using values for flight characteristics (flight speed, wing loading) and body measures (body mass, wing area) taken from the literature (Norberg and Rayner, 1987; Dietz et al., 2007) are given in Appendix B. For the somewhat arbitrary cut between low and medium manoeuvrable species, we also considered the foraging and echolocation behaviour of the involved species. With a contingency table, we analysed the interdependence of manoeuvrability classes with the number of recordings and the treatments.

In multiple comparisons, P values were corrected after Benjamini and Hochberg (1995). All statistical analyses were performed using 'R' (R Development Core Team, 2010) or 'DataDesk 6.2.1' (Data Description, Inc., Ithaca, NY).

3. Results

In 30 nights we sampled 1596 sequences containing bat echolocation calls that were further analysed. Some of the sequences included calls from several animals: 285 contained two, 22 three and one sequence contained four species, for a total of 1904 bat identifications. Of these, 1557 (81.8%) could be attributed to a species with high certainty (see Section 2.2). There was higher activity in managed orchards (1449 sequences, 93.1%) compared to the unmanaged ones (108 sequences, 6.9%). For the 22 strictly paired sites 632 sequences were recorded (see Section 2.4) and analysed as such (Table 1). The discriminant analysis of the geographical and topographical site factors not directly related to management (longitude, latitude, elevation, slope, aspect, $\cos(\text{aspect})$, $\sin(\text{aspect})$, street lengths, river lengths, built over area) showed no difference between managed and unmanaged orchards ($\Lambda = 1.141$, $\chi^2 = 3.4$, $P = 0.92$) demon-

Table 1

Number of echolocation sequences (*N* seq) and number of species (*N* spp.) identified in chestnut orchards per paired night survey and treatment. Numbers in brackets exclude sequences from *Pipistrellus pipistrellus*.

Survey	Managed		Unmanaged	
	<i>N</i> seq	<i>N</i> spp.	<i>N</i> seq	<i>N</i> spp.
1	15 (2)	3	0	0
2	13 (12)	4	0	0
3	45 (13)	8	6 (2)	2
4	8 (0)	1	2 (2)	1
5	61 (24)	5	40 (17)	4
6	83 (5)	4	0	0
7	15 (2)	3	10 (1)	2
8	17 (3)	2	0	0
9	34 (0)	1	1 (0)	1
10	1 (1)	1	7 (1)	2
11	9 (9)	1	8 (0)	1
12	42 (6)	5	3 (1)	2
13	21 (4)	4	0	0
14	33 (28)	4	0	0
15	2 (0)	1	9 (0)	1
16	28 (11)	6	8 (2)	3
17	13 (1)	2	0	0
18	7 (1)	2	7 (0)	1
19	5 (3)	3	0	0
20	48 (20)	4	0	0
21	18 (7)	5	1 (0)	1
22	12 (3)	4	0	0
Total	530 (155)	12	102 (36)	6

strating the variance to be independent of geographical location (Appendix A, Table 1). Accordingly, the number of sequences identified in each orchard could be compared pairwise.

In an ANOVA of the pairwise data the overall number of recorded echolocation call sequences differed significantly among species ($F_{11,81} = 6.47, P < 0.001$; Table 2) and treatment ($F_{1,83} = 7.47, P = 0.008$; Table 1). Species numbers were significantly higher in managed orchards (paired *t*-test, $t = 5.94, df = 21, P < 0.0001$). Out of the 21 species present in Ticino, twelve (57%; one Molossidae and eleven Vespertilionidae) were detected in managed orchards but only six species in unmanaged ones (29% of the 21 present species). None were exclusive to the unmanaged orchards (Tables 1 and 2). In both orchard types, *P. pipistrellus* showed the highest activity (73.1% of the overall sequences identified), followed by *Pipistrellus nathusii* and *Hypsugo savii* (7.8% each), and *P. kuhlii* (7.4%). The total activity (28 nights) of all species was also significantly higher in managed orchards (Wilcoxon test, $V = 220.5, P < 0.001$), even after removing *P. pipistrellus* from the analysis (Wilcoxon test, $V = 153, P < 0.001$). In managed chestnut orchards the activity ranged between 1 and 83 sequences per night, in unmanaged ones from 0 to 40. In the unmanaged orchards, there were 10 nights during which no bat signals were recorded at all.

3.1. Vegetation structure

Several vegetation variables clearly differed between treatments (see Appendix A, Table 1), as confirmed by the discriminant analysis applied to all vegetation variables ($\lambda = 0.1149, \chi^2 = 75.74, P = 0.001$; see Appendix C, Fig. 1). The analysis discriminated the sites into managed (class score of -0.713) and unmanaged (class score of 1.292) orchards. The variables that explained most on the discriminant axis were “Number of trees per ha with a diameter of 12.1–20 cm” (Canonical weight of 0.517), “Cover of shrub layer” (Canonical weight of 0.481) and “Cover of litter” (Canonical weight of 0.276).

We identified groups of managed orchards with similar characteristics using a cluster dendrogram (Fig. 2). Based on branch lengths, three groups of orchards could be distinguished: M₁ con-

Table 2 Species detected, Swiss Red List status (Duelli, 1994) with IUCN categories (LC: least concern, VU: near threatened, CR: critically endangered, NE: not evaluated, IUCN, 2001), body mass, wing area, wing loading, estimated flight speed, estimated realistic turning diameter, manoeuvrability class and number of sequences identified in managed (M) and unmanaged (U) chestnut orchards, including percentages, ratios (*N* sequences in managed/*N* sequences in unmanaged) and totals. Calculatory details are given in Appendix B.

