SAPROXYLIC BEETLE ASSEMBLAGES OF OLD HOLM-OAK TREES IN THE MEDITERRANEAN REGION: ROLE OF A KEYSTONE STRUCTURE IN A CHANGING HETEROGENEOUS LANDSCAPE

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RÉSUMÉ. — *Les assemblages de coléoptères saproxyliques des vieux chênes verts en région méditerranéenne: rôle d'une structure-clé dans un paysage hétérogène changeant.* — Une étude de la faune saproxylique a été conduite au printemps et en été dans un paysage méditerranéen soumis à des changements d'occupation des terres afin d'estimer l'influence relative de la composition paysagère *vs* les caractéristiques des arbres sur la biodiversité des coléoptères. La composition des assemblages d'espèces et le nombre de taxons échantillonnés sont apparus plus influencés par les caractéristiques des chênes verts que par la matrice paysagère environnante. Le nombre et le diamètre des troncs, le nombre de cavités et la quantité de bois mort visible étaient positivement corrélés soit avec le nombre total de taxons soit avec l'observation de taxons spécifiques. Les espèces méditerranéennes n'ont pas montré de préférence pour des environnements ouverts et les coléoptères mycétophages ne sélectionnaient pas particulièrement les conditions de boisements mésophiles. Nos résultats confirment le rôle déterminant des vieux arbres en tant que structures-clés pour la faune saproxylique mais jusqu'à présent ce rôle n'apparaît pas affecté par les changements paysagers résultant de l'abandon des terres. Cependant des pratiques spécifiques de gestion forestière demandent à être mises en œuvre afin de maintenir une population de vieux chênes verts en l'absence des pratiques traditionnelles d'occupation des terres qui les ont favorisés.
Mots-clés: Saproxyliques, *Quercus ilex,* modification du paysage, biodiversité.

SUMMARY. — A study of spring-summer saproxylic fauna was conducted in a Mediterranean landscape under land use change in order to estimate the relative influence of landscape composition vs tree characteristics on beetles' biodiversity. The composition of the species assemblages and the number of taxa sampled appeared more influenced by the characteristics of the sampled Holm oak trees than by the surrounding landscape matrix. The number and the diameter of trunks, the number of cavities and the quantity of visible dead wood were positively correlated either with the total number of taxa or with the observation of specific taxa. Mediterranean species did not show an overall preference for open surroundings, and mycetophagous beetles were not particularly selecting woody mesophilous conditions. Our results confirm the determinant role of old trees as keystone structures for the saproxylic fauna, but, up to now, this role does not seem to be affected by the changes in the landscape that resulted from land abandonment. However, specific forest management practices need to be implemented to maintain a population of old Holm oak trees in the absence of the traditional land use practices that favoured them.
Keywords: Saproxylic, *Quercus ilex*, landscape change, biodiversity.

The distribution of species and the structure of species assemblages depend on the characteristics of the local habitat, especially the availability of trophic resources, and on the surround-

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ing conditions providing or not connectivity among habitats. Measuring structural variables at specific spatial scales is critically important to understand the relationship between habitat heterogeneity and species diversity. The role of the different spatial scales will depend on how species perceive habitat heterogeneity. A species perception is likely to be controlled by its home range, its dispersal ability and by other habitat-specific spatial processes (Ranius, 2006). Tews *et al.* (2004) defined a 'keystone structure' as a distinct spatial structure providing resources, shelter or 'goods and services' crucial for other species. For example, dead wood in mixed beech-spruce forests may be a keystone structure, as the removal of this structure (through e.g. forest management) would significantly reduce saproxylic insect diversity (Schiegg, 2000). They suggest that biological diversity in these 'keystone structure ecosystems' may be more vulnerable than in multi-structured systems, as a reduction in quality or the loss of this structure induces severe consequences for a high proportion of taxonomic groups. On the other hand, many studies showed how the quality of the landscape matrix can affect the relationship between habitat heterogeneity and species diversity for various taxonomic groups (Dauber *et al*., 2003; Dunford & Freemark, 2004). Landscape characteristics are known to impact both local habitat quality and metapopulation dynamics. In the present context of land use change, landscape characteristics surrounding keystone structures are likely to evolve quickly which could affect how keystone structures function. Understanding the respective roles of keystones structures and landscape matrix is of particular interest, especially for species dependent upon keystone structures and distributed in highly heterogeneous landscapes.

