Insect Conservation and Diversity (2010) **3,** 236–245 doi: 10.1111/j.1752-4598.2010.00094.x

The influence of forest management and habitat on insect communities associated with dead wood: a case study in forests of the southern French Alps

GUY LEMPERIERE[1] and DAMIEN MARAGE[2,3] [1]Laboratoire d'Ecologie Alpine, Université Joseph Fourier, Grenoble Cedex, France, [2]AgroParisTech, Laboratoire d Etude des Ressources Foret Bois (LERFoB), ENGREF, Nancy, France and [3]INRA, Laboratoire d Etude Des Ressources Foret Bois (LERFoB), Centre INRA de Nancy, Champenoux, France

Abstract. 1. Dead wood plays a key role in the functioning of forest ecosystems and is appropriate for conservation purposes and for maintaining biodiversity. In this context, in mixed silver fir ancient forests of the southern French Alps, the respective influence of management status and decay stages were assessed together with assemblages of saproxylic invertebrates.

2. Although the structure of the saproxylic insect composition showed a strong dependence on the different stages of decaying wood, with groups of species restricted to one particular stage, the other part of this structure was only slightly influenced by the management status.

3. In early successional stages of dead wood that generate ephemeral habitats suitable for specialists, the assemblage of species could locally become extinct very quickly. In intermediate stages which were colonised by other assemblages of species, the richness and abundance of some groups were probably positively correlated with historical continuity at a local scale.

4. In the case of suitable long persistent habitats colonised by species with limited dispersal ability, some old established populations could be temporarily deprived of their potential habitats. However, the actual populations of invertebrates have gone through spatio-temporal discontinuities in a metapopulational context at the landscape level.

Key words. Alps, ancient forest, dead wood, ecological persistence, invertebrates, silver fir.

Introduction

Over the last few decades, there has been an increasing recognition that dead wood resources are critical elements of forest ecosystems. Standing dead trees (SDT) together with coarse woody debris (CWD) play a crucial role in the biodiversity and functioning of forest ecosystems (Harmon *et al*., 1986; Samuelsson *et al*., 1994). A wide range of plants and animals is strongly associated with dead wood especially cavity-nesting birds that can comprise 40% of the forest bird communities (Blondel, 1995; McComb & Lindenmayer, 1999). Saproxylic insects also pass through a part or their biological cycle on dead wood materials (Dajoz, 1974, 1998; Speight & Wainhouse, 1989). These functional groups play an active part in releasing nutrients in the biogeochemical cycles of forest ecosystems (Bormann & Likens, 1994). A decaying substrate is also associated with nitrogen-fixing bacteria that may contribute to soil nitrogen dynamics (Harmon *et al*., 1986). Furthermore, the decaying wood could be an important seedbed for regenerating trees, ferns and mosses (Harmon *et al*., 1986; Franklin *et al*., 1987; Peterken, 1996; Crites & Dale, 1997).

Tree mortality thus is generally the result of complex interactions among environmentally stochastic factors (Franklin

Correspondence: Guy Lemperiere, Laboratoire d'Ecologie Alpine, UMR-CNRS 5553, Université Joseph Fourier, BP 53, 38 041 Grenoble Cedex 9, France. E-mail: guy.lemperiere@unicaen.fr

et al., 1987) such as droughts, fungal pathogens, fire and storms. At various stages of tree development, mortality processes are different and lead to a fragmented distribution of dead wood habitats. Biotic and abiotic disturbances were more sensitive in the biostatic stage as defined by Koop and Hilgen (1987) as a mature or full-grown phase, as stem exclusions were rather rare in the innovation and aggradation stages as mentioned by Oldeman (1990) respectively as a gap opening constituting the developmental phase, i.e. the beginning of an internal dynamics of the ecosystem which leads to a gradual closure of the canopy and later phases of growth or aggradation phase.

These different mortality processes could interact with organisms dependent on dead wood. Tree species, diameter and decaying stages are factors that strongly regulate species composition (Andersson & Hytteborn, 1991; Bull *et al*., 1997; Crites & Dale, 1997; Dajoz, 1998). Forest management, both by clear-cutting and selective thinnings could alter and modify the spatial and temporal availability of dead wood (Kirby *et al*., 1991; Mc Carthy & Bailey, 1994; Green & Peterken, 1997). From an economical point of view, snags as breeding material for insects, capable of infecting living trees might be regarded as depreciating timber values. Moreover, in managed forests, snags can be seen as a threat to public safety (Peterken, 1996). Despite economic and safety considerations, the amount of dead wood, particularly SDT, has attracted attention of forest managers as part of their interest in maintaining biodiversity within forests managed for timber production (Ammer, 1991). Thus, the maintenance of snags has become an integrated part of forest management in France. At present, limited information is available concerning the amount and distribution of SDT in managed and unmanaged forests in France (Koop & Hilgen, 1987; Schnitzler & Borlea, 1998).

Existing frequency of snag in unmanaged ancient forests was assessed to provide a benchmark for natural forest conditions. Undisturbed forest stands may be important for biodiversity through their content of microhabitats or for the long periods available for colonisation (Norden & Appelqvist, 2001). The use of ecological continuity may lead to underestimate the importance of forest dynamics and dispersal, and to overestimate the importance of local land use history. If bioindicators of long-term habitat persistence are to be used, species with low dispersal capacity should be chosen.

