

Effect of deadwood management on saproxylic beetle richness in the floodplain forests of northern Italy: some measures for deadwood sustainable use

Francesca Della Rocca · S. Stefanelli ·
C. Pasquaretta · A. Campanaro · G. Bogliani

Received: 29 August 2013 / Accepted: 3 February 2014 / Published online: 13 February 2014
© Springer International Publishing Switzerland 2014

Abstract Saproxylic beetles may act as bio-indicators of high-quality mature woodlands, and their conservation is strongly linked to the quality and quantity of deadwood in a biotope. We tested the effect of deadwood accumulation and habitat variables on saproxylic species richness by investigating six sampling sites under different deadwood management practices that belong to both alluvial and riparian mixed forests of the Po plain, Italy. We sampled 43 obligate saproxylic species. The main factor predicting saproxylic species richness was the amount of deadwood measured by both log diameter and volume. We found a threshold of 0.22 m diameter (confidence interval CI 0.18–0.37 m) and 32.04 m³/ha volume (CI 16.09–64.09 m³/ha) below which saproxylic beetle richness would be significantly reduced and a threshold of 35 m³/ha dead wood volume (CI 33–40 m³/ha) over which species richness increases by <5 %. The other deadwood and environmental components influenced

saproxylic beetle richness to a lesser extent; some of them, however, should still be considered for proper management. Forest structure variables describing forest density such as large trees and basal areas have a negative effect on species richness. According to the results of our study, stumps and advanced decaying class are positively correlated, while small logs are negatively correlated to species richness. Thus, in extensively managed forests, the regular cutting of trees should be implemented to create artificial stumps, in order to assure a continuity of deadwood and, in the meantime, increase the number and width of openings in the forest. Moreover, prolonging rotation times can assure the presence of deadwood at intermediate/late stages of decay.

Keywords Floodplain forests · Coleoptera · Species richness · Threshold

F. Della Rocca (✉) · S. Stefanelli · G. Bogliani
DSTA - Department of Earth and Environmental Science,
University of Pavia, Via A. Ferrata 9, 27100 Pavia, Italy
e-mail: fdellarocca@gmail.com; francesca.dellarocca@unipv.it

C. Pasquaretta
Université de Strasbourg, IPHC, 23 rue Becquerel,
67087 Strasbourg, France

C. Pasquaretta
CNRS, UMR7178, 67037 Strasbourg, France

A. Campanaro
Centro Nazionale per lo Studio e la Conservazione della
Biodiversità Forestale “Bosco della Fontana” di Verona, Corpo
Forestale dello Stato, Verona, Italy

A. Campanaro
Dipartimento di Biologia e Biotecnologie “Charles Darwin”,
Università degli Studi di Roma “La Sapienza”, Rome, Italy

Introduction

Saproxylic beetles depend on deadwood, dying wood, or other saproxylic organisms during some part of their life cycle (Speight 1989). This functional group represents roughly 20–30 % of the invertebrate fauna in European broad-leaved forests (Vallauri et al. 2005), and their role in the process of coarse woody debris (CWD defined by Harmon et al. 1986) decomposition and nutrient recycling is well known (Harmon et al. 1986; Schläghamerský 2003). Due to their specificity for the deadwood substrate that characterizes mature timber habitat, saproxylic beetles can be considered one of the most reliable bio-indicators of high-quality mature woodlands (Speight 1989; Alexander 2004; Jonsson et al. 2005), and their conservation is strongly linked to the quality and quantity of deadwood in a landscape.

According to the European Red List of Saproxyllic Beetles (Niето and Alexander 2010), 11 % of the 436 saproxyllic beetles assessed are considered threatened throughout Europe. In fact, over the past 100 years in Italy, as in many other European countries, forests had been heavily exploited for commercial use, forestry practices, and subjected to the wrong management actions (Lombardi et al. 2008). These practices dramatically reduced the old growth forests and the dead wood availability causing a decline of saproxyllic beetle populations (McLean and Speight 1993). Urgent management measures are needed to preserve this forest habitat and its saproxyllic fauna. However, two decades after the Recommendation to the Council of Europe, which takes the importance and maintenance of deadwood into account, and after the indication of deadwood as key indicator of forest conservation at pan-European scale (indicator n. 4.5: MCPFE 2003) a very low number of effective results can be mentioned and most of them come from studies carried out in the boreal forests of northern Europe (Bouget et al. 2008).

Floodplain forests of the Italian Po plain, dominated by oak, elm, and lime trees, are among the scarcest and most endangered ecosystems in Europe (Schlaghamerský 2000). Active management applications are limited to some localized examples: the Nature Reserve Bosco Fontana (Cavalli and Mason 2003; Mason 2004; Campanaro et al. 2007) and some pilot studies in the Colli Euganei (Life Nature project LIFE03 NAT/IT/000119) and the Cilento and Valle di Diano National Park (Blasi et al. 2010).

Conserving dead wood in a forest is still viewed with diffidence by forestry managers, and there is still a general underestimation of the importance of deadwood in maintaining high biodiversity (Deuffic 2010). Two main reasons explain the general reticence of forest managers and policy makers to implement forest conservation measures aimed at maintaining deadwood. The first reason is a lack of knowledge regarding the saproxyllic fauna, especially that of Mediterranean countries (Buse et al. 2010).

The second reason is the absence of standardized and statistically based guidelines for deadwood management (Müller and Büttler 2010). As pointed out by Müller and Büttler (2010), many studies carried throughout the world demonstrate the necessity of increasing the amount of deadwood in a forest, but most of them provide only vague suggestions, and they do not provide an exact measure of the minimum amount of deadwood needed for maintaining saproxyllic diversity (Speight 1989; Grove and Meggs 2003; Christensen et al. 2005; Davies et al. 2008). Forest managers need clear, simple, and applicable guidelines based on common and comparable statistical tools. The aim of our study is to identify the minimum requirements for increasing saproxyllic beetle richness in the floodplain forests of northern Italy by suggesting a sustainable use of

dead wood and presenting a straight forward and statistically tested measure for forest managers. In this paper, we evaluated the effect of both deadwood quality and quantity on saproxyllic species richness and established a threshold range of deadwood volume and dead tree diameter below which saproxyllic beetle richness would be significantly reduced.

Methods

Study area

The study was conducted in the Ticino Valley Regional Park (Fig. 1). The park is located in northwest Italy and covers an area of about 97 km² along the banks of the Ticino River from its outlet at Lake Maggiore until its confluence with the Po River. The climate of the park is temperate sub-continental (Ferré et al. 2005). The weather is humid with a mean annual temperature of about 13 °C and an annual precipitation decreasing from north (1,200 mm) to south (700 mm) (Prigioni 1995). In 2002, the park was acknowledged as part of the “UNESCO Man and Biosphere Programme” as the MAB Biosphere Reserve “Valle del Ticino” (UNESCO 2005). It crosses the most urbanized area of the country and represents an important ecological corridor connecting the Alps to the Po floodplain. Ticino Park is the most extended natural area of the entire Po Valley and encompasses a mosaic of ecosystems such as large river habitats, wetlands, riparian woods, and patches of primary floodplain forest similar to the type that covered the entire valley until Roman colonization (1st Century b. c). Woodlands cover about 19,546 hectares or 21 % of the whole park and also include some habitat types listed in Annex 1 to the EU Habitat directive among which are Alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior* (habitat code 91E0*) and Riparian mixed forests of *Quercus robur*, *Ulmus laevis*, and *Ulmus minor*, *F. excelsior*, or *Fraxinus angustifolia* along the great rivers (habitat code 91F0).