The present work addresses this question by studying the distribution of saproxylic beetles, insects sensitive to stand conditions and characteristic of veteran trees (Key & Ball, 1993; Ball & Key, 1997; Franc, 1997; Grove, 2002; Brustel, 2004a; Jonsson *et al*., 2005), within a changing Mediterranean landscape characterized by a high spatial heterogeneity (Blondel & Aronson, 1999). Old Holm oak trees (*Quercus ilex*) are a typical feature in this context and of interest for the study of saproxylic beetles. Due to the recent land abandonment in the Mediterranean region, old Holm oak trees can now be found imbedded in a gradient of habitats that ranges from grassland to Holm oak woodland, with an intermediate stage consisting of shrublands. We expect saproxylic assemblages to be strongly affected by the nature of the context. We expect trees surrounded by woodlands to be in a context of increased wood availability and in a context of increased moisture and decreased climatic contrast (extension of mesophilous conditions) (Ranius & Jansson, 2000; Brin & Brustel, 2006). The relative importance of the presence of keystone structures and of the nature of the landscape matrix will be deduced from an analysis at two scales: that of the keystone structure (structure of old Holm oak trees) and the landscape scale (vegetation cover within 0.2 ha around the trees).

We addressed three main questions: (i) Does landscape type impact tree structure and insect species richness? (ii) What is the role of specific tree morphology variables or of the surrounding vegetation cover to explain insect species richness? (iii) What are the respective roles of tree morphology and vegetation cover to explain insect community composition?

MATERIAL AND METHODS

STUDY SITE

The study site was situated in the Pic Saint-Loup area, 20 km north of Montpellier (southern France) (43°47'N, 03°50'E). It covers a 2 km N-S x 2 km E-W karstic limestone plateau with south facing slopes and altitude ranging from 260 to 350 m. The climate is Mediterranean, with moist and cold winters. The annual average rainfall ranges from 950 to 1350 mm, average maximum temperature during the warmest month is 28°C and average minimum temperature during the coldest month is -1°C (Debussche & Escarre, 1983).

Until the middle of the 20th century grasslands were extensive in the study area. The shrublands were used for grazing sheep (meat production) and for the production of juniper oil. The oak woodlands were coppiced at 30 year intervals for charcoal (Debussche *et al*., 1987). The last peak of intensive use occurred during World War II in response to the need to produce meat (mutton) and charcoal for the inhabitants of the nearby city of Montpellier. Around the 1960s a period of rapid land abandonment started, with a decrease in the proportion of the study area used for grazing and a decrease in the sheep density from 1 sheep/ha to 0.25 sheep/ha in the areas still grazed (Larinier, 2003). Old trees, especially Holm Oak (*Quercus ilex*), were traditionally used as landmarks (isolated or aligned within or between fields and pastures) but also to provide shade and food supply (leaves and acorns) for livestock as well as wood for shepherds. Similarly to what occurred for other landscape components (e.g. water point, low walls), old trees disappeared or became surrounded by more complex vegetation structures during the last decades. After the 1980s, new land uses appeared on limited areas, especially bull and horse grazing in enclosures (Larinier, 2003). As a result, old Holm oak trees remained either isolated within grazed herbaceous plots, or became imbedded in shrubland or woodland.

Selection and characterization of the structure of the trees sampled

Aerial pictures from 1946 complemented by a field survey allowed to identify old Holm oak trees (*Quercus ilex*) and to define the landscape type in which the trees were located. We sampled 10 trees in grassland, 10 in shrubland and 8 in woodland (Fig. 1).

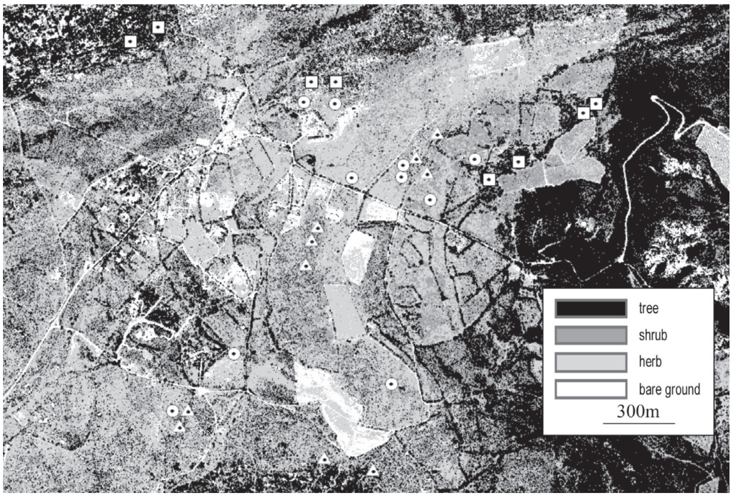

Figure 1. — Vegetation map for 2002 and localization of sampled trees (⊙= grassland, △= shrubland, ⊡ = forest).

To characterize Holm oak tree structure, we used 14 variables: the height (m), the width of the crown (m), the number of trunks (past coppicing practices), the mean height of trunk(s), the mean diameter of trunk(s) (measured just under the enlargement due to main branches insert), the number of main branches (directly inserted on the trunk), the number of shoots, the number of cavities in the trunk(s), the state of the trunk(s) (healthy = 1, decayed = 2, hollow = 3), the percentage of dead wood outside the crown, the percentage of dead wood inside the crown, the number of large pieces (diameter > 0.2 m) of dead wood within the crown, the cumulated length (m) of large pieces (diameter > 0.2 m) of dead wood on the ground and the number of large pieces (diameter > 0.2 m) of dead wood on the ground (Appendix 1).