The aim of this work was to evaluate the respective influence of habitat condition (i.e. decay stages of dead wood) and forest management on insect communities dependent on dead wood in ancient silver fir forests which were actually managed or unmanaged (reserve area). The baselines of our results should provide guidelines for the local forest managers in maintaining insect biodiversity associated with dead wood.

Material and methods

Study area

The study was carried out in the Petit Buëch experimental watershed located in the Hautes-Alpes (France) (44°35′N, 6°12′E), ca. 10 km northwest of Gap (Fig. 1). Covering a 57 km^2 area, the watershed elevation varies from 960 to 2700 m. The climate features stem from the AURELHY model of Météo France (Benichou & Le Breton, 1987) (data from 1961 to 1990). The mean annual rainfall is 1138 mm and the mean annual temperature value is 5.8 °C. Winters are cold with more than 100 days of frost and the snow cover usually lasts for ca. 150 days. The watershed lies essentially on a substratum from the Jurassic and Cretaceous periods.

Between 1300 and 1800 m, a silver fir-beech forest has developed (*Fagion sylvaticae*; *Geranion nodosi – Fagetum sylvaticae*) and is considered as Potential Natural Vegetation (Rameau, 1992). The most influential dynamic factors in this forest, namely landslides, avalanches, diseases and death, windfalls, and insect outbreaks lead to its structural heterogeneity, expressed in a silvatic mosaïc (Oldeman, 1990), the complex of distinct patches in various developmental phases (Leibundgut, 1993; Christensen & Emborg, 1996; Bobiec, 2002).

Sampling methods & design

Three forest units among a set of six forestry sites were selected to describe the amounts of SDT; one was harvested (Tavanet) and two were unexploited (Le Chapitre and Ufernet) for more than half a century (Table 1). According to the land use history derived from the Napoleonian cadastral map (1808), we selected only ancient forests, defined as areas covered with forests since the 18th century or before (Peterken,1996).

Management status, developmental phases and decay stages are three main factors that influence the pattern of forest insects (Dajoz, 1998; Jonsell *et al*., 1998; Spagarino *et al*., 2001; Maeto *et al*., 2002). SDT assessments were conducted as described in Marage and Lemperiere (2005). Samples were taken exclusively in the neutrophilous silver fir-beech forest as site conditions also seemed to have an effect on SDTs. The data set was obtained over a period of 2 years. Decay stages were assessed using the phases described by McComb and Lindenmayer (1999) (Fig. 2) and developmental phases described by Marage and Lemperiere (2005). SDT of each species tree were recorded on circular 400 m^{2}plots. On each plot, all trees were measured, if the DBH ≥7.5 cm (living or dead). The 7.5 cm threshold was chosen because it was the minimum diameter for trees recorded in the French National Forest Inventory. SDT were sampled only if they were at least 2 m tall. For each snag, height (m) was also recorded using a dendrometer (Bitterlich relascop). Trees were considered as SDT, when the photosynthetic capacity was lost corresponding with 3, 4, 5 and 6 classes of Thomas (1979). SDTs were classified into four classes, 7.5–27.5, 28–42.5, 43–62.5 cm, larger than 62.5 cm at DBH. Derived from the measurement with the Bitterlich relascop, the volume was estimated using the commercial formula as below:

$$V = \frac{\Pi}{4} D^2 \mathrm{Ht}(\mathrm{m}^3)$$

with Ht = height of the snag and D = diameter at middle-height.

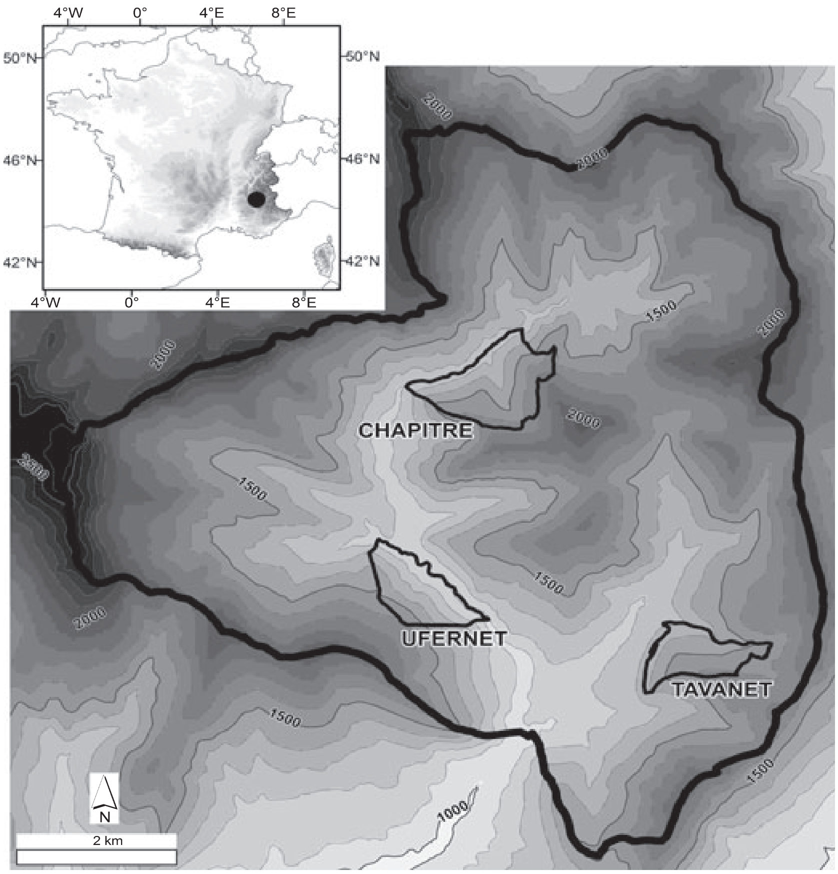

Fig. 1. Location of the three study sites in the Petit Buëch watershed, Hautes-Alpes France. Forests of Le Chapitre and Ufernet: unmanaged. Forest of Tavanet: managed.