Species	Red List status CH/IUCN	Body mass (g)	Wing area (dm ²)	Wing loading (N/m ²)	Flight speed (m/s)	Turning diameter (m)	Manoeuvrability	Identified in managed (M)	Identified in unmanaged (U)	Ratio M/U	Total percent (%)
<i>Pipistrellus pipistrellus</i>	n/LC	5.2	0.63	8.10	4.27	1.02	Medium	384 (72.5%)	78 (76.5%)	4.9	73.10
<i>Pipistrellus nathusii</i>	3/EN	6.7	0.67	9.81	4.70	1.23	Medium	47 (8.9%)	2 (2.0%)	23.5	7.75
<i>Pipistrellus kuhlii</i>	n/LC	4.7	0.54	8.54	4.37	1.07	Medium	43 (8.1%)	4 (3.9%)	10.8	7.44
<i>Hypsugo savii</i>	4b/NT	7.0	0.86	8.01	4.25	1.01	Medium	33 (6.2%)	16 (15.7%)	2.1	7.75
<i>Nyctalus leisleri</i>	4b/NT	16.9	0.86	19.28	6.59	2.42	Low	7 (1.3%)	1 (1%)	7.0	1.27
<i>Plecotus austriacus</i>	4b/NT	10.0	1.24	7.91	4.22	0.99	High	4 (0.8%)	0	-	0.63
<i>Eptesicus serotinus</i>	2/CR	22.3	1.80	12.15	5.24	1.53	Low	3 (0.6%)	0	-	0.47
<i>Pipistrellus pygmaeus</i>	-/NE	5.5	0.60	8.97	4.49	1.13	Medium	2 (0.4%)	1 (1%)	2.0	0.47
<i>Eptesicus nilssonii</i>	4a/NT	9.2	1.12	8.06	4.27	1.01	Medium	2 (0.4%)	0	-	0.32
<i>Nyctalus noctula</i>	3/VU	26.5	1.61	16.15	6.02	2.03	Low	2 (0.4%)	0	-	0.32
<i>Tadarida teniotis</i>	4a/NT	25.0	2.14	11.44	5.07	1.44	Low	2 (0.4%)	0	-	0.32
<i>Myotis daubentoni</i>	3/VU	7.0	0.98	7.01	3.97	0.88	High	1 (0.2%)	0	-	0.16
Total								530 (100%)	102 (100%)	5.2	100.00
Averages/sums								14	1	14	
								511	101	5.1	
								5	0	5	

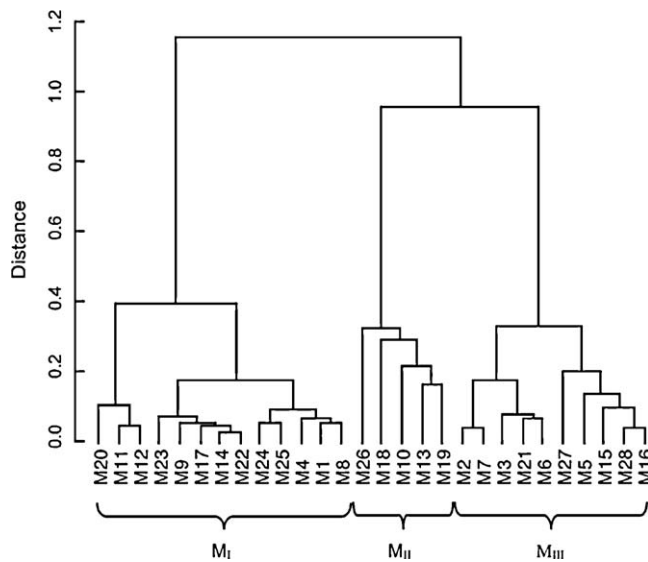


Fig. 2. Cluster dendrogram of managed orchards with forest structure variables. Bray–Curtis method was used to calculate the dendrogram. The numbers indicate survey night (corresponding to Table 1) and M indicates managed orchards. M_I , M_{II} and M_{III} are the three groups of managed orchards formed when considering branch lengths.

taining 13, M_{II} containing five and M_{III} containing 10 orchards. Six distinct Mann–Whitney U -tests revealed that there was a significant difference in the number of identified sequences (bat activity) between the managed groups (M_I , M_{III}) and the unmanaged orchards (U) ($M_I - U$: $W = 14.5$, $P = 0.006$; $M_{III} - U$: $W = 31$, $P = 0.020$), and between M_I and M_{II} ($W = 61$, $P = 0.018$). All other combinations were not significant (Fig. 3).

We performed a vegetation variable classification tree for the managed groups and unmanaged orchards (Fig. 4). The tree consists of three splits, with four terminal nodes representing the three managed orchards groups (M_I , M_{II} and M_{III} , see Fig. 2) and the unmanaged orchards. The variables under the nodes discriminate the following branches: number of shrubs and trees per hectare with <4 cm diameter, then shrub cover and tree height. Unmanaged chestnut orchards and managed group M_{II} have more than 150 shrubs and trees of <4 cm diameter per hectare. Orchards of the managed group M_{II} are distinguished from the unmanaged

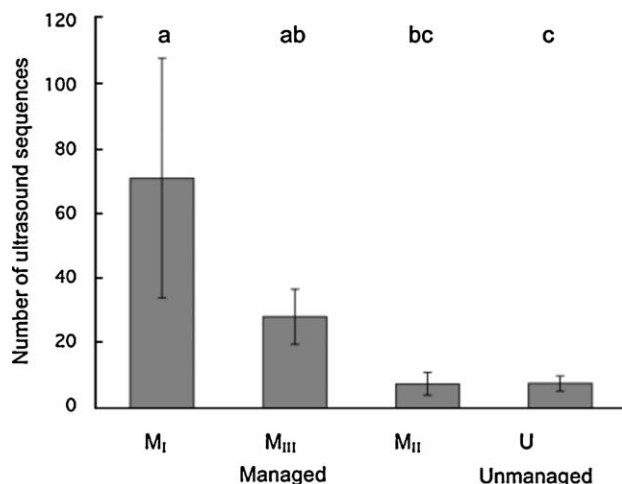


Fig. 3. Number of echolocation sequences recorded per group per night. Mean \pm SE are given. M_I , M_{II} and M_{III} are the groups of managed orchards created with the cluster dendrogram (see Fig. 2) and U the unmanaged group. Columns with different superscripts significantly differ in a Mann–Whitney U test.