Characterization of the landscape matrix

To characterize the landscape matrix surrounding sampled trees, we used infra-red aerial photographs taken in 2002. Photographs were ortho-rectified and geo-referenced to Lambert Conformal Conic system with a spatial resolution of 0.7 m in ENVI 4.0 (RSI Research Systems, 1996). We used a pixel classification of the aerial photographs (pixel size = 0.7 x 0.7 m) with four pixel classes: BARE GROUND (little or no vegetation), HERB (herbaceous vegetation), SHRUB (woody vegetation 0.5-2.5 m) and TREE (woody vegetation>3 m). We used a maximum-likelihood supervised method (Campbell, 1996) in ENVI to assign each pixel in the study area to one of the 4 pixel classes (Fig. 1). We tested the accuracy of the classification with a confusion matrix comparing ground truthed pixel classification to photographic based pixel classification for a test data set (around 5000 pixels) and obtained a kappa coefficient of 0.83, showing a good accuracy of the classification. Finally, we calculated the proportion of the 4 pixel classes within 25 m around each sampled tree.

Sampling of beetles

Each tree was equipped with one cross-vanes window flight trap (Polytrap™: Brustel, 2004b) from May 17th to July 11th 2005. Traps were hanged to intercept beetles flying within the crown at the top of the trunk. Insects were collected weekly and pooled to form one sample per tree. Individuals were identified at the species level except for Ciidae (one specimen), Malachiidae and Staphylinidae. We did not take into account these two last families in the study because each one corresponded to several species. Taxa were classified in ecological groups according to three types of classification: 1) their thermal sensitivity (Mediterranean thermophilous, non Mediterranean, unknown sensitivity), 2) their requirements in large pieces of dead wood, with or without hollows (yes, no, unknown) and 3) their trophic diet (mycetophagous, opophagous, predator, especially saproxylophagous, xylophagous). We observed 86 taxa belonging to 27 families (Appendix 2).

Statistical analyses

First, we tested the influence of the landscape matrix on tree structure, total insect species richness and species richness per ecological group. We checked for the homogeneity of tree structure among the three landscape types with a Kruskal-Wallis test for each one of the 14 variables (except for the categorical variable "state of trunks" for which we used a χ^2 test). Then, we used a non parametric Kruskal-Wallis test to compare the total insect species richness between the three landscape types and a χ^2 test to compare the species richness within each ecological group of the three classifications.

Second, we analysed the correlations between the characteristics of the trees / the surrounding vegetation and the species richness per tree with the Spearman rank test.

Finally, we analysed the respective roles of tree structure and landscape matrix on insect community structure with two Canonical Correspondence Analysis (CCA) (ter Braak, 1986, 1987; Lebreton *et al*., 1988a,b). The faunistic data-set consisted of a matrix of 86 taxa (presence-absence) from 28 samples. The two environmental data-sets consisted of a matrix of 14 variables for tree structure and a matrix of 4 variables for landscape matrix. Two CCA were successively performed with these two sets of data in order to estimate the relative influence of landscape matrix and tree characteristics on saproxylic beetle assemblages.

RESULTS

Landscape matrix had no significant effect on tree structure for 10 out of 14 variables (Tab. I). The width of crown was significantly higher in grassland, the percentage of dead wood outside the crown was significantly lower in shrubland and the amount of dead wood on the ground was significantly higher in woodland. Landscape matrix neither affected insect species richness (14.04 ± 3.75 taxa per tree; Kruskal-Wallis test = 1.05, $P = 0.59$) nor the number of taxa belonging to the different ecological groups (Tab. II).

Table I

Comparison of the tree characteristics between landscape types (Kruskal-Wallis test, except for State of trunks: Chi-square tests) (P values in bold are significant with a P <0.05 significance level)