Table 1. Sites features, alive and dead volume in silver fir ancient forests of the southern French Alps (volume: mean ± SE, $n = 48$).

Site	Management status	Area (ha)	Main species	Age of oldest tree	Date of last harvest	Living trees volume (m^3 ha^{-1})	SDT volume (m^3 ha^{-1})
Chapitre	Unmanaged (reserve area)	195	Silver fir	244	1951	510.0	70.30
Ufernet	Unmanaged	82	Silver fir	168	1954	358.3	36.20
Tavanet	Managed	85	Silver fir	125	1998	248.1	14.56

Standing dead trees basal area (g) was calculated and a necrotic index was computed as follows:

$$100\left[\frac{g_{SDT}}{g_{tot}}\right]$$

with $g_{tot} = g$ of living and dead tree.

Insect populations were sampled using trapping techniques every week from 1999 to 2001. A total of 20 interception traps (window traps) where displayed along transects in the three forests as given in Lott and Eyre (1996) with respectively 5 traps in Ufernet and Le Chapitre and 10 traps in Tavanet. Transect and quadrat methods were also used to determine the density of other groups of insects like mount building ants (Hym.Formicidae) (Boudjema *et al*., 2006), bark beetles (Col.Scolytidae) and weevils (Col.Curculionidae).

Data analysis

Direct gradient analysis [i.e. canonical correspondence analysis (CCA)] was performed on the data set to quantify the relationships between explanatory variables and the faunistic table (18 species × 48 samples). This method allows the simultaneous study of complex relations between species, and between species and their environment (ter Braak, 1987; Økland, 1996). In this procedure, a correspondence factor analysis (CFA) is first carried out to measure the multiple correlation ratio (MCR) and its unconstrained form correspondence analysis (CA). CCA is the most adequate ordination method, in accordance with the data table structure (i.e. unimodal response curves for most of the species) and because of its modelling properties (ter Braak, 1987;

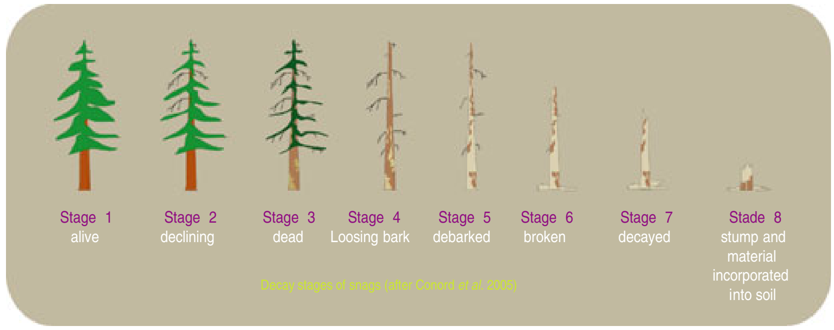

Fig. 2. Decaying stages of standing dead trees (SDT). After Lemperiere *et al.*, 2005.

Table 2. Categories of habitat and management variables.

	Categories	Frequency (%)
Habitat variable		
Decay stages of dead wood	a. Stage II	18.8
	b. Stages III–IV	35.4
	c. Stages V, VI, VII	16.7
	d. Both stage present	29.2
Management variable		
Management status	e. Managed	45
	f. Unmanaged	55

Prodon & Lebreton, 1994). The basic principle of CCA is to constrain the ordination axes to be linear combinations of explanatory variables (Lebreton *et al.*, 1991).

Moreover, the respective and combined influence of habitat conditions (i.e. stages of decay) and management regimes (i.e. management regime and developmental phases) can be studied by partial CCA or CCA with variance partitioning (ter Braak, 1987; Sabatier *et al.*, 1989; Økland & Eilertsen, 1994; Økland, 1999). It allows the statistical removal of the effect of a predominant factor masking the effects of secondary factors which are still of interest (Yoccoz & Chessel, 1988). Different combinations of the categorical variables (Table 2) were used to partition the variance in different ways (i.e. separate and combined effects), based on sample projections in different orthonormal bases (Sabatier *et al.*, 1989; Chessel,1997).

Statistical significance of the effect of each variable or combination of variables was tested according to a Monte-Carlo permutation test with 2000 permutations (Thioulouse *et al.*, 1997). Moreover, the ratio of total inertia of each separate CCA to total inertia of unconstrained CA can be considered as a MCR (in %) (Sabatier *et al.*, 1989). It allows evaluation of the percentage of total faunistic variation explained by a given variable or combination of variables (Lebreton *et al.*, 1991). The ratio of total inertia to the number of factors (i.e. the number of categories of explanatory variables), noted I/F; was calculated to compare the explanatory power of variables and combination of variables with different numbers of categories.