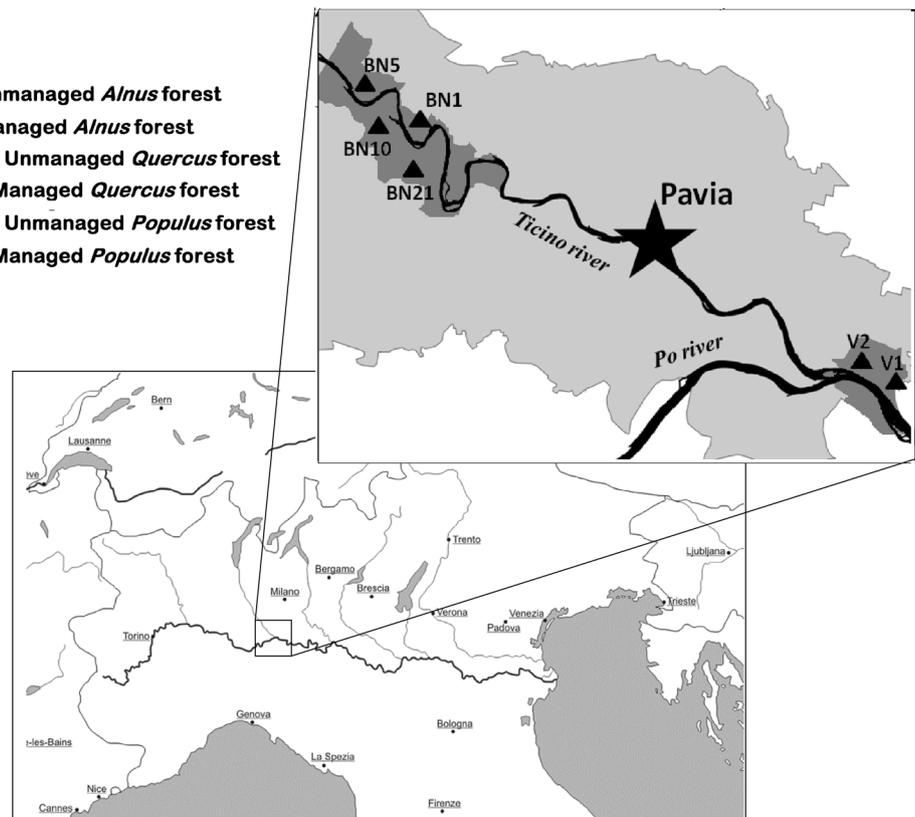
The study sites are located on the southern stretches of the Park and are included in two Natura 2000 sites, Site of Community Importance (SCI) “Boschi Siro Negri e Moriano” (IT2080014) and SCI “Boschi di Vaccarizza” (IT2080019).

Study design

Our study was designed to analyse the effects of deadwood accumulation and habitat variables on saproxyllic richness. We analysed data from 36 traps located in 6 sampling sites: 2 riparian mixed forests (habitat code 91F0) with dominance of *Q. robur* (called here on in this paper *Quercus*

Fig. 1 Location of the study area and study sites. Each triangle indicates one sampled forest

V1: Unmanaged *Alnus* forest
V2: Managed *Alnus* forest
BN10: Unmanaged *Quercus* forest
BN5: Managed *Quercus* forest
BN21: Unmanaged *Populus* forest
BN1: Managed *Populus* forest



forests) and 4 Alluvial forests (habitat code 91E0*). Alluvial forests included 2 riparian forests of *F. excelsior* and *A. glutinosa* (Corine Biotopes code 44.3, called in this paper “*Alnus* forests”) and 2 arborescent galleries of tall *Salix alba*, *S. fragilis* and *Populus nigra* (Corine code 44.13: called in this paper “*Populus* forests”). We selected 1 managed and 1 unmanaged forest per habitat type, considering unmanaged forests those which had not been influenced by direct human disturbance for at least 20 years (Paillet et al. 2010). In the managed forests the principal silvicultural management adopted is coppice or coppice with high forests.

In each sampling site, we selected 6 fallen trees on the basis of their decomposition status following the decay classification described by the Italian manual “Biosoil-Biodiversity Project” (Cindolo and Petriccione 2006). We selected 3 specific decaying classes: class 1, recently dead tree with trunk intact, class 2, wood still solid for the most part with <10 % of its structure changed due to decomposition (box cutter penetrates <1 cm), class 3, wood decayed from 10 to 25 %, which can be verified by using a sharp box cutter (penetrates about 1 cm). We placed 1 trap per tree in the centre of a circular plot of 11 m radius (equals to 400 m²) for a total of 36 traps in the whole study area. The distance between two plots and also between the plot and the forest border was more than 20 m. We also

measured the diameter at breast height (DBH) of each sampled tree.

Saproxylic beetles

Saproxylic beetles were sampled using eclector traps which are a not-widely used method to catch beetles living in decaying wood (Albrecht 1990; Schmitt 1992; Alinvi et al. 2007). The traps consisted of a 1 m wide black polypropylene fabric weed barrier which enclosed the fallen dead tree. A hole was made in the cloth, and a lid for a translucent plastic bottle cover with a 70 % ethanol solution was fastened on it. Beetles emerging from the trap were caught inside the bottle screwed into this lid (Johansson et al. 2006). All traps were checked continuously from May to October 2010 in order to cover the seasonal activity of all the species. Bottles were emptied at 2 week intervals to obtain a total of 12 collections. Beetles were separated from other insects and identified to species level by many experts (see acknowledgements). In this paper, we considered only obligate saproxylic beetles belonging to 21 families. We considered obligate saproxylic beetles those species which depend on dead wood in at least part of their lifecycle (Gibb et al. 2006), and this category was assigned by the experts (see acknowledgements) on the basis of their knowledge of the species.

Table 1 Variables measured for each of the 36 sampling plots. 13 variables describe characteristics of forest structure and deadwood surrounding the sampled tree

Variables	Description	Range of value
<i>Forest structure</i>		
BAS_A	Basal area	1.30–73.76 m ² /ha
B_TREE	Number of trees with a diameter >10 cm	1–30
S_TREE	Number of trees with a diameter <10 cm	0–40
DWV	Total dead wood volume	1.87–206.42 m ³ /ha
<i>Trap's tree parameters</i>		
T_DIAM	Diameter at breast height of the tree where trap is present	11–70 cm
T_DEC	Decaying class of the tree where trap is present	1–3
<i>Dead wood volume grouped by category</i>		
LO	Big logs volume	0–128.69 m ³ /ha
SLO	Small logs volume	0–19.60 m ³ /ha
ST	Stump volume	0–76.43 m ³ /ha
S	Snags volume	0–63.46 m ³ /ha
STR	Standing trees volume	0–141.05 m ³ /ha
FTR	Fallen trees volume	0–109.09 m ³ /ha
<i>Dead wood volume grouped by decaying class</i>		
DC1	Decaying class 1	0–103.98 m ³ /ha
DC2	Decaying class 2	0–143.98 m ³ /ha
DC3	Decaying class 3	0–90.54 m ³ /ha

T_Diam and T_Dec are variables describing the sampled tree

Environmental variables

We measured a total of 15 variables that we “a priori” considered as potentially important for the local species richness of saproxylic beetles within each sampling plot (Table 1). Two variables described the diameter and the decaying class of the sampled tree and 13 variables described habitat features of the plot surrounding the sampled tree. To quantify deadwood volume, we recorded all wood pieces with a minimum diameter of 5 cm and grouped them into six categories (Cindolo and Petriccione 2006): small logs (piece of fallen stem or branch with a diameter between 5 and 10 cm), big logs (piece of wood with a diameter of at least 10 cm), stumps (short, vertical pieces created by cutting, with a height smaller than 130 cm), snags (standing deadwood without branches, with a height >130 cm and with a DBH >10 cm), fallen trees, and standing dead trees. For each category we established the decaying class and recorded the diameter. In the case of fallen trees and standing dead trees (including snags), we recorded the diameter at breast height (DBH), whereas, for all others categories we measured it at half length. We calculated the volume of the dead trees using the general

stand volume equation (Castellani et al. 1984) and the volume of logs and snags by assuming it to be a cylinder and using the length and diameter at half length (Bässler et al. 2008). Within each sampling plot, we counted all the living trees and recorded the species and the diameter at DBH. Afterward, we calculated the following forest stand attributes: (1) Small tree density: measured as the number of trees with a DBH < 10 cm; (2) Big tree density: measured as the number of trees per ha⁻¹ with a DBH ≥ 10 cm; (3) Basal area (m² ha⁻¹).

Data analysis

Saproxylic beetles

We used the pooled sample of 36 traps in the analysis. As a measure of species richness we used the number of species caught in each plot. As a measure of species abundance, we used the number of individuals.

To evaluate if the number of species sampled is representative of the whole saproxylic fauna living in the Italian floodplain forests, we computed a sample size-based rarefaction curve and a coverage-based rarefaction curve (Chao and Jost 2012; Müller et al. 2013) using the software iNEXT (interpolation/extrapolation) available online at <http://chao.stat.nthu.edu.tw/inext/>. With the coverage based rarefaction analysis we can estimate the coverage deficit of our sampling effort that is, in other word, the probability that the next sampled individual belongs to a new species not previously collected (Olszewski 2004). We used the coverage based rarefaction curves also to compare species richness among different communities. This approach goes a step further than the traditional rarefaction technique because compares sample of equal completeness instead of equal size, satisfying a replication principle which is an essential property for characterizing diversity (Jost 2010; Chao and Jost 2012). By standardizing samples on coverage, we are sure that communities have the same sampling completeness and the unsampled species constitute the same proportion of the total individuals in each community. Obviously, when samples from different communities have the same degree of completeness, they can be compared directly, without any need of rarefaction (Chao and Jost 2012). For all the estimates we calculated a 95 % confidence band using a bootstrap sampling method with 100 replicates. Differences in species richness among habitat type and among management type were also evaluated with the permutational multivariate analysis of variance (PERMANOVA) comparing each variable separately (univariate approach). PERMANOVA is a semi-parametric test analogous to multivariate analysis of variance but with pseudo-*F* ratios and *p* values generated by resampling (permutation) the resemblance measures of the

actual data; thus it is less sensitive to assumptions of parametric tests that are frequently violated by ecological data sets (Anderson 2001; Anderson et al. 2008). The PERMANOVA analysis was performed using the R package *Vegan*, *Adonis* function (Oksanen et al. 2012).