orchards (U) by a shrub cover of less than 22%. The other two groups of managed orchards (M_I and M_{III}) have less than 150 shrubs of <4 cm diameter per hectare and are only separated by tree heights (< and >1900 cm, respectively).

3.2. Insect availability

The taxonomic group with the highest dry mass was the Lepidoptera (Table 3). Insect dry weight (Wilcoxon test, $V = 175$, $P = 0.245$), total insect number ($V = 148$, P -value = 0.084), and mean insect weight per individual per night (Wilcoxon test, $V = 174.5$, $P = 0.237$) did not differ significantly between treatments. With the exception of Heteroptera, none of the insect groups differed in dry weight or number of insects between treatments. We reanalysed the data, pooling Coleoptera, Diptera, Lepidoptera and Trychoptera as the predominant insect groups in the diet of bats (Wickramasinghe et al., 2004), but again found no significant difference between managed and unmanaged orchards (Wilcoxon test, $V = 183$, $P = 0.318$).

3.3. Selectivity of vegetation structure according to bat traits

We classified the detected species into high, medium and low manoeuvrable (Table 2) according to their flight morphology, wing loading and flight speed, and also considering their foraging and echolocation behaviour (Appendix B). As we expected, we found differences in their relative distribution between forest treatments, with low manoeuvrable bat species appearing more often in managed treatments, and high manoeuvrable species more prevalent in unmanaged orchards. However, despite considerably higher activity in managed orchards (Table 2), a contingency table did not show a significant influence of treatment on the distribution of recorded sequences per manoeuvrability classes ($\chi^2 = 2.02$, $df = 2$, $P = 0.365$). Nevertheless, activity of low manoeuvrable species was heavier biased towards managed orchards (Table 2).

4. Discussion

4.1. Managed versus unmanaged chestnut orchards

This study provides an example of a human activity that is beneficial to bats. There were twice as many bat species (12 species) and a five-fold increase in bat activity (530 echolocation sequences) in managed chestnut orchards compared to unmanaged ones (6 species, and 102 sequences). In addition, no bat species was detected in unmanaged orchards exclusively. Although vegetation structure differed significantly between treatments, with the unmanaged orchards being denser and closer, management of chestnut orchards does not appear to influence the number and biomass of the bat's prey. These results strongly suggest that vegetation structure rather than prey abundance is a key factor affecting foraging activities. Therefore, management directly influences habitat use of bats due to interaction with flight manoeuvrability (Patriquin and Barclay, 2003). Thinning or understory management as practiced in traditional orchards likely improves accessibility into the vegetation matrix and facilitates foraging, and consequently increases both efficiency and diversity in resource exploitation (Norberg, 1977). Studies on the effect of forest management, with concurrent monitoring of differentially thinned forests and stands of varying densities, most often show highest activity and diversity in less dense forests and more open areas (Krusic et al., 1996; Humes et al., 1999; Erickson and West, 2003; Loeb and Waldrop, 2008).

The effects of forestry and agricultural practices on bats have been evaluated in different parts of the world. Although logging with polycyclic loggings system in Trinidad and reduced impact