		Grassland	Shrubland	Forest
Height of tree (m)	$KS = 0.975$; $P = 0.6143$	6.68 ± 1.21	7.17 ± 0.64	7.23 ± 1.89
Width of crown (m)	$KS = 6.243$; $\mathbf{P = 0.0441}$	8.28 ± 1.65	6.46 ± 1.06	6.81 ± 2.44
Number of trunks	$KS = 2.588$; $P = 0.2742$	1.20 ± 0.42	1.0 ± 0.0	1.25 ± 0.46
Mean height of trunk(s)	$KS = 3.966$; $P = 0.1377$	1.67 ± 0.30	1.61 ± 0.38	1.97 ± 0.36
Mean diameter of trunk(s)	$KS = 0.026$; $P = 0.9871$	0.70 ± 0.31	0.63 ± 0.12	0.64 ± 0.16
Number of main branches	$KS = 1.557$; $P = 0.4592$	3.60 ± 0.97	3.40 ± 1.35	2.88 ± 1.13
Number of shoots	$KS = 1.330$; $P = 0.5142$	0.80 ± 1.03	0.83 ± 2.20	1.13 ± 1.55
Number of cavities on the trunk(s)	$KS = 0.099$; $P = 0.9518$	1.10 ± 1.85	2.90 ± 5.61	5.25 ± 8.05
% of dead wood outside the crown	$KS = 6.240$; $\mathbf{P = 0.0442}$	3.90 ± 2.42	1.90 ± 1.37	3.50 ± 1.69
% of dead wood inside the crown	$KS = 2.711$; $P = 0.2578$	2.10 ± 1.66	2.40 ± 1.65	3.00 ± 1.31
Nb. of large pieces of dead wood within the crown	$KS = 2.736$; $P = 0.2546$	1.20 ± 1.62	0.50 ± 0.71	1.25 ± 1.04
Cum. length of lg. pieces of d. wood on the ground	$KS = 10.363$; $\mathbf{P = 0.0056}$	2.04 ± 4.13	0.52 ± 1.64	5.43 ± 5.72
Nb. of large pieces of dead wood on the ground	$KS = 8.503$; $\mathbf{P = 0.0142}$	2.10 ± 3.70	0.50 ± 1.58	3.00 ± 2.33
State of trunks	$\chi^2 = 0.159$; $df = 4$; $P = 0.997$			

The number of taxa was significantly and positively related with the diameter and the state of trunks, the percentage of dead wood inside the crown, the number of large pieces of dead wood within the crown, the cumulated length (m) of large pieces of dead wood on the ground and the number of large pieces of dead wood on the ground (Tab. III). Conversely the number of taxa was significantly and negatively correlated with the number of main branches. The species richness was also significantly and negatively correlated with the percentage of herbs (Tab. III).

TABLE II

Number of taxa within each ecological group for the three classifications: thermal sensitivity, need for wood and trophic diet

		Grassland	Shrubland	Forest
Thermal sensitivity		*Chi*^{2}= 0.201; *df*= 4; *P*=0.995		
	Mediterranean thermophilous	7	7	6
	Non Mediterranean	41	42	39
	Unknown	4	3	3
Species looking for large pieces of dead wood		*Chi*^{2}= 3.523; *df*= 4; *P*= 0.474		
	Yes	12	6	12
	No	37	43	34
	Unknown	3	3	2
Trophic diet		*Chi*^{2}= 3.571; *df*= 8; *P*= 0.894		
	Opophagous	1	1	1
	Saproxylophagous	30	25	25
	Xylophagous	11	18	15
	Mycetophagous	7	4	5
	Predator	3	4	2

TABLE III

Spearman rank correlation between the characteristics of the sampled trees and of the surrounding matrices with the number of species trapped in each tree (P values in bold are significant with a P <0.05 significance level)

Scale	Parameters	Spearman correlation	*P*
Tree	Height of tree (m)	-0.182	0.353
	Width of crown (m)	-0.162	0.410
	Nb. of trunks	0.013	0.949
	Mean height of trunk(s)	0.275	0.156
	Mean diameter of trunk(s)	0.516	**0.005**
	Nb. of main branches	-0.441	**0.019**
	Nb. of shoots	0.183	0.350
	Nb. of cavities	0.006	0.977
	State of trunk(s)	0.411	**0.030**
	% dead w. outside crown	0.206	0.293
	% dead w. inside crown	0.553	**0.002**
	Nb. large pieces dead wood	0.411	**0.030**
	Length lg. p. dead w. ground	0.464	**0.013**
	Nb. lg. p. dead w. ground	0.594	**0.0009**
Landscape	% of trees	0.233	0.232
	% of shrubs	0.035	0.861
	% of herbs	-0.420	**0.026**
	% of bare ground	0.162	0.409

The two first axes of the CCA using tree characteristics explained 23.5% of the variance (Fig. 2). The faunistic contrasts were almost entirely explained by the characteristics of the trees (species-environment correlations = 0.981 for axis 1 and 0.961 for axis 2) and the number of cavities had the highest positive correlation along axis 1 (r = 0.836) and the number of trunks the highest positive correlation along axis 2 (r = 0.512). Oedemeridae and Buprestidae had high positive scores along axis 1 while Mycetophagidae, Erotylidae and Lucanidae had high positive scores along axis 2.