Multivariate analyses were performed in three steps: (i) analysis of the effect of habitat conditions (decay stages of dead wood), (ii) analysis of the effect of forest management, (iii) analysis of the additive effect of combinations of habitat and management variables, to obtain the best multivariate model for predicting faunistic composition dependent on this ancient forest. All the multivariate analyses were performed with ADE-4 software (Thioulouse *et al.*, 1997).

Results

Effect of decay stages

The effect of habitat conditions was the most determinant factor with highest total inertia (1.001), inertia per factor (0.250) and MCR (20.8%), both significant at $P < 0.001$ according to a Monte-Carlo test with 2000 permutations (Table 3). As a result, the composition of the saproxylic insect fauna of these ancient forests could be largely predicted by the different decay stages only. The entomocenotic sequences were characterised by an ordination from declining silver firs subjected to attacks by the fir weevil, *Pissodes piceae* III. (Col.Curculionidae) together with a complex of secondary 'pests' or insects including adults and larvae of *Cryphalus piceae* Ratz., *Pityokteines curvidens* Germar and *Pityokteines spinidens* Reitter, *Pityophthorus pityographus* Ratz. (Col.Scolytinae), *Urocerus gigas* L. (Hym.Siricidae), then saproxylophagous insects colonising SDT 5–10 years after the first colonisation such as the Elateridae species *Melanopus castanipes* Paykull and the Eucnemidae species *Xylophilus corticalis* Paykull and *Epiphanis cornutus* Eschscholtz and colonies of the carpenter ant *Camponotus herculeanus* on axis 1. On axis 2, from specialists both on stage I to stage VII to more ubiquitous species, an overlap of xylophagous and saproxylophagous insects feeding on decaying wood with both adult and larval stages was observed (Fig. 3).

Table 3. Variance partitioning of canonical correspondence analysis and partial canonical correspondence analysis (CCA).

	I	*F*	*I/F*	MCR (%)	*P*
Effects of habitat					
Decay stages of dead wood	1.001	4	0.250	0.208	***
Effects of management status					
Management status	0.235	2	0.117	0.048	*
Additive effects of habitat and management					
Decay stages + management	1.230	6	0.205	0.255	***

I is total inertia of CCA, *F* is the number of factors (i.e. the number of categories per variable), MCR is a multiple correlation ratio measuring the quality of the prediction of sample scores by explanatory variables (% of total variance explained), it is calculated by the ratio: total inertia of CCA/total inertia of unconstrained CA, which is 4.809; *P* is the significance level according to the Monte-Carlo test with 2000 permutations, with $^*P < 0.05$, $^{**}P < 0.01$ and $^{***}P < 0.001$.

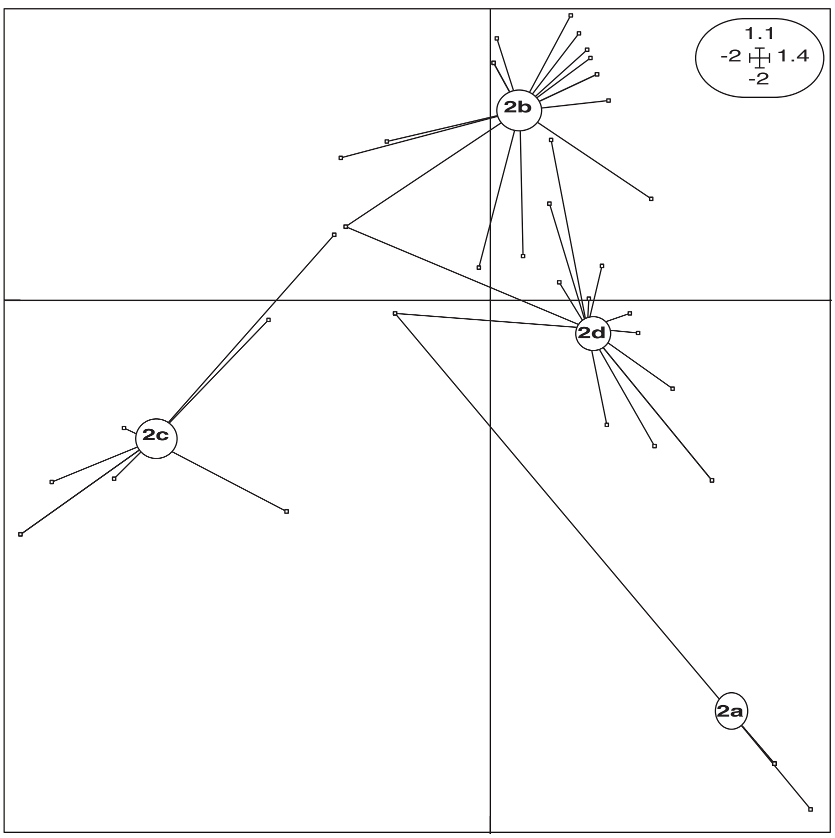

Fig. 3. Sample ordination by canonical correspondence analysis (CCA) with effect of the different decay stages of dead wood. 2a = Stage I, 2b = Stage II–III, 2c = stages V–VI–VII, 2d = mixed stages. Each circle is located at the barycenter of samples occurring in each category.

Effect of management status

The influence of management status on entomocenoses was 4.8%, and the inertia for this factor was equal to 0.235, only significant at $P < 0.05$ (Table 3). Management status was less influential than habitat conditions in explaining species composition. Taking into account the management variables, in our context, was insufficient to allow prediction of the saproxylic insect composition of these ancient forests. As insect species have distinct habitat requirements and occur in particular decay stages of dead wood more than others, their response to forest management was less obvious.