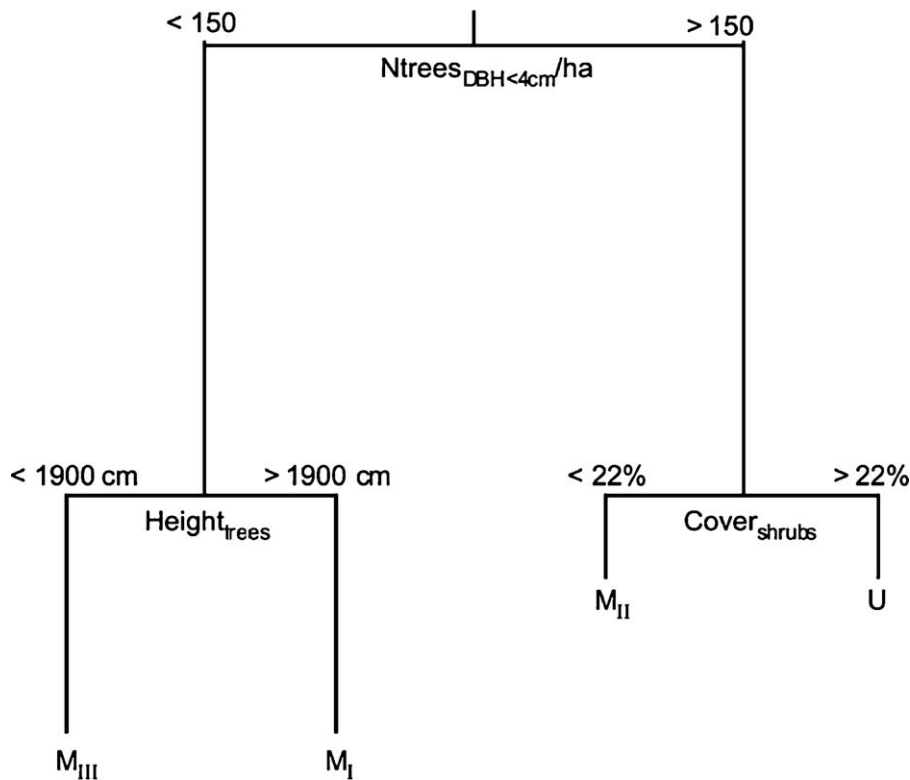


Fig. 4. Classification tree created with the environmental variables sampled in the chestnut orchards. M_I , M_{II} and M_{III} are the groups of managed orchards made by cluster dendrogram (Fig. 2) and U corresponds to unmanaged orchards. The vertical depth of each split is proportional to the variation explained. $N_{trees_{DBH<4cm/ha}}$ = number of trees with a diameter of <4 cm per 1 ha; $Height_{trees}$ = tree height [cm] and $Cover_{shrubs}$ = shrub cover [%].

logging in Amazonian forests seem to be compatible with the conservation of bat diversity (Clarke et al., 2005a), they negatively affect rare species (Presley et al., 2008). In boreal forests, silvicultural methods that create a mosaic of patches are recommended for conservation of a high bat species numbers even if thinning seems to have only a minimal effect on habitat use by bats (Patriquin and Barclay, 2003; Lacki et al., 2007). Generally, insectivorous bats prefer open stands to those with important structural clutter (Krusic et al., 1996; Loeb and O'Keefe, 2006).

Dense vegetation, as encountered in unmanaged orchards, causes acoustic clutter that affects foraging efficiency (Fenton, 1990; Schnitzler and Kalko, 2001). The impact of clutter on bat activity along forest edges has been demonstrated experimentally (Brigham et al., 1997), and clutter has recently been found to reduce

habitat use by bats (Loeb and O'Keefe, 2006). Some bat species consistently avoid regions of high structural clutter and prefer to commute and forage along more open structures as trails, gaps and edges (Walsh and Harris, 1996; Lloyd et al., 2006; Caras and Korine, 2009; Hein et al., 2009). Opening up the vegetation can thus create flight corridors for commuting bats.

Sampled habitat types differed considerably in structure and in foliage density, which could potentially affect bat detectability. To estimate such an effect, we tried to quantify possible sound absorption by leaves for a typical signal of 40 kHz, emitted at 100 dB SPL over a distance of 20 m, an appropriate critical distance for field-recording with a 12 Bit analogue-to-digital converter (72 dB dynamic range). Geometric spreading loss would attenuate the signal by 46 dB, and atmosphere attenuates another 20 dB

Table 3

Average number of insects (N , $MN \pm SE$) and their dry weights (WT , $MN \pm SE$) sampled per night, separated in 12 taxonomic groups and two treatments. Wilcoxon test P -values: *n.s.* not significant.

Taxonomic group	N			WT (mg)		
	Managed	Unmanaged	P -Values	Managed	Unmanaged	P -Values
Blattaria	2.3 ± 0.5	3.1 ± 0.8	<i>n.s.</i>	16.4 ± 4.6	18.3 ± 4.5	<i>n.s.</i>
Coleoptera	51.9 ± 9.4	62.9 ± 9.5	<i>n.s.</i>	749.7 ± 205.5	788.9 ± 135.5	<i>n.s.</i>
Diptera	258.4 ± 53.2	351.7 ± 63.6	<i>n.s.</i>	187.5 ± 50.2	154.3 ± 25.7	<i>n.s.</i>
Ephemeroptera	0.4 ± 0.2	0.6 ± 0.3	<i>n.s.</i>	0.5 ± 0.3	4.1 ± 3.5	<i>n.s.</i>
Heteroptera	5.1 ± 1.5	9.4 ± 1.9	<i>n.s.</i>	31.9 ± 9.2	123.1 ± 37.4	*
Homoptera	10.2 ± 1.9	20.4 ± 10.1	<i>n.s.</i>	16.0 ± 4.6	22.5 ± 12.0	<i>n.s.</i>
Lepidoptera	450.9 ± 78.4	525.7 ± 86.3	<i>n.s.</i>	4194.0 ± 549.8	5016.7 ± 685.6	<i>n.s.</i>
Hymenoptera	35.9 ± 6.9	34.4 ± 6.0	<i>n.s.</i>	100.1 ± 17.5	82.4 ± 16.9	<i>n.s.</i>
Neuroptera	4.7 ± 0.8	7.4 ± 1.6	<i>n.s.</i>	15.6 ± 2.9	23.3 ± 4.9	<i>n.s.</i>
Plecoptera	0.1 ± 0.0	0.1 ± 0.1	<i>n.s.</i>	0.2 ± 0.1	0.2 ± 0.2	<i>n.s.</i>
Thysanoptera	0.4 ± 0.4	0.2 ± 0.2	<i>n.s.</i>	1.1 ± 1.1	0.2 ± 0.1	<i>n.s.</i>
Trichoptera	61.9 ± 12.6	67.2 ± 16.4	<i>n.s.</i>	334.7 ± 72.6	404.6 ± 93.9	<i>n.s.</i>
Total	882.2 ± 123.7	1083.1 ± 130.9	<i>n.s.</i>	5652.2 ± 690.7	6631.3 ± 780.5	<i>n.s.</i>

* $P \leq 0.05$.

(Lawrence and Simmons, 1982). Foliage dampens sound linearly with frequency and would reduce our test signal by about 3.3 dB (Marten and Marler, 1977). Thus, foliage contributes only 4.8% to total signal attenuation (4% at 30 kHz, 5.6% at 60 kHz). Patriquin et al. (2003) have found small (25 kHz) to no effect (40 kHz) of forest types and structures on signal detection thresholds. As activity levels differed 5.2-fold between treatments, acoustic effects cannot account for the differences in recorded bat activity, which we thus confidently attribute to reflect bat occupancy.