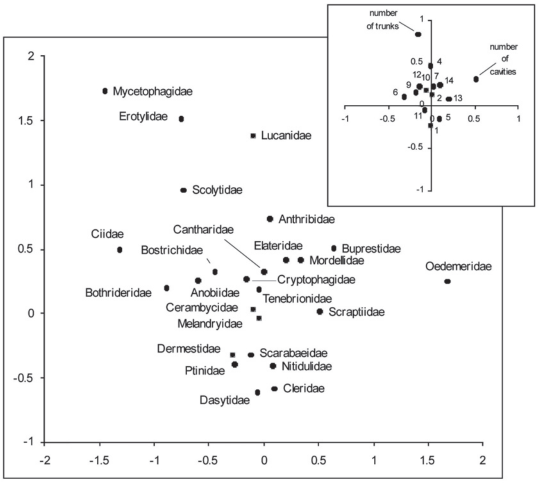

Figure 2. — Plot of families (mean value of taxa scores) on the two first axes of Canonical Correspondence Analysis performed with tree characteristics (axis 1 = 11.8%, axis 2 = 11.7%). The correlation of the descriptors with the first two canonical axes is plotted in the window (1 = height of tree, 2 = width of crown, 4 = mean height of trunk(s), 5 = mean diameter of trunk(s), 6 = number of main branches, 7 = number of shoots, 9 = state of trunk(s), 10 = % of dead wood outside the crown, 11 = % of dead wood inside the crown, 12 = number of large pieces of dead wood within the crown, 13 = cumulated length of large pieces of dead wood on the ground, 14 = number of large pieces of dead wood on the ground).

The two first axes of the CCA using characteristics of the landscape matrix explained 60.2% of the variance (Fig. 3). The correlations between landscape parameters and species were slightly higher than 0.9 (species-environment correlations= 0.908 and 0.922 for axes 1 and 2, respectively). The percentages of trees ("tree") and herb ("grassland") showed high opposite correlations along the first axis (r = 0.879 and -0.861, respectively) while the second axis opposed the percentages of bare ground ("soil") and shrubs ("shrubland") (r = 0.712 and -0.535, respectively). Almost all families were grouped at the centre of the plot. Lucanidae and Bothrideridae had positive scores on axes 1 and 2 respectively.

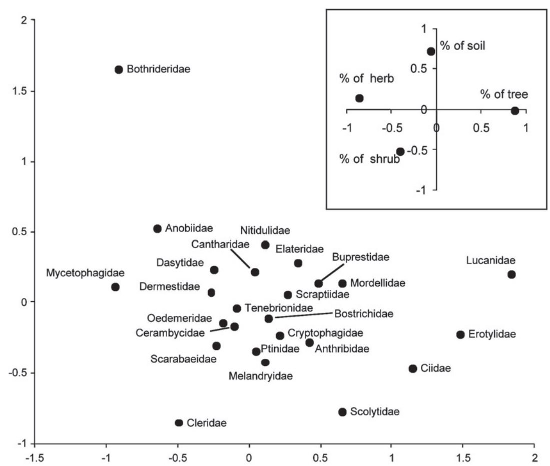

Figure 3. — Plot of families (mean value of species coordinates) on the two first axes of Canonical Correspondence Analysis performed with landscape parameters (axis 1= 33.2%, axis 2= 27.0%). The correlation of the descriptors with the first two canonical axes is plotted in window.

DISCUSSION

Consequences of land abandonment

In the studied area, the spring-summer saproxylic fauna showed a very homogeneous distribution across the landscape. This low influence of the presence or not of forest regrowth is an original result when compared to observations issued either from northerly parts of the Western Palaearctic or from other parts of the Mediterranean region. Indeed, in the former, forest regrowth in sites with free-standing large oaks was detrimental to many saproxylic beetle species (Ranius & Jansson, 2000). In the latter, the regrowth of the oak forest induced the disappearance of the more thermophilous and Mediterranean species as well as the increase in abundance of a medio-European complex of species in older and closer stands (Brin & Brustel, 2006). It is possible that the absence of a marked effect of the structure of the surrounding vegetation on the composition of the insect fauna we collected in old trees is explained by the limited contrast in bioclimatic conditions between the open and wooded matrices. The local regrowth of the Holm oak forest that followed land abandonment started recently (traditional land uses lasted until the fifties) and did progress slowly in the particularly dry edaphic context (karstic south facing slopes and plateau at the foot of the Pic Saint-Loup, 658 m). As a result forests are still at an early maturation stage characterized by small trees and an open understory. In this context saproxylic assemblage may mainly reflect the characteristics of their immediate habitat (the old trees studied).

Role of local versus landscape conditions

The comparison between CCAs showed that the faunal composition of the species assemblages was more influenced by the characteristics of the trees than by landscape parameters. For example, Oedemeridae and Buprestidae were more frequently observed near cavities (especially *Ischnomera xanthoderes* and *Latipalpis plana* which needed decay wood corresponding to dead or cut branches). More generally the number of taxa depended on the availability of large pieces of dead wood directly measured by the quantity of dead wood in the tree or on the ground and indirectly estimated by the diameter of trunks.