To identify species' preference for habitat type or forest management type, we applied the indicator species analysis *IndVal* (Dufrene and Legendre 1997) by using the software *PC-ORD* (McCune and Mefford 1999). Species having an *IndVal* >20 % and a *p* value of <0.05 were considered as indicator species.

Factors affecting species richness

We carried out multi-model inference (MMI) and model average to evaluate the effect of the environmental and deadwood variables on species richness. We first log-transformed number of species and individuals to approach a normal distribution and standardized the variables to deal with collinearity among predictors (Schielzeth 2010) by dividing continuous variables by two standard deviation units, because binary predictors were involved in the models (Gelman et al. 2008). Then, we ran the model selection for three different datasets using the R Package *MuMIn* (Barton 2009). The first dataset contained four forest structure variables including basal area, number of small trees, number of big trees, and deadwood volume. The second dataset included deadwood volume and six different deadwood categories: logs, small logs, stumps, snags, fallen trees, and standing trees. To have comparable values among the plots, we calculated the percentage of each category dividing their absolute value by the total deadwood volume present in the plot. The third dataset was built using the variable deadwood volume and three deadwood decaying classes. Also in this case, the categories were calculated as the proportion between their absolute value and the deadwood volume in the plot. We also included the interactions between deadwood volume and decaying classes.

We ran linear mixed effect models (Pinheiro and Bates 2000) to explain saproxylic richness and abundance using the above mentioned variables as fixed effects and plot identity as random effect for each model selection.

We first ran a Multi-model inference to compare candidate models and ranked them according to the Akaike Information Criterion (Akaike 1985) corrected for small sample sizes (AICc) and their normalized Akaike weights (AICw) (Burnham and Anderson 2002), with the empirical rule of Richards (2005). When the candidate models differed in AICc by <2 units, we accepted the one with the lowest AICc as the best fit but considered other acceptable models in the discussion. We also compared the evidence ratio between the lowest AICc score and the one of interest

following the formula described in Burnham and Anderson (2002).

We applied a full model average method to calculate the relative weight of evidence for each predictor involved in the models by summing the model weights over all models in which each term appeared (Symonds and Moussalli 2011).

We applied the zero method model average, because the aim was to evaluate whether different factors have different effects on the response variables (Nakagawa and Freckleton 2011).

By performing a one-way ANOVA, we tested the effect of Tree decaying classes on saproxylic species richness and abundance. In order to be certain that deadwood volume (DWV) and its correlation with species richness wouldn't affect the results, we checked if DWV was balanced among the tree decaying classes using a one-way Anova test.

Then, we analysed the relationship between tree diameter, species richness, and abundance and between tree diameter and deadwood volume by performing a Spearman Rank Correlation test.

Amount of deadwood

We used two different approaches to determine the minimum volume and diameter of dead wood needed to conserve the maximum richness of saproxylic beetles. In the first approach, we applied the conditional inference tree (CIT) analysis (Müller and Hothorn 2004; Hothorn and Zeileis 2008). This method, available in the R package *party* (Hothorn et al. 2006), allowed us to find a species richness shift along a gradient of dead wood amount and diameter using deadwood volume and tree diameter as dependent variables. The lower limit of the range is extremely important because identify the minimum requirements for increasing saproxylic beetle richness (Müller and Büttler 2010). The split value is an indication of the optimal compromise between saproxylic conservation and deadwood harvesting and it might be called "the sustainable use of deadwood". The upper limit can be considered the quantity of deadwood needed to guarantee an improvement in the effects of saproxylic richness. Thus, different values can be chosen on the basis of different management requirements.

In the second approach, we first calculated the regression curves describing the relationship between species richness and two dependent variables: deadwood volume and tree diameter.

Then, we identified as a cut-point (threshold) of deadwood volume, the asymptote reached by the curve that corresponds to an incremental change in species richness <5 % with the addition of two more samples (Milanesi et al. 2012).

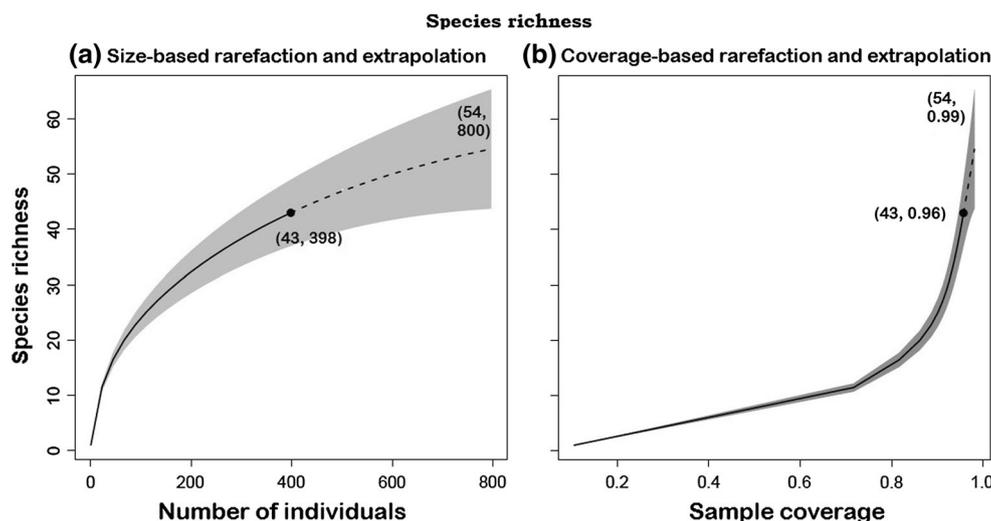


Fig. 2 **a** Size-based rarefaction curve (*solid line*) and extrapolation (*dashed line*) up to twice the saproxylic species actually collected. **b** Coverage-based rarefaction curve and extrapolation curve. The *shaded area* is the 95 % confidence interval based on a bootstrap method with 100 replications. Reference samples are indicated by

In both of the approaches, we calculated a 95 % confidence band using a bootstrap sampling method with 1,000 replicates to statistically underline the uncertain range of the threshold value, which is very useful for management actions (Roff 2006).

Results

Saproxylic beetles

We found a total of 398 individuals from 43 obligate saproxylic beetle species (see Table 5 in “Appendix”).

Sample-size based rarefaction curve of the whole dataset did not reach an asymptote but the slope of the curve is small indicating that the sampling is nearly complete and most of the species are represented. As shown in Fig. 2, an extrapolate estimate of species richness at twice the sampling effort (794 individuals) would lead to an increasing of only 11 more species. These species might be extremely rare and difficult to detect as underlined by the coverage – based rarefaction curve. In this figure we can see that our sampling effort reach almost the maximum coverage, with an estimate sample completeness of 96 % (SE = 0.3 %) and a coverage deficit of 4 %. This value indicates that the 4 % of the individuals in the community belongs to the 11 species not detected by the sample.

The three habitat type, as well as the two management type forests, have nearly identical sample coverage values (Fig. 3) implying they are equally complete. Therefore the raw data by themselves can be directly compared (Chao and Jost 2012). Species richness didn’t differ among the three habitat types

solid black dots and in parentheses the x- and y-axis coordinates. The sample size is equal to 398 individuals corresponding to sample coverage of 0.96 (**b**). A double sample size (800 individuals) corresponds to an increasing of 11 more species (**a**) and an increasing in sample coverage of 3 % (**b**)

(PERMANOVA test: Pseudo-F = 3.280; $p = 0.072$) while it was significantly higher in unmanaged forests (PERMANOVA test: Pseudo-F = 1.331; $p = 0.001$) (Table 2). The species indicator analysis revealed 5, 4 and 2 species with a significant indicator value respectively for *Populus*, *Quercus* and *Alnus* forests and 8 and 3 species with a significant indicator value respectively for unmanaged and managed forests (Table 3).