At a landscape level, managed chestnut orchards represent small islands of open stands within a dense and relatively homogenous forest matrix (50–60% coverage). As both treatments held the same density of large trees (DBH > 50 cm), abandonment did not affect the original structure of the orchards trees, but did affect the gaps between them by increasing the density of shrubs, small trees, and chestnut shoots. Erickson and West (2003) found bat activity to be negatively correlated with tree density and such density dependent reactions may be species specific (Patriquin and Barclay, 2003). Bat activity in managed chestnuts orchards with a shrub density higher than 150 stems/ha did not significantly differ from that assessed in unmanaged stands. Humes et al. (1999) found higher activity of many bat species in old-growth forests (average 155 trees/ha) and in thinned stands (average 184 trees/ha) than in unthinned stands (average 418 trees/ha). Our threshold of 150 trees/ha compares favourably to these findings.

A mosaic of different habitats is likely to enhance the overall biodiversity in agricultural landscapes. Selective management of overgrown chestnut orchards generates such a mosaic of open and closed patches, which diversifies habitats available to bats. Similar to our finding of changed activity pattern after management, selective logging was shown to shift activity and diversity patterns in tropical forests too (Peters et al., 2006).

4.2. Effect of the abandonment on the species assemblage: winners and losers

Studies in forest systems showed that most bats avoid structurally cluttered habitats. Their activity concentrates in less complex but heterogeneous habitats that allow for easier navigation (Gehrt and Chelvig, 2003; Lumsden and Bennett, 2005). We expected to find bat species with low manoeuvrability to appear more often in managed orchards, and manoeuvrable species to focus on the unmanaged. Our study supported the prediction for the species with low manoeuvrability as we found large and medium large species (such as *Eptesicus serotinus*, *Nyctalus noctula*, and *Nyctalus leisleri*) foraging almost exclusively in the managed areas. However, most other species, regardless of manoeuvrability, also showed a preference for the managed chestnut orchards. All five species registered most frequently (>5 sequences) showed a 2.1–23.5 times higher activity in managed forests and there was no difference in habitat use, as indicated by the proportion of activity among low, medium or high manoeuvrability species among habitats. Species with high manoeuvrability were rarely recorded in general. This may be due to lower abundance as well as lower detectability of these species. There was only one record of a low-manoevrability bat (*N. leisleri*) in an unmanaged forest, compared to 14 detections of low manoeuvrability bats in managed ones. *H. savii* was the species with the highest relative use of unmanaged chestnut forests, even though its flight manoeuvrability was judged as medium.

We can relate the turning diameters, as we defined here (10-fold minimum turning radius at slowest speed, Table 2 and Appendix B) to the forest parameters measured in the two treatments. Tree density translates into median distances between trees of any diameter of 2.2 m ($Q_{25\%} = 1.9$, $Q_{75\%} = 2.7$ m) in unmanaged and 8.9 m ($Q_{25\%} = 7.1$, $Q_{75\%} = 10.1$ m) in managed forests. Thus, although turn-

ing flight is possible for all species in the unmanaged forests, even highly manoeuvrable bat species are at least challenged to efficiently fly in unmanaged chestnut orchards (Aldridge, 1987), and may not operate optimally between minimum power and maximum range speed (Norberg and Rayner, 1987). Furthermore, the closing vegetation structure in unmanaged forests results in drastically higher levels of echolocation clutter.

4.3. Species not registered

Most of the species that were not detected during the study but are present in the southern Alps (i.e. *Myotis blythii*, *M. brandti*, *M. mystacinus*, *M. emarginatus*, *M. nattereri*, *M. myotis*, and *Plecotus auritus*), are rare (Duelli, 1994), live in a restricted area and are therefore difficult to detect. However, a study on habitat use by bats in Italy found *Myotis* spp. to be moderately active in chestnut woodlands (Russo and Jones, 2003). Therefore, we cannot exclude that *Myotis* spp. were present in the surrounding areas but avoided feeding at our sites. Species with very low amplitude calls, such as *Plecotus* spp., may also not have been detected adequately (Waters and Jones, 1995). Although acoustic monitoring is considered more appropriate for measuring flight activity than mist-netting or harp-trapping (e.g. O'Farrell and Gannon, 1999; Lumsden and Bennett, 2005), none of these methods detects all species with equal chance. We could not identify to species 18% of the bat sequences we had recorded. Some bats, for example *P. kuhlii* and *P. nathusii*, may echolocate very similarly and their call spectrograms can overlap (Obrist et al., 2004a). However, the paired experimental design ensured equal sampling between treatments, rendering the relations between treatments for any given species reliable.

4.4. Conclusions and practical implications

Abandonment of chestnut orchards leads to a decline in bat species richness and activity. Conversely, the management of chestnut orchards in the traditional way opens up the orchards, enabling foraging access for a variety of bat species, which only occasionally hunt in abandoned orchards with dense vegetation. The results of our study are consistent with the conclusions by Laiolo et al. (2004) concerning the avifauna and those by Crampton and Barclay (1998) concerning the Chiroptera, in supporting the suitability of old, more openly structured orchards as habitat for bats and birds. Foresters restoring former chestnut orchards eliminate the invading woody vegetation, prune the old and grafted chestnut trees and reconstitute the herb layer by sowing grass species. Subsequent management of the restored orchards consists in pasturing the area, collecting the fruits and removing litter. When restoring orchards, foresters tend to avoid suppressing former orchard trees, regardless of the existing tree density. In our study, the managed orchards with a relatively high proportion of shrubs and small trees (M_{II}) did not significantly differ in bat activity from unmanaged ones (U). Overall, this indicates that (a) regular management is important to maintain suitable habitat for bats, and (b) density of small trees left standing should not exceed 150 ha⁻¹. Consequently, only fully managed, open and undergrowth-free stands influence the activity pattern of many bat species. Additionally, significantly higher number of bats roost in managed chestnut orchards (Spada et al., 2008). If regular management stops or becomes too occasional, the viability of the orchards as foraging and roosting habitat decreases within a short time due to the rapid colonization of tree and shrub species (Conedera et al., 2000). Foresters and farmers should be encouraged to restore and support silvo-pastoral systems such as chestnut orchards to create and maintain open stands in multifunctional forests (McNeely, 1994).