Considering a small area (4 km^2) with homogeneous abiotic conditions, our study showed that saproxylic assemblages were mainly explained by the local characteristics of their habitat and that the composition of the surrounding vegetation actually played a minor role. The Mediterranean species did not show a preference for open plots (although several uncommon Mediterranean species were observed, as *Mycetochara quadrimaculata*, *Ischnomera xanthoderes*, *Latipalpis plana*, *Chlorophorus ruficornis*, *Ogmoderes angusticollis*). Mycetophagous beetles did not particularly select mesophilous woodland conditions. Moreover, except the amount of dead wood on the ground, all the determining characteristics of the trees studied were independent from the surrounding vegetation. The relative higher abundance of dead branches on the ground near the trees studied in a forested context could be the result of higher competition for light (Ball & Key, 1997) or possibly to a more frequent removal of dead wood in open habitats.

As saproxylic beetles depend on dead wood, they selected trees with many trunks and cavities but with few main branches, the typical Holm oak tree apt to play the role of a keystone structure is a short tree (for its age) regularly cut (coppice), showing wounds and surrounded by fallen dead branches (Ranius, 2002).

Implications for management

The presence of the keystone structure represented by old Holm oak trees is closely related to past charcoal production and traditional farmland practices (production of tools, consumption of leaves by flocks, etc.). Consequently one may fear that the probable future extension of forest and the ensuing spread of mesophilous conditions that result from land abandonment may reduce habitat availability not only for thermophilous Mediterranean species but also for the saproxylic fauna as a whole. Useful measures to protect local saproxylic species assemblages do not require large scale landscape management but only practices able to substitute for traditional land uses, such as the regular pruning of some trees (Key & Ball, 1993; Ball & Key, 1997; Franc, 1997; Grove, 2002; Brustel, 2004a; Jonsson *et al.*, 2005) or favouring the accumulation of dead wood on the ground, especially in grasslands and shrublands, by limiting its collection.

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APPENDIX 1

Characteristics of sampled trees and surroundings (see details in text)

	Grassland										Shrubland										Forest							
	G1	G2	G3	G4	G5	G6	G7	G8	G9	G10	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	F1	F2	F3	F4	F5	F6	F7	F8
Tree structure																												
height of tree (m)	6	6.6	5.6	5.5	5.3	7.1	8.6	8.3	7.8	6	8.3	7.4	7.1	7.2	7.1	5.9	7.1	7.2	6.6	7.8	10	6	7.5	8.9	8.5	5.2	6.3	5.1
width of crown (m)	9.3	10.1	8.4	6.7	6.4	11	9.3	8.2	7.3	6.1	5.8	8	5.4	6	5.4	5.8	7.2	8.4	6.4	6.2	11	4.8	4.2	6.1	7.7	6.8	8.8	4.7
nb. of trunks	2	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	2	1
m. height of trunk(s)	1.5	1	1.5	1.5	1.7	1.8	1.9	2	1.9	1.9	1	1.35	1.2	1.5	1.8	1.4	2.1	2.1	1.9	1.7	1.7	1.9	2.3	2	1.8	2.2	2.5	1.4
m. diam. of trunk(s)	0.5	0.6	1.5	0.45	0.5	0.85	0.55	0.65	0.7	0.7	0.6	0.6	0.5	0.55	0.7	0.55	0.6	0.7	0.55	0.9	0.7	1	0.5	0.5	0.6	0.7	0.6	0.6
nb. of main branches	4	5	3	4	3	4	5	3	3	2	5	2	2	2	2	3	4	5	5	4	4	2	1	4	3	2	4	3
nb. of shoots	1	0	0	0	0	1	1	2	3	0	0	1	7	0	0	0	0	0	0	0	0	0	0	0	3	3	3	0
nb. of cavities	6	1	0	0	1	0	1	2	0	0	1	18	0	4	0	5	0	0	1	0	0	0	0	0	0	20	7	15
state of trunk(s)	3	1	3	2	1	3	1	1	2	2	1	2	3	2	3	2	1	1	1	3	1	1	1	2	2	3	2	3
% dead w. outside	4	1	8	4	3	2	7	1	3	6	1	2	1	1	1	1	3	1	3	5	2	2	6	4	3	6	2	3
% dead w. inside	1	1	6	1	1	2	4	1	2	2	1	1	6	2	3	2	3	1	1	4	1	4	3	4	2	5	2	3
nb. lg. pc. dead w.	1	0	5	1	0	0	0	3	1	1	0	0	2	0	1	0	1	0	0	1	1	1	0	0	1	3	2	2
l. dead w. ground	0	0	13.5	1	0	0	2	0	2	1.9	0	0	0	0	0	0	0	0	0	5.2	12	16	0	7.5	2	2.5	2.5	1.2
nb. lg. pc. dead w. ground	0	0	12	1	0	0	2	0	3	3	0	0	0	0	0	0	0	0	0	5	1	7	0	3	3	5	4	1
Landscape																												
% of tree	9	16.96	8.992	8.825	5.4	10.63	16.32	6.611	3.6	12	19	23.39	26	45.82	15	14.73	14	10	10.14	17	49	61	71	61	38	32	71	72
% of shrub	23	24.24	35.86	35.11	39	47.88	45.53	9.879	35	31	37	32.23	39	31.83	51	49.44	43	50	27.73	40	30	21	18	25	39	35	20	19
% of grass	62	55.3	54.49	51.98	56	40.82	31.57	78.3	53	36	41	43.08	34	19.45	33	35.42	39	38	56.47	39	20	17	11	14	11	17	7.5	5.2
% of soil	5.8	3.498	0.654	4.086	0.5	0.672	6.576	5.21	8.6	21	2.9	1.298	1.2	2.895	1.3	0.413	3.3	2.3	5.658	3.5	0.1	1.3	0.3	0.4	12	16	1	3.5