Factors affecting species richness

Multi model inference for the forest structure dataset showed that the best predictor model included only the deadwood volume variable which was positively and significantly related to species richness (Table 4, and in “Appendix” Table 6). The second structure variable, in order of importance, was the big trees which was negatively, but not significantly, related to species richness. Considering the effect of deadwood volume categories on saproxylic richness, the multi model inference showed that the best model included deadwood volume, small logs volume, and stumps volume (Table 4). Deadwood volume was positively related to species richness, and it was the only variable that showed a strong and significant effect on species richness; small logs and stumps are the second and third variable in order of importance and had respectively a negative and positive effect (Table 6 in “Appendix”). Finally, by investigating the effect of the three deadwood volume decaying classes on species richness, we found that the best model included both deadwood volume and the third decaying class (Table 4). The two explanatory variables were both positively related to species richness, but only deadwood volume was significant (Table 6 in “Appendix”).

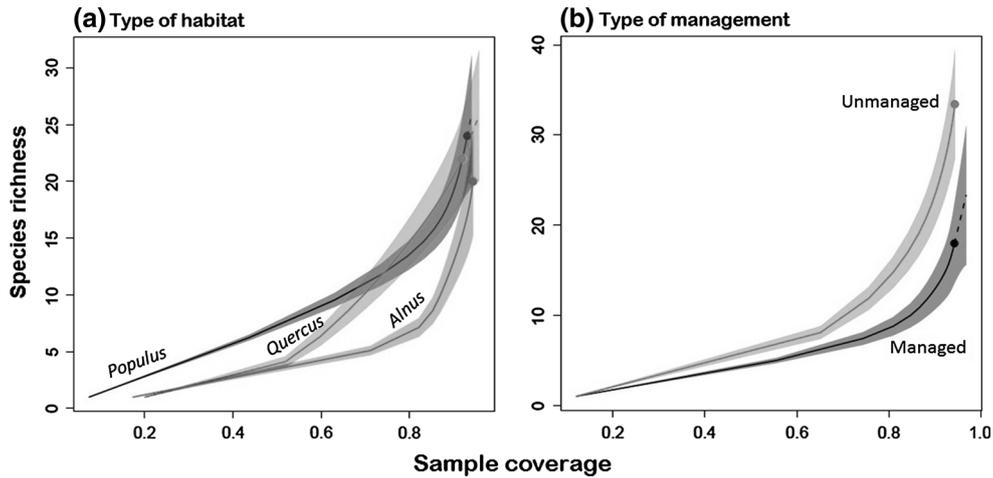


Fig. 3 Comparison of saproxylic species richness among **a** the three habitat types: *Populus*, *Quercus* and *Alnus* forests and **b** between managed and unmanaged forests. The figures show coverage-based rarefaction and extrapolation curves with 95 % confidence interval based on a bootstrap method with 100 replications (shaded areas).

Reference samples are indicated by solid black dots. The sample coverage reaches **a** the 0.93, 0.91, 0.94 in *Populus*, *Quercus* and *Alnus* forest respectively and **b** 0.94 in both managed and unmanaged forests

Table 2 Total number of species and individuals observed (Tot. obs.) in each forest type and mean number of species and individuals collected in each plot

Categories	Forest type	N species			N individuals		
		Tot. obs.	Mean/plot	SD	Tot. obs.	Mean/plot	SD
Habitat type	<i>Populus</i>	24	4.92	±3.20	141	12.25	±8.74
	<i>Quercus</i>	22	3.64	±2.24	107	8.91	±8.82
	<i>Alnus</i>	20	4	±2.25	150	12.5	±12.61
Forest management	Managed	18	3.06	±2.23	153	8.17	±7.70
	Unmanaged	34	5.41	±2.45	245	14.59	±11.48

Table 3 The preference of single species for one of the three habitat types and for managed or unmanaged forests: only species with IndVal (IV) >20 % and $p < 0.05$ are shown

Species	IV <i>Populus</i>	IV <i>Quercus</i>	IV <i>Alnus</i>	IV Managed	IV Unmanaged
<i>Aegomorphus clavipes</i>	33.33				
<i>Valgus hemipterus</i>	42.97				30.79
<i>Silvanus unidentatus</i>	33.22				
<i>Bitoma crenata</i>	46.33				35.35
<i>Rhopalocerus rondanii</i>	23.48				44.7
<i>Driophytorus corticalis</i>		32.54			57.95
<i>Epurea guttata</i>		41.28			
<i>Oxylaemus cylindricus</i>		36.84			
<i>Melanotus villosus</i>		21.74			45.45
<i>Calambus bipustulatus</i>		48.2			
<i>Pychnomerus terebrans</i>					32.15
<i>Aeletes atomarius</i>					24
<i>Cryptolestes duplicatus</i>					23.05
<i>Dorcus parallelepipedus</i>			43.99		
<i>Corticeus unicolor</i>			25	37.36	
<i>Cetonia aurata</i>				28.27	
<i>Hylis sp</i>				23.66	

Table 4 Model selection with Akaike's information criterion corrected for small sample size (*AICc*) for the three datasets

	K	AICc	$\Delta AICc$	wi	Evidence ratio
<i>Forest structure</i>					
B_TREE + BAS_A + DWV + S_TREE + B_TREE*DWV + BAS_A*DWV + DWV*S_TREE	9	17.5	11.22	0	273.14
Null model (intercept model only)	2	12.48	6.25	0.01	22.76
DWV	3	6.22	0	0.16	1
B_TREE + DWV	4	6.47	0.24	0.15	1.13
B_TREE + BAS_A + DWV	5	7.38	1.15	0.09	1.78
<i>Dead wood volume category</i>					
DWV + ST + LO + FTR + S+SLO + STR + DWV*ST + + DWV*LO + DWV*FTR + DWV*S + DWV*SLO + DWV*STR	13	29.78	24.19	0.00	178,974.7
Null model (intercept model only)	2	12.48	6.89	0.00	31.34
DWV +ST + SLO	5	5.59	0.00	0.04	1
DWV + SLO	4	5.93	0.33	0.03	1.17
DWV + SLO + DWV*STR	5	6.15	0.56	0.03	1.32
<i>Dead wood volume decaying class</i>					
DWV + DC1 + DC2 + DC3 + DWV*DC1 + DWV*DC2 + DWV*DC3	7	12.31	8.02	0.00	55.14
Null model (intercept model only)	2	12.48	8.19	0.00	60.03
DWV + DC3	4	4.29	0.00	0.19	1
DWV + DC2	4	4.85	0.56	0.15	1.32
DWV	3	6.22	1.93	0.08	2.62

Full and null models are presented with the three best models considered for each analysis. Selected models are shown in bold