However, these efforts have a price. A survey (Rudow and Borter, 2006) on 46 orchard restoration projects in Switzerland, covering

210 ha and project budgets of 6.5 Mio. Swiss Francs (SFr.) revealed substantial restoration costs of an average SFr. 55,000 ha⁻¹, 73% thereof being labour costs. The Swiss Federation, the Cantons or NGO foundations paid the majority of these costs, thereby conserving a traditional landscape and triggering renewed interest of tourism. To make the continued management and laborious harvesting of chestnuts economically feasible and practical, two Swiss federal bills regulating agricultural subsidizations are applicable. Following the ecological compensation scheme for agricultural areas managed under ecological, sustainable and natural conditions (Schweizerischer Bundesrat, 1998), an amount of SFr. 15 can be paid per year and tree managed in chestnut orchards. An additional bill governs quality control in such ecologically cultivated areas: up to SFr. 1000 ha⁻¹ and year can be subsidized for ideally structured and interconnected orchards (Schweizerischer Bundesrat, 2001). Taken together, and considering the renewed interest of gastronomy in sweet chestnuts, a propagation of chestnut orchard restoration and their continued management is foreseeable, also to the benefit of bats.

Acknowledgments

We would like to thank the Forester Service of the Canton Ticino and the private orchard owners for providing help and permissions to sampling the data. We are grateful for the fieldwork of Franco Fibbioli, Simone Degiacomi and Nathalie Tzaud. We thank Heather Cole for improving the English, and we acknowledge the contribution of anonymous reviewers to a considerably amended manuscript.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2010.12.010.