Additive effect of decay stage of dead wood and management status

Results showed that 25.5% of variability was explained by additive effects of the different decay stage of dead wood and the management status.

Species ordination by CCA of the additive effect of decay stage of dead wood and management status (Fig. 2) is very close to that obtained by unconstrained CA. Thus, it indicated that ancient unmanaged forests that allow the persistence of a sylvatic mosaïc with the integrity of a silvigenesis cycle contained all the decay stages of dead wood. In contrast, the ancient managed forest was generally characterised by a silvicultural cycle in which degradation phases were absent. The relationship between management status and quantity of SDT tested by a one-way ANOVA was significant at $P < 0.01$ (F-ratio = 4.77, n = 48). SDT volume had an average of 65.2 ± 18.1 m^3 ha^{-1} in unmanaged forests as compared to 14.6 ± 6.0 m^3 ha^{-1} in managed forests (Fig. 4).

Biocenotic sequences according to decay stages and management status

Records and observations of successional biocenosis on SDT but also on early stages of infestations have been assessed on silver fir. Six major stages were identified (Table 4) even though, the presence of the Fir budworm *Choristoneura murinana* Hbn. (Lep.Tortricidae) and records of defoliations by this insect with a limited and localised impact was confirmed in 1999 and 2000 (stage I).

In stage II, on declining silver firs, attacks by the fir weevil, *P. piceae* Ill. (Col.Curculionidae), were recorded together with the below mentioned secondary 'pests' including adults and larvae of *C. piceae* Ratz., *P. curvidens* Germar and *P. spinidens* Reitter, *P. pityographus* Ratz. (Col.Scolytinae), *U. gigas* L. (Hym.Siricidae). Those insects were collected in trees belonging to the aggradation and biostatic stages of both managed and unmanaged forests. The colonisation and decline of trees took from 12 to 24 months and this rooting process started from the outside of the trees.

Table 4. List of invertebrates sampled on dead wood of managed (M) and unmanaged (U) silver fir forests.

Species	Stage II	Stages III–IV	Stages V–VI	Stage VII
Coleoptera				
Curculionidae				
Pissodes piceae	+ + +(M, U) (352)			
Scolytinae				
Pityokteines curvidens	+ + +(M, U) (1822)			
Pityokteines spinidens	+ + +(M, U) (1507)			
Pityophthorus pityographus	+ + +(M, U) (1436)			
Cryphalus piceae	+ + +(M, U) (118)			
Cerambycidae				
Anastrangalia dubia		+ +(M, U) (30)		
Anastrangalia sanguinolenta		+(M, U) (5)		
Brachyleptura hybrida		+(U) (3)		
Clytus lama		+ +(M, U) (11)		
Evodinus clathratus		+(M, U) (5)		
Molorchus minor		+(M, U) (5)		
Oxymirus cursor		+(U) (2)		
Pidonia lurida		+(U) (5)		
Rhagium bifasciatum		+ + +(M, U) (57)		
Rhagium inquisitor		+(U) (4)		
Pyrochroidae				
Pyrochroa coccinea		+(M, U) (1)		
Elateridae				
Ampedus erythrogonus		+(U) (2)		
Ampedus melanurus		+(U) (2)		
Ampedus nigrinus		+(U) (1)		
Hypoganus cinctus		+(U) (1)		
Melanopus castanipes		+(U) (1)	+(U) (1)	
Eucnemidae				
Xylophilus corticalis			+(U) (1)	
Epiphanis cornutus			+(U) (1)	
Carabidae				
Carabus auronitens				+(U) (5)
Cychrus attenuatus				+ +(U) (9)
Pterostichus cristatus				+ +(U) (23)
Hymenoptera				
Siricidae				
Urocerus gigas	+(M,U) (2)			
Formicidae				
Formica lugubris				+ + +(M,U) (*)
Camponotus herculeanus	–	–	+ +(U) (*)	–

–, absence; +, 1–5 individuals; + +, 6–20 individuals; + + +, > 21 individuals.
Numbers of individuals are represented within brackets; *presence of a colony.

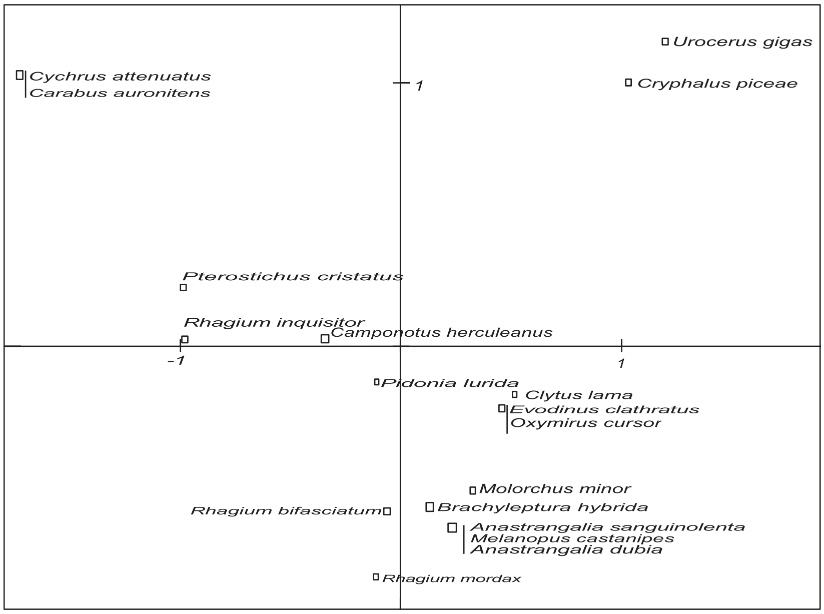

Fig. 4. Species ordination by canonical correspondence analysis (CCA) with additive effect of the decay stages of dead wood and management status.