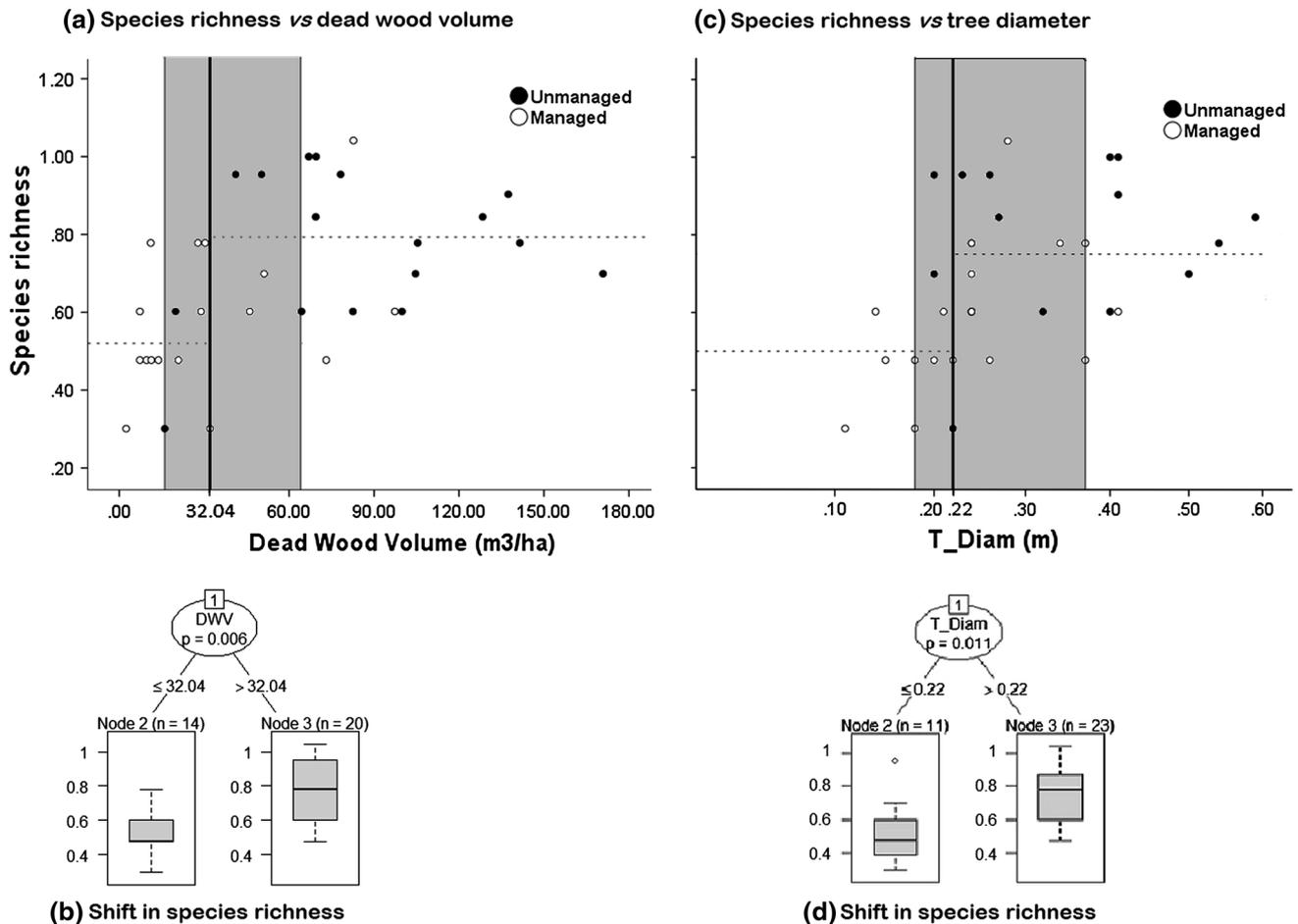


Fig. 4 Threshold for saproxylic beetles. Scatterplots in figures (a–c) show species richness versus dead wood volume (a) and versus dead wood diameter (c). The vertical line indicates the threshold value of deadwood volume and diameter for the maximum difference in species richness with a 95 % confidence interval (gray shading,

calculated using 1,000 bootstraps). Plots in figures b–d show a shift in species richness at 32.04 m³/ha (b) and at 22 cm diameter (d). The two classes obtained (nodes labelled 2 and 3), differ significantly in species richness ($p = 0.006$ for deadwood volume; $p = 0.011$ for diameter)

Saproxylic species richness was also affected by tree diameter with higher number of species in trees with bigger diameters ($r_s = 0.51, p < 0.01, n = 36$). On the contrary, no correlation was found between tree diameter and species abundance ($r_s = 0.302, p = 0.08, n = 36$).

a shift of species richness at 0.22 m diameter ($p < 0.01$) and a confidence interval comprised between 0.18 and 0.37 cm (Fig. 4). The relationship between deadwood diameter and species richness is better explained by the linear regression function $Y = 2.44x + 0.41$ ($R^2 = 0.19; F_{1,34} = 15.455; p < 0.01$) while the relationship between deadwood volume and species richness is better explained by the logarithmic function $Y = 0.25 + 0.11 * \log x$ ($R^2 = 0.33; F_{1,34} = 7.743; p < 0.001$). In this case, the curve approached an asymptote when dead wood volume was 35 m³/ha with a confidence interval comprised between 33 and 40 m³/ha (Fig. 5).

We also analysed the effect of tree decaying classes on saproxylic species richness and abundance, and we found no difference among the three decaying classes ($F_{2,34} = 0.43, p = 0.65$; species richness; $F_{2,34} = 0.30, p = 0.74$; species abundance).

Amount of deadwood

When we applied the Conditional Inference Tree between species richness and deadwood volume, we found a threshold value of 32.04 m³/ha ($p < 0.01$) with a confidence interval comprised between 16.09 and 64.09 m³/ha (Fig. 4). Moreover, applying the Conditional Inference Tree to species richness with tree diameter as predictor, we found a threshold value with

Discussion

Saproxylic beetles

Despite the relatively low number of species caught by eclector traps compared to the other most commonly used

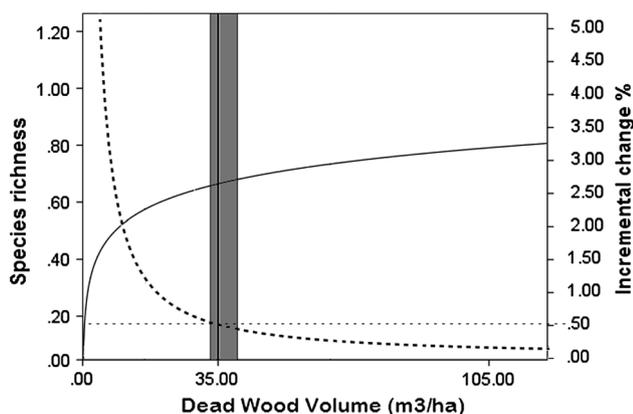


Fig. 5 Deadwood threshold for saproxylic beetles corresponding to an incremental change of 5 % in species richness. The *dashed curve* is the incremental change, while the *solid curve* is the species richness. The *vertical line* indicates the threshold value of 35 m³/ha for a 5 % incremental change in species richness with a 95 % confidence interval (*gray shading*)

traps (Schiegg 2000; Ranius and Jansson 2000; Wikars et al. 2005), this method was strongly informative at the within-site level, and the resulting information was useful for describing the influence of local and microhabitat environmental factors to saproxylic species. We identified some species which are good indicators of a specific habitat, such as *Rhopalocerus rondanii* (Zoopheridae) and *Oxylaemus cylindricus* (Bothrideridae), both rare and with a limited distribution (Franc 1997; Schlaghamerský 2000), which showed a significant association respectively for poplar and oak forests. We also found that some species considered as generalists in the literature (Audisio 1993; Méndez and Quirós 2005) such as *Valgus hemipterus* (Scarabeidae), *Epurea guttata* (Nitidulidae), and *Dorcus parallelipedus* (Lucanidae), in our study showed a significant tendency to be associated with a specific habitat: respectively for poplar, oak, and alder forests.

Our results support the view that two distinct communities exist with respect to silvicultural practices. In managed forests where deadwood is regularly removed, we found a restricted number of species all common and generalist (Hurka 2005, Carpaneto, *pers. comm.*) such as *Cetonia aurata* (Scarabeidae) and *Corticium unicolor* (Tenebrionidae); conversely, in the mature and well-preserved woodlands there was a significantly greater number of common and generalist species such as *V. hemipterus*, *Bitoma crenata*, and *Melanotus villosus* but also some rare and specialist species such as *R. rondanii* and *Pycnomerus terebrans* (both Zopheridae), which are highly linked to veteran trees (Schlaghamerský 2000). We also found a rare but generalist species such as *Aletes atomarius* (Histeridae) (Penati *pers. comm.*). The higher values for the species richness and abundance of unmanaged forests are in accordance with the results of other study cases (e.g. Müller et al. 2008).

Factors predicting species richness

Multi model inference seems to be a suitable method for disentangling the source of variation due to the intertwined factors affecting species richness. It focuses on the variance explained by each variable included in the model rather than on significant relationships between a response variable and its possible predictors. Therefore, by evaluating the weight of each variable, it is possible to better understand the ecological mechanisms driving variation in saproxylic species richness to allow for the proper setup of more specific management measures. We found that the amount of deadwood present is the main factor affecting saproxylic species richness in a forest when expressed as both volume and size while the other deadwood and environmental components influence saproxylic beetles to a lesser extent. Interactions among deadwood volume and variables in the three datasets were never significant, emphasizing how the relative importance of the variables found in the model-inference and model average was not derived by a possible cumulative effect with deadwood volume.

Among the forest structure variables, our study pointed out the negative effect of living trees with a diameter more than 10 cm on species richness. Although the presence of big trees in a forest is an index of a mature biotope, it also causes reduced exposure to sunlight, which is not an optimal condition for many saproxylic beetles (Kaila et al. 1997; Martikainen 2001) especially for the species dwelling in oak and Eurasian aspen (*Populus tremula*) forests (Franc 2007; Franc and Götmark 2008).