References

- Aldridge, H.D.J.N., 1987. Turning flight in bats. *J. Exp. Biol.* 128, 419–425.
- Arita, H.T., 1993. Rarity in neotropical bats—correlations with phylogeny, diet, and body-mass. *Ecol. Appl.* 3, 506–517.
- Benayas, J., Martins, A., Nicolau, J., Schulz, J., 2007. Abandonment of agricultural land: an overview of drivers and consequences. *CAB Rev.: Perspect. Agric. Vet. Sci. Nutr. Nat. Resour.* 2, 1–14.
- Benjamini, Y., Hochberg, Y., 1995. Controlling the false discovery rate—a practical and powerful approach to multiple testing. *J. Roy. Stat. Soc. B: Met.* 57, 289–300.
- Blondel, J., Aronso, J., 1999. *Biology and Wildlife of the Mediterranean Region*. Oxford University Press Inc., New York.
- Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest communities of Southern Wisconsin. *Ecol. Monogr.* 27, 326–349.
- Brigham, R.M., Grindal, S.D., Firman, M.C., Morissette, J.L., 1997. The influence of structural clutter on activity patterns of insectivorous bats. *Can. J. Zool.* 75, 131–136.
- Caras, T., Korine, C., 2009. Effect of vegetation density on the use of trails by bats in a secondary tropical rain forest. *J. Trop. Ecol.* 25, 97–101.
- Castro-Arellano, I., Presleya, S.J., Saldanha, L.N., Willig, M.R., Wunderle, J.M., 2007. Effects of reduced impact logging on bat biodiversity in terra firme forest of lowland Amazonia. *Biol. Conserv.* 138, 269–285.
- Ceballos, G., Brown, J.H., 1995. Global patterns of mammalian diversity, endemism, and endangerment. *Conserv. Biol.* 9, 559–568.
- Clarke, F.M., Pio, D.V., Racey, P.A., 2005a. A comparison of logging systems and bat diversity in the Neotropics. *Conserv. Biol.* 19, 1194–1204.
- Clarke, F.M., Rostant, L.V., Racey, P.A., 2005b. Life after logging: post-logging recovery of a neotropical bat community. *J. Appl. Ecol.* 42, 409–420.
- Conedera, M., Krebs, P., 2008. History, present situation and perspective of chestnut cultivation in Europe. In: Abreu, C.G., Peixoto, F.P., Gomes-Laranjo, J. (Eds.), *Proceedings of the Second Iberian Chestnut Congress*, Vila Real (P). *Acta Hort.* 23–27.
- Conedera, M., Manetti, M.C., Giudici, F., Amorini, E., 2004. Distribution and economic potential of the Sweet chestnut (*Castanea sativa* Mill.) in Europe. *Ecol. Mediterr.* 30, 179–193.
- Conedera, M., Stanga, P., Lischer, C., Stöckli, V., 2000. Competition and dynamics in abandoned chestnut orchards in southern Switzerland. *Ecol. Mediterr.* 26, 101–112.
- Crampton, L.H., Barclay, R.M.R., 1998. Selection of roosting and foraging habitat by bats in different-aged aspen mixedwood stands. *Conserv. Biol.* 12, 1347–1358.
- Crome, F.H.J., Richards, G.C., 1988. Bats and gaps—microchiropteran community structure in a Queensland rain-forest. *Ecology* 69, 1960–1969.
- Davy, C.M., Russo, D., Fenton, M.B., 2007. Use of native woodlands and traditional olive groves by foraging bats on a Mediterranean island: consequences for conservation. *J. Zool.* 273, 397–405.
- De'ath, G., Fabricius, K.E., 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. *Ecology* 81, 3178–3192.
- Dietz, C., Helversen, O.V., Nill, D., 2007. *Handbuch der Fledermäuse Europas und Nordwestafrikas*. Kosmos Verlags-GmbH.
- Dirnböck, T., Dullinger, S., Grabherr, G., 2003. A regional impact assessment of climate and land-use change on alpine vegetation. *J. Biogeogr.* 30, 401–417.
- Duchamp, J.E., Swihart, R.K., 2008. Shifts in bat community structure related to evolved traits and features of human-altered landscapes. *Landscape Ecol.* 23, 849–860.
- Duelli, P., 1994. Rote Listen der gefährdeten Tierarten in der Schweiz. Schweiz Bundesamt für Umwelt Wald und Landschaft. Eidgenössische Drucksachen- und Materialzentrale (EDMZ), Bern.
- Erickson, J.L., West, S.D., 2003. Associations of bats with local structure and landscape features of forested stands in western Oregon and Washington. *Biol. Conserv.* 109, 95–102.
- Fenton, M.B., 1990. The foraging behaviour and ecology of animal-eating bats. *Can. J. Zool.* 68, 411–422.
- Gehrt, S.D., Chelmsvig, J.E., 2003. Bat activity in an urban landscape: patterns at the landscape and microhabitat scale. *Ecol. Appl.* 13, 939–950.
- Harvey, C.A., Villalobos, J.A.G., 2007. Agroforestry systems conserve species-rich but modified assemblages of tropical birds and bats. *Biodivers. Conserv.* 16, 2257–2292.
- Hayes, J.P., Loeb, S.C., 2007. The influence of forest management on bats in North America. In: Lacki, M.J., Hayes, J.P., Kurta, A. (Eds.), *Bats in Forests: Conservation and Management*. John Hopkins University Press, Baltimore, pp. 207–235.
- Hein, C.D., Castleberry, S.B., Miller, K.V., 2009. Site-occupancy of bats in relation to forested corridors. *Forest Ecol. Manage.* 257, 1200–1207.
- Humes, M.L., Hayes, J.P., Collopy, M.W., 1999. Bat activity in thinned, unthinned, and old-growth forests in western Oregon. *J. Wildl. Manage.* 63, 553–561.
- Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* 54, 187–211.
- IUCN, 2001. *IUCN Red List Categories and Criteria: Version 3.1*. IUCN Species Survival Commission, IUCN, Gland, Switzerland/Cambridge, UK, p. ii + 30 pp.
- Jaberg, C., Bohnenstengel, T., Amstutz, R., Blant, J.-D., 2007. Utilisation du milieu forestier par les chauves-souris (Mammalia: Chiroptera) du canton de Neuchâtel—implications pour la gestion sylvicole. *Schweiz. Z. Forstwes.* 157, 254–259.
- Keller, M., 2005. *Field Manual for the Third Swiss National Forest Inventory 2004–2007*. Swiss Federal Research Institute WSL, Birmensdorf, Switzerland, p. 393.
- Krusic, R.A., Yamasaki, M., Neefus, C.D., Pekins, P.J., 1996. Bat habitat use in White Mountain National Forest. *J. Wildl. Manage.* 60, 625–631.
- Lacki, M.J., Hayes, J.P., Kurta, A. (Eds.), 2007. *Bats in Forests: Conservation and Management*. John Hopkins University Press, Baltimore.
- Laiolo, P., Rolando, A., Valsania, V., 2004. Avian community structure in sweet chestnut coppiced woods facing natural restoration. *Rev. Ecol. -Terre Vie* 59, 453–463.
- Lawrence, B.D., Simmons, J.A., 1982. Measurements of atmospheric attenuation at ultrasonic frequencies and the significance for echolocating bats. *J. Acoust. Soc. Am.* 71, 585–590.
- Legendre, P., Legendre, L., 1998. *Numerical Ecology*. Elsevier, Amsterdam.
- Lloyd, A., Law, B., Goldingay, R., 2006. Bat activity on riparian zones and upper slopes in Australian timber production forests and the effectiveness of riparian buffers. *Biol. Conserv.* 129, 207–220.
- Loeb, S.C., O'Keefe, J.M., 2006. Habitat use by forest bats in South Carolina in relation to local, stand, and landscape characteristics. *J. Wildl. Manage.* 70, 1210–1218.
- Loeb, S.C., Waldrop, T.A., 2008. Bat activity in relation to fire and fire surrogate treatments in southern pine stands. *Forest Ecol. Manage.* 255, 3185–3192.
- Lumsden, L.F., Bennett, A.F., 2005. Scattered trees in rural landscapes: foraging habitat for insectivorous bats in south-eastern Australia. *Biol. Conserv.* 122, 205–222.
- MacDonald, D., Crabtree, J.R., Wiesinger, G., Dax, T., Stamou, N., Fleury, P., Lazpita, J.G., Gibon, A., 2000. Agricultural abandonment in mountain areas of Europe: environmental consequences and policy response. *J. Environ. Manage.* 59, 47–69.
- Marten, K., Marler, P., 1977. Sound transmission and its significance for animal localisation. I. Temperate habitats. *Behav. Ecol. Sociobiol.* 2, 271–290.
- McNeely, J.A., 1994. Lessons from the past—forests and biodiversity. *Biodivers. Conserv.* 3, 3–20.
- Menzel, M.A., Carter, T.C., Menzel, J.M., Ford, W.M., Chapman, B.R., 2002. Effects of group selection silviculture in bottomland hardwoods on the spatial activity patterns of bats. *Forest Ecol. Manage.* 162, 209–218.
- Mickleburgh, S.P., Hutson, A.M., Racey, P.A., 2002. A review of the global conservation status of bats. *Oryx* 36, 18–34.
- Neuweiler, G., 1984. Foraging, echolocation and audition in bats. *Naturwissenschaften* 71, 446–455.
- Norberg, R.A., 1977. Ecological theory on foraging time and energetics and choice of optimal food-searching method. *J. Anim. Ecol.* 46, 511–529.
- Norberg, U., Rayner, J.M.V., 1987. Ecological morphology and flight in bats (Mammalia: Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Phil. Trans. R. Soc. Lond. B* 316, 335–427.