In stages III and IV, adult and larval stages of xylophagous and saproxylophagous insects feeding on decaying wood belonged to the families Cerambycidae, Pyrochroidae and Elateridae. Most adults were collected near trees belonging to the degradation stage on SDT in both managed and unmanaged forests.

In stages V and VI, saproxylophagous insects colonised SDT 5–10 years after the first colonisation. Elateridae and Eucnemidae were recorded. Colonies of the carpenter ant *C. herculeanus* were also recorded in large numbers. Those insects were recorded on trees belonging to the degradation stage on SDT in unmanaged forests.

In a longer term process, strongly decaying wood (stage VII) on silver fir was observed in the degradation stage of unmanaged forests on SDT. It was found to be a suitable overwintering habitat for Carabid beetles when the base of trees was not colonised by the mount building ant *Formica lugubris* Zett. (Hym.Formicidae) (Lemperiere *et al*., 2002).

A major difference in the way dead wood could be assessed on beech as compared to silver fir was linked with the slow rotting process which occured from the heart to the outside of the tree. Two stages (stages III and IV) were assessed in the aggradation and biostatic stages in both managed and unmanaged forests. The adult Cerambycid species *Cerambyx scopolii* Fuesslins, *Clytus arietis* L., *Rhagium bifasciatum* Fabricius and *Rhagium mordax* Degeer, *Saperda scalaris* L. and the adult Elateridae *Ampedus erythrogonus* Müller were recorded. In the degradation stage of unmanaged forests, on the dead parts of old trees like trunk cavities or dead branches, where the decay was very slow, or on strongly decaying wood (stage VII), the presence of insects like the protected Cerambycid species *Rosalia alpina* L. or *Prionus coriarius* L. was recorded.

Adults of *Alosterna tabacicolor* Degeer, *Aromia moschata* L., *Pachytodes cerambyciformis* Schrank, *Ropalopus insubricus* Germar (Col.Cerambycidae) whose larvae developed on different broadleave trees (*Fraxinus excelsior* L., *Acer pseudoplatanus* L.) were also collected on flowering plants in open areas.

Most stages on both Silver fir and Beech were favourable habitats for many orders like Diptera (families Sciaridae, Lonchaeidae, Tipulidae…), Coleoptera (families Buprestidae, Staphylinidae, Lymexylonidae, Melandryidae) or mycetophagous insects that were not investigated in this study.

A strong effect was observed with the tree species as beech represented only a small proportion of SDT in the study area. In the same time, this tree species was hosting the protected longhorn species *R. alpina* L. (Col.Cerambycidae) which is included in the red list of the UICN and on the annexes II and IV of the 'Habitat' Directive and could then be considered as a priority habitat for conservation.

Discussion

Respective influence of management status and decay stages

Among the explanatory variables considered in this study, the most important factor determining biocenosis composition of ancient forests of the southern French Alps was the decay stage of dead wood, i.e. the insect habitat. Although the structure of the saproxylic insect composition showed a strong dependence on the different stages of decaying wood, with groups of species restricted to one particular stage, there was some influence from forest management status and other factors not taken into account in our study could certainly have influenced this biocenotic sequence.

Snags appeared to be relatively abundant in our case study (Marage & Lemperiere, 2005). Many authors observed that a large reduction of SDT was typical of managed forests (Andersson & Hytteborn, 1991; Kirby *et al*., 1991; Guby & Dobbertin, 1996; Green & Peterken, 1997). Because the environmental constraints were almost similar between sites, the natural disturbances erased the effects of silvicultural practices. This point supported the significance of the degradation stage in the overall structure of the forest ecosystem as mentioned by Leibundgut (1993) and Peterken (1996), even if land use and harvest planning history studies revealed that unmanaged forests were different from managed forests (Lamoisson, 2000).

Forestry implications

One of the underlying goals of our study was to provide initial baseline data regarding forest management in this area. The management of SDT resources must be considered according to the spatial arrangement and dynamics of all components of habitats for each species or functional group to provide a continuum of snag habitat across the landscape in a metapopulational context.

Species dependent on temporary substrates (e.g. snag or dead log) must be able to cope with the temporal and spatial gaps that could occur when individual substrate units were lost. Jonsson (2000) indicated that CWD could be very common both in space and time in natural forests. It is likely that species with fairly low dispersal ability and/or very special substrate demands have persisted. Presently, these species might have problems with increasing temporal and spatial gaps in the availability of dead wood within managed stands due to increasing distance between remnant old growth stands.

In the same time, silvicultural practices were beneficial for species whose adults live in open areas on flowering plants as it was the case for some that were observed (Kaila *et al*., 1997). Some of these insects could be considered as 'tourists' (Jonsson *et al*., 2005) for which trunks, logs and stumps constitute mating and egg laying sites for adults and breeding sites for larvae. Such practices also had an impact on the species composition of ant communities (Lemperiere *et al*., 2002).

In our case, the spatial pattern of forests and especially the neighbourhood of unmanaged and managed sites together with environmental stochasticity factors (i.e. storms) could fill the temporary gaps and allow the maintenance of biodiversity.