APPENDIX 2

List of species trapped in each sampled tree (trophic diet: m= mycetophagous, o= opophagous, p= predator, sx= especially saproxylophagous, x= xylophagous; lg. p.: 1= species looking for large pieces of wood (sometime with hollows); Med: 1= Mediterranean species)

Family	species	troph	lg. p.	Med.	Grassland										Shrubland										Forest							
					G1	G2	G3	G4	G5	G6	G7	G8	G9	G10	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	F1	F2	F3	F4	F5	F6	F7	F8
Anobiidae	*Dorcatoma serra*	M	1	0				1																								
Anobiidae	*Stagetus elongatus*	M	1	0										1																		
Anobiidae	*Xestobium rufovillosum*	Sx	1	0																		1										
Anthribidae	*Rhaphitropis oxyacanthae*	Sx	0	0						1	1																		1		1	
Bostrichidae	*Scobicia chevrieri*	X	0	0								1	1						1				1									
Bostrichidae	*Sinoxylon sexdentatum*	X	0	1																											1	
Bostrichidae	*Xylopertha praeusta*	X	0	0											1		1		11													
Bothrideridae	*Ogmoderes angusticollis*	P	0	1				1				1		1																		
Buprestidae	*Agrilus angustulus*	X	0	0																									1			
Buprestidae	*Agrilus hastulifer*	x	0	0														1											1			
Buprestidae	*Agrilus laticornis*	x	0	0																									1			
Buprestidae	*Agrilus obscuricollis*	x	0	0												1																
Buprestidae	*Anthaxia hungarica*	x	0	1																									2			
Buprestidae	*Anthaxia millefolii*	x	0	0														1						1								
Buprestidae	*Anthaxia umbellatarum*	x	0	0														1														
Buprestidae	*Latipalpis plana*	x	0	1	2		3		3		1	3	3	3	2	3			2	3			1		2	2	3		1	4	3	1
Cantharidae	*Malthinus seriepunctatus*	sx	?	?				1								1														1	1	1
Cantharidae	*Malthinus flaveolus*	sx	?	?			2				1			1					1													
Cerambycidae	*Callimus abdominale*	x	0	0			3		1				1				2								1	1	3		1			1
Cerambycidae	*Cerambyx cerdo*	x	1	0								1	2																	1		
Cerambycidae	*Cerambyx welensii*	x	1	1									1					1						1						1		
Cerambycidae	*Chlorophorus ruficornis*	x	0	1	2		3				1		1	2		1				1	1			1								
Cerambycidae	*Clytus rhamni*	x	0	0													1															
Cerambycidae	*Corymbia fontenayi*	x	1	1																											1	

Family	species	troph	lg. p.	Med.	Grassland										Shrubland										Forest							
					G1	G2	G3	G4	G5	G6	G7	G8	G9	G10	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	F1	F2	F3	F4	F5	F6	F7	F8
Cerambycidae	*Deroplia genei*	x	0	0												1										1						
Cerambycidae	*Gracilia minuta*	x	0	0																		1										
Cerambycidae	*Phymatodes testaceus*	x	0	0						1									1		1										1	
Cerambycidae	*Poecilium lividus*	x	0	0		1	2			1	2	2	1						9			1	3	2			1					
Cerambycidae	*Stenopterus rufus*	x	0	0				1																								
Cerambycidae	*Stictoleptura cordigera*	x	0	1			1											1														
Cerambycidae	*Stictoleptura fulva*	x	0	0							1						1		1					1				1				
Ciidae	one species from unidentified genus	m	0	0																								1				
Cleridae	*Clerus mutillarius*	p	0	0															2													
Cleridae	*Denops albofasciatus*	p	0	1															2				1									
Cleridae	*Opilo domesticus*	p	0	0													1		1													
Cleridae	*Opilo pallidus*	p	0	0												1																
Cryptophagidae	*Cryptophagus pallidus*	m	0	0		2		1	1													1				3	4	1			1	
Dasytidae	*Danacea pallipes*	sx	0	?		1																										
Dasytidae	*Haplocnemus impressus*	sx	0	?			6							2	6	3	8	4	2	13	7		2		1	4						1
Dasytidae	*Dasytes flavipes*	sx	0	0		1		4		1		4	1	3	6	1	5	6			1	2	1	3	2	5	4		2	2	4	4
Dermestidae	*Anthrenus* sp.	sx	0	0							1																					
Dermestidae	*Attagenus pelio*	sx	0	0																1												
Dermestidae	*Attagenus piceus*	sx	0	0		1																										
Dermestidae	*Ctesias serra*	sx	0	0																				1							2	
Dermestidae	*Trogoderma glabrum*	sx	0	0		1								1																		
Elateridae	*Brachygonus megerlei*	p	1	0																							1					
Elateridae	*Cardiophorus gramineus*	p	1	0			1																									
Elateridae	*Elater ferrugineus*	p	1	0				1																						1	2	
Elateridae	*Lacon punctatus*	sx	1	0																										2		
Elateridae	*Melanotus crassicollis*	sx	0	0	1		16		9		7			38	5	12	5	5	4	4		4	12	9	3	34	1	1	4	5	3	1
Erotylidae	*Triplax russica*	m	1	0																								3			1	
Lucanidae	*Lucanus cervus*	sx	1	0																											1	1