- O'Farrell, M.J., Gannon, W.L., 1999. A comparison of acoustic versus capture techniques for the inventory of bats. *J. Mammal.* 80, 24–30.
- Obrist, M.K., Boesch, R., Flückiger, P.F., 2004a. Variability in echolocation call design of 26 Swiss bat species: consequences, limits and options for automated field identification with a synergetic pattern recognition approach. *Mammalia* 68, 307–322.
- Obrist, M.K., Boesch, R., Flückiger, P.F., Dieckmann, U., 2004b. Who's calling? Acoustic bat species identification revised with synergetics. In: Thomas, J., Moss, C., Vater, M. (Eds.), *Echolocation in Bats and Dolphins*, Proceedings of the Biosonar Conference 1998. University of Chicago Press, Chicago, pp. 484–491.
- Patriquin, K.J., Barclay, R.M.R., 2003. Foraging by bats in cleared, thinned and unharvested boreal forest. *J. Appl. Ecol.* 40, 646–657.
- Patriquin, K.J., Hogberg, L.K., Chruszcz, B.J., Barclay, R.M.R., 2003. The influence of habitat structure on the ability to detect ultrasound using bat detectors. *Wildl. Soc. Bull.* 31, 475–481.
- Peters, S.L., Malcolm, J.R., Zimmerman, B.L., 2006. Effects of selective logging on bat communities in the southeastern Amazon. *Conserv. Biol.* 20, 1410–1421.
- Presley, S.J., Willig, M.R., Wunderle, J.M., Saldanha, L.N., 2008. Effects of reduced-impact logging and forest physiognomy on bat populations of lowland Amazonian forest. *J. Appl. Ecol.* 45, 14–25.
- R Development Core Team, 2010. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0. <http://www.R-project.org>.
- Ripley, B., 2010. Tree: Classification and Regression Trees. R Package Version 1.0-28., <http://CRAN.R-project.org/package=tree>.
- Rudow, A., Borner, P., 2006. Erhaltung der Kastanienkultur in der Schweiz—Erfahrungen aus 46 Selvenrestaurationsprojekten. *Schweiz. Z. Forstwes.* 157, 413–418.
- Russo, D., Jones, G., 2003. Use of foraging habitats by bats in a Mediterranean area determined by acoustic surveys: conservation implications. *Ecography* 26, 197–209.
- Safi, K., Kerth, G., 2004. A comparative analysis of specialization and extinction risk in temperate-zone bats. *Conserv. Biol.* 18, 1293–1303.
- Schaub, M., Gimenez, O., Sierro, A., Arlettaz, R., 2007. Use of integrated modeling to enhance estimates of population dynamics obtained from limited data. *Conserv. Biol.* 21, 945–955.
- Schnitzler, H.U., Kalko, E.K.V., 2001. Echolocation by insect-eating bats. *BioScience* 51, 557–569.
- Schweizerischer Bundesrat, 1998. Verordnung über die Direktzahlungen an die Landwirtschaft (Direktzahlungsverordnung, DZV). 910.13, 52 p.
- Schweizerischer Bundesrat, 2001. Verordnung über die regionale Förderung der Qualität und der Vernetzung von ökologischen Ausgleichsflächen in der Landwirtschaft (Öko-Qualitätsverordnung, ÖQV). 910.14, 16 p.
- Spada, M., Szentkúti, S., Zambelli, N., Mattei-Roesli, M., Moretti, M., Bontadina, F., Arlettaz, R., Tosi, G., Martinoli, A., 2008. Roost selection by non-breeding Leisler's bats (*Nyctalus leisleri*) in montane woodlands: implications for habitat management. *Acta Chiropt.* 10, 81–88.
- Stierlin, H.R., Ulmer, U., 1999. Forest structure. In: Brassel, P., Brändli, U.-B. (Eds.), *Results of the Second Swiss National Forest Inventory 1993–1995*. Swiss Federal Research Institute WSL, Birmensdorf, Switzerland, pp. 103–150.
- Walsh, A.L., Harris, S., 1996. Foraging habitat preferences of vespertilionid bats in Britain. *J. Appl. Ecol.* 33, 508–518.
- Waters, D.A., Jones, G., 1995. Echolocation call structure and intensity in five species of insectivorous bats. *J. Exp. Biol.* 198, 475–489.
- Weller, T.J., Cryan, P.M., O'Shea, T.J., 2008. Broadening the focus of bat conservation and research in the USA for the 21st century. *Endang. Species Res.* 8, 129–145.
- Wickramasinghe, L.P., Harris, S., Jones, G., Jennings, N.V., 2004. Abundance and species richness of nocturnal insects on organic and conventional farms: effects of agricultural intensification on bat foraging. *Conserv. Biol.* 18, 1283–1292.
- Zingg, P.E., 1990. Akustische Artidentifikation von Fledermäusen (Mammalia: Chiroptera) in der Schweiz. *Rev. Suisse. Zool.* 97, 263–294.