Biodiversity implications and consequences

The death of trees in a forest could be caused by several abiotic factors (pollution, drought stress, unsuitable sites) and/or biotic factors (presence of pathogens, defoliations, attacks by bark beetles under biocenotic sequences (Dajoz, 1974; Coudroy, 1984).

The presence of different forms of dead wood could be considered to be the result of the decay of a certain percentage of trees or parts of trees and measured in numbers of individuals per hectare or in volume per hectare as previously mentioned. This dead wood habitat could then vary in quality or forms and quantity and has been characterised by a long series of processes as described by McComb and Lindenmayer (1999) and Dajoz (1998).

For instance, stage II is an early successional stage of dead wood. This stage generates an ephemeral habitat which is suitable for specialist Curculionids and Scolytids living on silver fir and most often with one generation per year over 2–3 years in our case study. When the habitat becomes unsuitable, this assemblage of species which possesses a high dispersal ability could locally become extinct.

The following newly created habitats, stages III and IV could be considered as intermediate stages which are colonised by other assemblages of Cerambycidae and Elateridae species. In our study case, the richness and abundance of the studied groups were probably positively correlated with historical continuity at a local scale (Jonsson, 2000). Stages V and VI were persistent habitats that were colonised by species with limited dispersal ability excluding social insects. Some old established populations and the generations to come could then be temporarily deprived of their potential habitats and the necessary spatio-temporal and functional continuum could be affected in managed stands.

However, the actual populations of insects have gone through spatio-temporal discontinuities in a metapopulational context at the landscape level (Jonsson *et al*., 2005; Hanski 1998) without crucial impact of the distribution of this material on species richness.

The value of dead wood for conservation purposes could be of great importance as a large number of invertebrates are associated with this material. For invertebrates, a minimum volume of SDT ha^{-1} was required for habitat, microhabitat and species conservation and this volume had to be compatible with the management purposes of the forest. If the value of SDT and dead wood in general is high for conservation purposes and for maintaining the biodiversity and accordingly a minimum volume of SDT per ha is required for habitat and species conservation, it still has to be estimated in a case per case strategy.

There are still investigations to be carried out on other major indicator groups as mentioned earlier in this study and by different authors (Cancela Da Fonseca, 1993) to assess gains and losses according to the management status. Again it is difficult to estimate the gains and losses of diversity or species richness because of the restricted number of functional groups we assessed. However, we could suggest that an appropriate way to assess and monitor dead wood material (SDT and CWD) and its associated fauna could be carried out using the network of trophic levels and species diversity through a complexity index as developed by Cancela Da Fonseca (1993) for the soil fauna keeping in mind that as far as the final decay stages were concerned, cenotic levels and their species composition were more closely related with the fauna of the soil surface (Cancela Da Fonseca, 1993) defining dead wood as an epigenous organic annex of the soil (Gobat *et al.,* 2003).

In addition to its biodiversity value, dead wood has been used as fuel for centuries and still continues to be used by local populations (e.g. agdals zones in Morocco, where dead wood is still collected).

If Kirby (2001) mentioned that 'the more dead wood there is, the wider its size range and the wider the range of circumstances in which it occurs, the greater are the chances of it supporting a rich invertebrate fauna', then a local and temporary forest pest problem could be considered as a potential and optional candidate for maintaining the habitat diversity of this material and its presence accepted by forest managers.

In conservation areas, an integrated forest management could then be a compromise between forest pest management and conservation management to maintain and/or restore ecological processes (decay stages phases) at a large scale without artificially creating this material.

Acknowledgements

We would like to thank the 'Office National des Forêts' (France) for granting permission to sample in their forests and Dr K. Day for reviewing the English manuscript.

References

Ammer, U. (1991) Implications of the results of research on dead wood for forestry practice. *Forstwissenschaftliches Centralblatt*, **110**, 149–157.

Andersson, L.I. & Hytteborn, H. (1991) Bryophytes and decaying wood: a comparison between managed and natural forest. *Holarctic Ecology*, **14**, 121–130.

Benichou, P. & Le Breton, O. (1987) Prise en compte de la topographie pour la cartographie des champs pluviométriques statistiques. *La Météorologie*, **19**, 25–42.

Blondel, J. (1995) *Biogéographie. Approche Écologique et Évolutive*. Masson, Paris.

Bobiec, A. (2002) Living stands and dead wood in the Bialowieza forest: suggestions for restoration management. *Forest Ecology and Management*, **165**, 125–140.

Bormann, F.H. & Likens, G.E. (1994) *Pattern and Process in a Forested Ecosystem*. Springer-Verlag, New York, New York.

Boudjema, G., Lemperiere, G., Deschamps-Cottin, M. & Molland, D.G. (2006) Analysis and nonlinear modeling of the mound-building ant Formica lugubris spatial multi-scale dynamic in a larch-tree stand of the southern French Alps. *Ecological Modelling*, **190**, 147–158.

ter Braak, C.J.F. (1987) The analysis of vegetation-environment relationship by canonical correspondence analysis. *Vegetatio*, **69**, 69–77.

Bull, E.L., Parks, C.G. & Torgersen, T.R. (1997) *Trees and Logs Important to Wildlife in the Interior Columbia River Basin*. USDA Forest Service Pacific NW Region, Portland, Oregon.