Our model selection procedure suggested that volumes of small logs and stumps are the main categories that have an effect on species richness, and their effect works in opposite directions. Generally, forests with a high amount of small logs are young and, therefore, it is expected to have a low amount of all the others categories of deadwood with, consequently, a low number of saproxylic species. The only category positively correlated to species richness is the amount of stumps. This finding contrasts with previous studies in which stumps were directly correlated with the intensity of management and, consequently, with a reduced volume and diversity of deadwood which leads to a lower number of saproxylic species (Ehntröm 2001; Sitonon et al. 2000). However, as described by Brin et al. (2011), the repeated provision of stumps in managed stands may favor species able to breed in both logs and stumps, thus, accentuating the loss in log-specific fauna but not in the overall number of species. Moreover, stumps, because of their similarity to snags for being partially underground and having roots, and to logs, because of their smaller size and their contact to the ground level, could contribute to maintaining some degree of persistence and continuity for deadwood in managed forests (Hjälten et al. 2007). Despite

the importance of stumps as described above, only five national inventories in Europe take stumps into consideration, and Italy is not one of those countries (Rondeux and Sanchez 2010).

The importance of decomposition classes for saproxylic species richness is another variable which should be taken into account for forest management but has been neglected so far. There is controversial and confusing information available and not many relevant publications on this topic (Jonsell 2008; Lassauce et al. 2011). Our MMI model suggests that a trend towards increasing species richness could be strengthened by the decay stages of deadwood in the surroundings, with positive effects of the later stages.

Amount of deadwood

Some studies have highlighted the role of threshold ranges and have also proposed several management measures, but they focus exclusively on deadwood volume (Müller et al. 2010). In our analysis, we found a threshold range for both deadwood volume and tree diameter. When log diameter is below 18 cm and deadwood volume is $16 \text{ m}^3/\text{ha}$, saproxylic beetle fauna will be seriously underrepresented. A sustainable use of deadwood would be reached at $35 \text{ m}^3/\text{ha}$, leaving in the forest all the dead trees with a diameter not smaller than 22 cm. Moreover at $35 \text{ m}^3/\text{ha}$, the number of species starts to increase $<5 \%$, thus, a further increase in deadwood doesn't entail a stronger growth of species number. Species richness continues to increase up to the upper limit, although at a lower rate. Pignatti et al. (2009) reported the estimates produced by the Italian National Inventory of Forests and Forests Carbon Sinks for the amount of deadwood in Italian forests (INFC), which is $8.8 \text{ m}^3/\text{ha}$. They also indicate that 76 % of the forests have standing dead trees with a diameter $<10 \text{ cm}$ and 96 % have a diameter $<20 \text{ cm}$. It means that for a large part of the Italian forests, saproxylic species richness will decrease.

Some local exceptions to this national scenario exist as is the case of some unmanaged fluvial forests (with *S. alba* and *Q. robur*) in the Central Appennines surveyed by Lombardi et al. (2008), where the mean deadwood volume reported is 30.1 and $56.3 \text{ m}^3/\text{ha}$ (respectively), and Bosco Fontana, a lowland forest in the Po Plain in which the mean deadwood volume is $64.26 \pm 51.69 \text{ m}^3/\text{ha}$ (Travaglini et al. 2007). Also the Ticino valley National Park hosts some unmanaged floodplain forests with an estimated deadwood volume upper then $64 \text{ m}^3/\text{ha}$ such as the Integral Nature Reserve “Bosco Siro Negri one of our sampling site (BN10) with a mean deadwood volume of $112 \text{ m}^2/\text{ha}$ ”. The Reserve, established in 1973, is characterized by the presence of unmanaged riparian mixed forests dominated by *Q. robur* which covered a large part of the Po Valley before the Romans (Perracino 2010).

Conclusions

The development of guidelines for deadwood management is contingent on a better understanding of the relationship between deadwood variables and saproxylic richness. This is the first study which quantifies the effect of deadwood harvesting in the managed floodplain forests of northern Italy and to suggest a sustainable use of deadwood by simultaneously analysing both deadwood quality and quantity. Among these forests, those in which the removal of dead wood has not been practiced for at least 20 years harbour not only a higher number of saproxylic species, but also higher species diversity with both generalist and specialist saproxylic beetles. We demonstrated that a sustainable use of deadwood is possible. We found that the amount of deadwood and the diameter of the trees are the most important aspects affecting saproxylic species richness, and they both need to be considered for deadwood management. Promoting an increase in deadwood volume without an indication of the size of trees and logs to be left in a forest is not enough for ensuring the saproxylic conservation. All the other factors, such as deadwood type or deadwood stage of decay, have a secondary effect but should be still considered for correct policy management. Stumps, for example, were shown to be important for saproxylics as they play a key role in the survival of many species (Hjälten et al. 2007). Management guidelines could oversee a programmed cutting of trees for the creation of artificial stumps to assure a continuity of deadwood. Finally, additional conservation measures for forests subjected to deadwood harvesting are to prolong rotation times to assure the presence of deadwood at intermediate/late stages of decay.

Acknowledgments We would like to thank the Fondazione CARIPLO and the Ticino Park (Parco Lombardo della Valle del Ticino) for funding our research. Francesco Sartori generously supported part of the research which was carried out inside the Riserva Naturale Integrale “Bosco Siro Negri” through a fund from the Italian Ministry for the Environment (Ministero dell’Ambiente e della Tutela del Territorio e del Mare) and authorized us to carry out the research within the integral reserve. Marco Bardiani, Fabio Mazzocchi, Emma Minari, and Liana Fedrigoli, belonging to the Centro Nazionale Biodiversità Forestale “Bosco Fontana” di Verona, for their help on trap design and forest structure surveys. Marco Sutti for his help in collecting environmental variables. We thank all the experts who helped us with beetle determination: Maurizio Pavesi, Michele Zilioli, and Fabrizio Rigato from the Natural History Museum of Milan; Paolo Audisio; Giuseppe Carpaneto; Giuseppe Platia; Gianfranco Salvato; Fabio Penati; Paolo Cornacchia; Enzo Colonnelli; Claudio Canepari; Carlo Pesarini; Wolfgang Rucker. I also thank Nicklas Jansson for his suggestions on saproxylic beetle ecology at the beginning and during this research project, and Pietro Milanesi for the statistical analysis suggestions and for reviewing the final version of this manuscript.

Appendix

See Tables 5 and 6.

Table 5 List of the saproxylic species collected

Saproxylic species	<i>n</i>	Populus forests		Quercus forests		Alnus forests	
		Unmanaged (BN21)	Managed (BN1)	Unmanaged (BN10)	Managed (BN5)	Unmanaged (V1)	Managed (V2)
Total species	43	18	17	19	10	14	8
<i>Total individuals</i>	398	69	72	85	22	91	59
Histeridae	2	1	2	1	1	1	1
<i>Aeletes atomarius</i>	2		2				
<i>Paromalus flavicornis</i>	43	6	3	4	1	18	11
Zopheridae	4	3	1	2	1		
<i>Pychnomerus terebrans</i>	1			1			
<i>Bitoma crenata</i>	9	6	3				
<i>Rhopalocerus rondanii</i>	11	8		3			
<i>Colobicus hirtus</i>	2	1			1		
Curculionidae	1			1			
<i>driophytorus corticalis</i>	2			2			
Anthribidae	2			1			1
<i>Platystomos albinus</i>	1						1
<i>Phaenotherion fasciculatum</i>	1			1			
Elateridae	6			4		3	1
<i>Melanotus villosus</i>	1			1			
<i>Cardiophorus anticus</i>	1					1	
<i>Ampedus pomorum</i>	3			2		1	
<i>Ampedus pomonae</i>	1					1	
<i>Laeon punctatus</i>	4			2		1	2
<i>Calambus bipustulatus</i>	1			1			
Melasidae	2		1				1
<i>Melasis buprestoides</i>	1						1
<i>Hylis sp</i>	1						
Lissomidae	1		1				
<i>Drapetes mordelloides</i>	1						
Latridiidae	1	1	1	1	1	1	1
<i>Enicmus rugosus</i>	17	9	2	1	2	3	
Mycetophagidae	1	1	1	1	1	1	1
<i>Litargus conexus</i>	9	1	1	4	1	2	
Cerambycidae	4	2	2	1	1	1	1
<i>Aegosoma scabricorne</i>	14		5		2		
<i>Aegomorphus clavipes</i>	2	2					
<i>Neoclytus acuminatus</i>	1	1					