Family	species	troph	lg. p.	Med.	Grassland										Shrubland										Forest							
					G1	G2	G3	G4	G5	G6	G7	G8	G9	G10	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	F1	F2	F3	F4	F5	F6	F7	F8
Malachiidae	several species	sx	?	?				2					1									1			1							
Melandryidae	*Abdera biflexuosa*	m	0	0			1												1			1		1								
Melandryidae	*Abdera quadrifasciata*	m	1	0						1								1								1					2	
Melandryidae	*Conopalpus brevicollis*	m	0	0	1		18		1	2			2	7			6	4		1				1	2	8	4	1	8	13	7	7
Mordellidae	*Mordellistena confinis*	sx	0	0							2				1												2			2	1	
Mycetophagidae	*Mycetophagus quadriguttatus*	m	0	0				1																								
Nitidulidae	*Epurea fuscicollis*	op	0	0														1														1
Nitidulidae	*Soronia grisea*	op	0	0									1																			
Oedemeridae	*Ischnomera xanthoderes*	sx	?	1	1														1			1								1	2	
Oedemeridae	*Oedemera flavipes*	sx	0	0												1																
Ptinidae	*Ptinus variegatus*	sx	0	0		1	1		4	6	5	1	1	2	1	2	4	1	1	1	1	3	1	2	4	12	7	5		1		
Ptinidae	*Ptinus palliatus*	sx	0	0						1															1							2
Ptinidae	*Ptinus sexpunctata*	sx	0	0																	1											
Scarabaeidae	*Cetonia aurata*	sx	0	0		1			1	2	1	1	5		1	1		1		30	2	1	10									
Scarabaeidae	*Eupotosia affinis*	sx	0	1			1											1														
Scarabaeidae	*Potosia cuprea*	sx	0	0						1			1						1	4								1		1	2	
Scolytidae	*Scolytus intricatus*	x	0	0															1													
Scolytidae	*Xyleborus monographus*	x	0	0																											1	
Scraptiidae	*Anaspis humeralis*	sx	0	0				4				1					1			3	1											
Scraptiidae	*Anaspis lurida*	sx	0	0									3		1						1				1	4	4		5	3	1	2
Scraptiidae	*Anaspis maculata*	sx	0	0																						1				1		
Scraptiidae	*Anaspis pulicaria*	sx	0	0	1					1			1	3	3	1	3	2			6	2	1	1	1	4	6		1	3	1	
Scraptiidae	*Anaspis regimbarti*	sx	0	0		2		1	1			1	1	2	2						1	2		4		4		2			1	1
Scraptiidae	*Scraptia dubia*	sx	0	0			1																			1				1		
Scraptiidae	*Scraptia fuscula*	sx	0	0						1										1						6						
Scraptiidae	*Scraptia testacea*	sx	0	?																						4						
Staphylinidae	several species	p	0	0		2			3		1		4	1	1		5	3	6	3	3	1			2	4	5	1	5	1	13	1
Tenebrionidae	*Isomira* sp.	sx	0	0																						1						

Family	species	troph	lg. p.	Med.	Grassland										Shrubland										Forest							
					G1	G2	G3	G4	G5	G6	G7	G8	G9	G10	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	F1	F2	F3	F4	F5	F6	F7	F8
Tenebrionidae	*Mycetochara maura*	sx	0	0	9	5	9	9	1	18	3	9		7		6		9		5	11	1	1	24		32	60	45	7	34	43	210
Tenebrionidae	*Mycetochara quadrimaculata*	sx	1	0	3		5	1											3												2	
Tenebrionidae	*Prionychus ater*	sx	1	0	2		3	3			6	1																1				1
Tenebrionidae	*Prionychus fairmairei*	sx	1	0	1		1				2							1						1		1				2	4	
Tenebrionidae	*Pseudocistela ceramboides*	sx	1	0			1																									
Tenebrionidae	*Tenebrio obscurus*	sx	1	0			1											1						4								