Table 5 continued

Saproxyllic species	n	Populus forests		Quercus forests		Alnus forests	
		Unmanaged (BN21)	Managed (BN1)	Unmanaged (BN10)	Managed (BN5)	Unmanaged (V1)	Managed (V2)
<i>Xylotrechus rusticus</i>	18		18				
Scarabeidae	2	1	2				
<i>Cetonia aurata</i>	1		1				
<i>Valgus hemipterus</i>	12	10	2				
Lucanidae	1	1	1	1	1	1	1
<i>Dorcus parallelepipedus</i>	86	4	23	9	1	37	12
Nitidulidae	2		1		2	1	
<i>Epurea guttata</i>	7		3		1	3	
<i>Epurea aestiva</i>	1				1		
Laemophleidae	2	1		2		1	
<i>Cryptolestes duplicatus</i>	3			3			
<i>Placonotus testaceus</i>	5	1		3			1
Erotylidae	1	1			1		
<i>Dacne bipustulata</i>	3	1			2		
Silvanidae	3	2	1	2		2	
<i>Silvanus unidentatus</i>	5	4				1	
<i>Silvanus bidentatus</i>	1			1			
<i>Uleiota planatus</i>	19	11	4	3		1	
Monotomidae	2	2		1	1	1	1
<i>Rhizophagus bipustulatus</i>	74	6		38	4	17	9
<i>Monotoma longicollis</i>	1	1					
Tenebrionidae	6	2	3	1		2	1
<i>Prionychus sp.</i>	1					1	
<i>Diachina fagi</i>	2	1	1				
<i>Diaperis boleti</i>	1		1				
<i>Stenomax aeneus</i>	2	2					
<i>Corticium unicolor</i>	25					3	22
<i>Uloma culinaris</i>	2		1	1			

For each forest the number of species (bold) and the number of individuals per species (italics) is given

Table 6 Parameter estimates of fixed effects for selected models

	Estimate	SE	Adjusted SE	z value	<i>p</i> (z value)	RVI
<i>Forest structure</i>						
(Intercept)	1.556	0.042	0.044	35.24	<2e−16***	
DWV	0.225	0.093	0.097	2.331	0.019*	0.92
B_Tree	−0.191	0.108	0.112	1.704	0.088	0.67
Bas_A	−0.122	0.110	0.114	1.066	0.286	0.4
Bas_A:DWV	−0.331	0.237	0.247	1.341	0.179	0.31
S_Tree	−0.091	0.097	0.101	0.905	0.365	0.14
B_Tree:DWV	−0.078	0.213	0.222	0.346	0.729	0.11
DWV:S_Tree	−0.054	0.209	0.218	0.250	0.803	0.04
<i>Dead wood volume category</i>						
(Intercept)	1.559	0.041	0.043	36.053	<2e−16***	
DWV	0.234	0.093	0.096	2.421	0.0155*	0.93
SLO	−0.274	0.229	0.233	1.171	0.241	0.70
ST	0.144	0.094	0.098	1.470	0.142	0.51
LTR	−0.149	0.288	0.292	0.510	0.609	0.34
LO	0.159	0.218	0.223	0.712	0.476	0.32
S	0.100	0.094	0.097	1.025	0.305	0.32
STR	−0.123	0.191	0.195	0.634	0.526	0.30
DWV*SLO	0.243	0.227	0.236	1.031	0.302	0.19
DWV*STR	−0.120	0.120	0.125	0.959	0.337	0.06
DWV*CS	0.051	0.286	0.297	0.172	0.863	0.06
DWV*FTR	0.124	0.218	0.224	0.555	0.578	0.05
DWV*S	−0.239	0.305	0.319	0.752	0.4520	0.05
DWV*LO	0.009	0.382	0.393	0.023	0.981	0.03
<i>Dead wood volume decaying class</i>						
(Intercept)	1.557	0.041	0.042	36.320	<2e−16***	
DWV	0.276	0.085	0.089	3.091	0.001**	0.98
DC 3	0.164	0.095	0.099	1.654	0.098	0.60
DC2	−0.167	0.105	0.108	1.539	0.123	0.53
DC1	−0.043	0.121	0.124	0.352	0.724	0.38
DWV*DC3	−0.088	0.214	0.223	0.395	0.693	0.12
DWV*DC2	0.033	0.182	0.190	0.178	0.859	0.10
DWV*DC3	0.032	0.171	0.178	0.184	0.853	0.07

Variables are standardized (z)

p* < 0.05; *p* < 0.01;****p* < 0.001

References

- Akaike H (1985) Prediction and entropy. In: Atkinson AC, Fienberg SE (eds) A celebration of statistics. Springer, New York, pp 1–24
- Albrecht L (1990) Grundlagen, Ziele und Methodik der waldökologischen Forschung in Naturwaldreservaten. Schriftenreihe Naturwaldreservate in Bayern 1. München, Germany
- Alexander KNA (2004) Revision of the index of ecological continuity as used for saproxylic beetles. English Nature Research Report 574. English Nature, Peterborough
- Alinvi O, Ball JP, Danell K, Hjäältén J, Pettersson RB (2007) Sampling saproxylic beetle assemblages in dead wood logs: comparing window and elector traps to traditional bark sieving and a refinement. *J Insect Conserv* 11(2):99–112
- Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecol* 26:32–46
- Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E, Plymouth
- Audisio P (1993) Fauna d'Italia XXXII. Coleoptera Nitidulidae—Kateretidae. Calderini, Bologna
- Barton K (2009) MuMIn: multi-model inference. R package version 0.12.2/r18
- Bässler C, Förster B, Monin C, Müller J (2008) The BIOKLIM-Project: biodiversity research between climate change and wilding in a temperate montane forest. The conceptual framework. *Waldökologie, Landschaftsforschung und Naturschutz* 7:21–33
- Blasi C, Marignani M, Copiz R, Fipaldini M, Del Vico E (2010) Le Aree Importanti per le Piante nelle Regioni d'Italia: il presente e il futuro della conservazione del nostro patrimonio botanico. Progetto Artiser, Roma
- Bouget C, Brustel H, Zagatti P (2008) The French information system on saproxylic beetle ecology (FRISBEE): an ecological and

- taxonomical database to help with the assessment of forest conservation status. *Terre Vie-Rev Ecol* 10:33–36
- Brin A, Bouget C, Brustel H, Jactel H (2011) Diameter of downed woody debris does matter for saproxylic beetle assemblages in temperate oak and pine forests. *J Insect Conserv* 15:653–669
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York
- Buse J, Levanony T, Timm A, Dayan T, Assmann T (2010) Saproxylic beetle assemblages in the Mediterranean region: impact of forest management on richness and structure. *Forest Ecol Manag* 259:1376–1384
- Campanaro A, Hardersen S, Mason F (2007). Piano di gestione della Riserva Naturale Statale e Sito Natura 2000 “Bosco della Fontana”. Quaderni Conservazione Habitat, 4. Cierre edizioni, Verona
- Castellani C, Scrinzi G, Tabacchi G, Tosi V (1984) Inventario Forestale Nazionale Italiano. Tavole di cubatura a doppia entrata. MAF/ISAF, Trento
- Cavalli R, Mason F (2003) Techniques for re-establishment of dead wood for saproxylic fauna conservation. LIFE nature project NAT/IT/99/6245 Bosco della Fontana (Mantova, Italy). Gianluigi Arcari Editore, Mantova
- Chao A, Jost L (2012) Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology* 93:2533–2547
- Christensen M, Hahn K, Mountford EP, Ódor P, Standovar T, Rozenbergar D, Diaci J, Wijdeven S, Meyer P, Winter S, Vrska T (2005) Dead wood in European beech (*Fagus sylvatica*) forest reserves. *Forest Ecol Manag* 210:267–282
- Cindolo C, Petriccione B (2006) Progetto biosoil—biodiversity. Valutazione della biodiversità forestale sulla Rete sistemica di Livello I. Manuale Nazionale, Italia. Corpo forestale dello Stato, Roma
- Davies ZG, Tyler C, Stewart GB, Pullin AS (2008) Are current management recommendations for conserving saproxylic invertebrates effective? *Biodivers Conserv* 17:209–234
- Deuiffic P (2010) Du bois mort pour la biodiversité. Des forestiers entre doute et engagement. *Revue Forestière Française* 1(42):71–85
- Dufrene M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol Monogr* 67:345–366
- Franc V (1997) New records of Coreidae (Heteroptera) and Erotylidae (Coleoptera) from Slovakia. *Biologia*. Bratislava 52(5):662
- Franc N (2007) Standing or downed dead trees—does it matter for saproxylicbeetles in temperate oak-rich forest? *Can J For Res* 37:2494–2507
- Franc N, Götmark F (2008) Openness in management: hands-off vs partial cutting in conservation forests, and the response of beetles. *Biol Conserv* 141(9):2310–2321
- Gelman A, Pittau MG, Yajima M, Su YS (2008) An approximate EM algorithm for multilevel generalized linear models. Technical report, Department of Statistics, Columbia University
- Gibb H, Hjältén J, Ball JP, Atlegrim O, Pettersson RB, Hilszczański J, Johansson T, Danell K (2006) Effects of landscape composition and substrate availability on saproxylic beetles in boreal forests: a study using experimental logs for monitoring assemblages. *Ecogr* 29:191–204
- Grove S, Meggs J (2003) Coarse woody debris, biodiversity and management: a review with particular reference to Tasmanian wet eucalypt forests. *Aust For* 66:258–272
- Harmon ME, Franklin JF, Swanson FJ, Sollins P, Gregory SV, Latting JD, Anderson NH, Cline SP, Aumen NG, Sedell JR, Lienkaemper GW, Cromack K, Cummins KW (1986) Ecology of coarse woody debris in temperate ecosystems. *Adv Ecol Res* 15:133–299
- Hjältén J, Johansson T, Alinvi O, Danell K, Ball JP, Pettersson R, Gibb H, Hilszczański J (2007) The importance of substrate type, shading and scorching for the attractiveness of dead wood to saproxylic beetles. *Basic Appl Ecol* 8:364–376
- Hothorn T, Zeileis A (2008) Generalized Maximally Selected Statistics. *Biometrics* 64:1263–1269
- Hothorn T, Buhlmann P, Dudoit S, Molinaro A, Vander Laan M (2006) Survival ensembles. *Biostat* 7: 355–373. Johansson T, Gibb H, Hilszczański J, Pettersson RB, Hjältén J, Atlegrim O, Ball J.P., Danell K (2006). Conservation-oriented manipulations of coarse woody debris affect their value as habitat for spruce-infesting bark and ambrosia beetles (Coleoptera: Scolytinae) in northern Sweden. *Can J For Res* 36:174–185
- Johansson T, Gibb H, Hilszczański J, Pettersson RB, Hjältén J, Atlegrim O, Ball JP, Danell K (2006) Conservation-oriented manipulations of coarse woody debris affect their value as habitat for spruce-infesting bark and ambrosia beetles (Coleoptera: Scolytinae) in northern Sweden. *Can J For Res* 36:174–185
- Jonsell M, Weslien J, Ehnström B (1998) Substrate requirements of red-listed saproxylic invertebrates in Sweden. *Biodivers Conserv* 7:749–764
- Jonsson BG, Krusys N, Ranius T (2005) Ecology of species living on dead wood—Lessons for dead wood management. *Silva Fennica* 39:289–309
- Jost L (2010) The relation between evenness and diversity. *Diversity* 2:207–232
- Kaila L, Martikainen P, Punttila P (1997) Dead trees left in clearcuts benefit saproxylic Coleoptera adapted to natural disturbances in boreal forest. *Biodivers Conserv* 6:1–18
- Lassauce A, Paillet Y, Jactel H, Bouget C (2011) Deadwood as a surrogate for forest biodiversity: meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. *Ecol Indicators* 11:1027–1039
- Lombardi F, Lasserre B, Tognetti R, Marchetti M (2008) Deadwood in relation to stand management and forest type in Central Apennines (Molise, Italy). *Ecosystems* 11:882–894
- Martikainen P (2001) Conservation of threatened saproxylic beetles: significance of retained aspen *Populus tremula* on clear-cut areas. *Ecol Bull* 49:205–218
- Mason F (2004) Dinamica di una foresta della Pianura Padana. Bosco della Fontana—Primo contributo Monitoraggio 1995. Seconda edizione con Linee di gestione forestale. Gianluigi Arcari Editore, Mantova
- McCune B, Mefford MJ (1999) PC-ORD. Multivariate analysis of ecological data, version 4. MjM Software Design, Gleneden Beach, OR, USA
- McLean IFG, Speight MCD (1993) Saproxylic invertebrates—the European context. In: Kirby KJ, Drake CM (eds) Dead wood matters: the ecology and conservation of saproxylic invertebrates in Britain. *Eng Nat Sci* 7:21–32
- MCPFE (2003) Improved pan-European indicators for sustainable forest management as adopted by MCPFE expert level. Meeting 7–8 Oct 2002, Vienna, Austria
- Méndez M, Quirós AR (2005) Vida en la madera muerta: los escarabajos lucanidos de Cantabria. *Locustella* 3:9–18
- Milanesi P, Meriggi A, Merli E (2012) Selection of wild ungulates by wolves (*Canis lupus L. 1758*) in an area of the Northern Apennines. *Ethol, Ecol & Evol* 24:81–96
- Müller J, Büttler R (2010) A review of habitat thresholds for dead wood: a baseline for management recommendations. *Eur J Forest Res* 129:981–992
- Müller J, Hothorn T (2004) Maximally selected two-sample statistics as a new tool for the identification and assessment of habitat

- factors with an application to breeding-bird communities in oak forests. *Eur J Forest Res* 123:219–228
- Müller J, Müller AJ, Bussler H (2013) Some of the rarest European saproxylic beetles are common in the wilderness of Northern Mongolia. *J Insect Conserv* 17:989–1001
- Nakagawa S, Freckleton RP (2011) Model averaging, missing data and multiple imputation: a case study for behavioural ecology. *Behav Ecol Sociobiol* 65:103–116
- Nieto A, Alexander KNA (2010) European Red List of Saproxylic Beetles. Publications Office of the European Union, Luxembourg
- Oksanen J, Blanchet FG, Kindt R, Legendre R, Minchin PR, O'Hara RB et al (2012) *Vegan: community ecology package*. R Package Version 2.1-17 edn
- Olszewski TD (2004) A unified mathematical framework for the measurement of richness and evenness within and among multiple communities. *Oikos* 104:377–387
- Paillet Y, Bergès L, Hjältén J, Ódor P, Avon C, Bernhardt-Römermann M, Bijlsma RJ et al (2010) Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. *Cons Biol* 24:101–112
- Perracino M (2010) *Atlante dei SIC della Provincia di Pavia. Regione Lombardia e Fondazione Lombardia per l'Ambiente*, Milano
- Pignatti G, De Nadale F, Gasparini P, Paletto A (2009) Il legno morto nei boschi italiani secondo l'Inventario Forestale Nazionale. *Forest@* 6:365–375
- Pinheiro JC, Bates DM (2000) *Mixed Effects Models in S and S-Plus*. Springer-Verlag, New York
- Prigioni C (1995) Guidelines for the feasibility study of reintroduction of the otter *Lutra lutra* in Italy: the Project of the Ticino Valley (North-Western Italy). *Hystrix* 7:255–264
- Ranius T, Jansson N (2000) The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. *Biol Conserv* 95:85–94
- Richards SA (2005) Testing ecological theory using the information-theoretic approach: examples and cautionary results. *Ecology* 86:2805–2814
- Roff DA (2006) *Introduction to computer-intensive methods of data analysis in biology*. Cambridge University Press, Cambridge
- Rondeux J, Sanchez C (2010) Review of indicators and field methods for monitoring biodiversity within national forest inventories. Core variable: Deadwood. *Environ Monit Assess* 164:617–630
- Schiegg K (2000) Effects of dead wood volume and connectivity on saproxylic insect species diversity. *Ecosci* 7(3):290–298
- Schielzeth H (2010) Simple means to improve the interpretability of regression coefficients. *Met Ecol Evol* 1:103–113
- Schlaghamerský J (2000) The saproxylic beetles (Coleoptera) and ants (Formicidae) of Central European hardwood floodplain forests. *Folia Fac Sci Nat Univ Masaryk Brun* 103
- Schlaghamerský J (2003) Saproxylic invertebrates of floodplains, a particularly endangered component of biodiversity. In: Mason F, Nardi G, Tisato M, (eds) *Proceedings of the international symposium "dead wood: a key to biodiversity"*, Mantova
- Schmitt M (1992) Buchen-Totholz als Lebensraum für xylobionte Käfer. *Waldhygiene* 19:97–191
- Siitonen J, Martikainen P, Punttila P, Rauh J (2000) Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. *Forest Ecol Manag* 128:211–225
- Speight MCD (1989) *Saproxylic invertebrates and their conservation*. Strasbourg, Council of Europe, Nature and Environment Series 42, pp 81
- Symonds MRE, Moussalli A (2011) A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behav Ecol Sociobiol* 65:13–21
- Travaglini D, Botalico F, Brundu P, Chirici G, Minari E (2007) Sampling deadwood within Bosco della Fontana. In: Gianelle D, Travaglini D, Mason F, Minari E, Chirici G, Chemini C (eds) *Canopy analysis and dynamics of a floodplain forest*. Cierre Grafica Editore, Verona, pp 59–68
- Vallauri D, André J, Dodelin B, Eynard-Macher R, Rambaud D (2005). *Bois mort et à cavités. Un clé pour des forêts vivantes*. Tec and Doc (Ed), Paris
- Wikars L-O, Sahlin E, Ranius T (2005) A comparison of three methods to estimate species richness of saproxylic beetles (Coleoptera) in logs and high stumps of Norway spruce. *Can Entomol* 137(3):304–324