Cancela Da Fonseca, J. (1993) Community composition: complexity versus diversity. *Bulletin Ecology*, **24**, 31–40.

Chessel, D. (1997) *Ordination Sous Contraintes*. Documentation de la Programmathèque ADE-4, Lyon, France.

Christensen, M. & Emborg, J. (1996) Biodiversity in natural versus managed forest in Denmark. Conservation of biological diversity in temperate and boreal forest ecosystems. *Forest Ecology and Management*, **85**, 47–51.

Coudroy, J.P. (1984) Enchaînement biocénotique des insectes xylophages du Sapin (*Abies alba* L.) en vallée d'Ossau: description des deux premiers groupes d'espèces. *Documents D'écologie Pyrénéenne III–IV*, 97–100.

Crites, S. & Dale, M.R.T. (1997) Diversity and abundance of bryophytes, lichens and fungi in relation to woody substrate and successional stage in aspen mixedwood boreal forests. *Canadian Journal of Botany*, **76**, 641–651.

Dajoz, R. (1974) Les insectes xylophages et leur rôle dans la dégradation du bois mort. *Ecologie Forestière* (ed. by P. Pesson), pp. 257–287. Gauthier-Villars, Paris, France.

Dajoz, R. (1998) *Ecologie des Insectes Forestiers*. Gauthier-Villars, Paris, France.

Franklin, J.F., Shugart, H.H. & Harmon, M.E. (1987) Tree death as an ecological process. *BioScience*, **37**, 550–556.

Gobat, J.M., Aragno, M. & Matthey, W. (2003) *Le Sol Vivant*. Presses Polytechniques et Universitaires Romandes.

Green, P. & Peterken, G.F. (1997) Variation in the amount of dead wood in the woodlands of the Lower Wye Valley UK, in the relation to the intensity of management. *Forest Ecology and Management*, **98**, 229–238.

Guby, N.A.B. & Dobbertin, M. (1996) Quantitative estimates of coarse woody debris and standing dead trees in selected Swiss forests. *Global Ecology and Biogeography Letters*, **5**, 327–341.

Hanski, I. (1998) Metapopulation dynamics. *Nature*, **396**, 41–49.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K. & Cummins, K.W. (1986) Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research*, **15**, 133–302.

Jonsell, M., Weslien, J. & EHNSTROeM, B. (1998) Substrate requirements of red-listed saproxylic invertebrates in Sweden. *Biodiversity and Conservation*, **7**, 749–764.

Jonsson, B.G. (2000) Availability of coarse woody debris in a boreal old-growth *Picea abies* forest. *Journal of Vegetation Science*, **11**, 51–56.

Jonsson, B.G., Kruys, N. & Ranius, T. (2005) Ecology of species living on dead wood – lessons for dead wood management. *Silva Fennica*, **39**, 289–309.

Kaila, L., Martikaïnen, P. & Puntil, P. (1997) Dead trees left in clear-cuts benefit saproxylic Coleoptera adapted natural disturbance in boreal forest. *Biodiversity and Conservation*, **6**, 1–18.

Kirby, P. (2001) *Habitat Management for Invertebrates: A Practical Handbook*. Royal Society for Protection of Birds edn, Join Conservation Commitee, The lodge sandy bedfordshire.

Kirby, K.J., Webster, S.D. & Anctzak, A. (1991) Effects of forest management on stand structure and quantity of fallen dead wood: some British and Polish examples. *Forest Ecology and Management*, **43**, 167–174.

Koop, H. & Hilgen, P. (1987) Forest dynamics and regeneration mosaic shifts in unexploited beech (*Fagus sylvatica*) stands at Fontainebleau (France). *Forest Ecology and Management*, **20**, 135–150.

Lamoisson, A. (2000) *Reconstitution Historique et Analyse de la Gestion Forestière du Bassin Versant de Rabou-Chaudun aux 19ème et 20ème Siècles (Hautes-Alpes)*. INA-PG, Paris, France.

Lebreton, J.D., Sabatier, R., Banco, G. & Bacou, A.M. (1991) Principal component and correspondence analyses with respect to instrumental variables: an overview of their role in studies of structure–activity and species–environment relationships. *Applied Multivariate Analysis in SAR and Environmental Studies* (ed. by J. Devillers and W. Karcher), pp. 85–114. Kluwer, Dordrecht, The Netherlands.

Leibundgut, H. (1993) *Europäische Urwälder*. Paul Haupt, Berne.

Lemperiere, G., Bourbon, G., Buray, A. & Franchini, S. (2002) Etude des populations de fourmis rousses dans cinq sites du bassin deGap-Chaudun (Hautes-Alpes). *Revue Forestiere Francaise*, **54**, 419–428.

Lemperiere, G., Conord, C., Fleury, S. & Day, K. (2005) 'Dr Saproxyl et Mr Pest': compromis ou conflits potentiels entre santé de la forêt et biodiversité. Eds Tec et Doc Lavoisier.

Lott, D.A. & Eyre, M.D. (1996). Invertebrate Sampling Methods in Environmental Monitoring Surveillance and Conservation using Invertebrates. EMS Publications edn, Newcastle-upon-Tyne, UK.

Maeto, K., Sato, S. & Miyata, H. (2002) Species diversity of longicorn beetles in humid warm temperate forests: the impact of forest management practices on old-growth forest species in southwestern Japan. *Biodiversity and Conservation*, **11**, 1919–1937.

Marage, D. & Lemperiere, G. (2005) The management of snags: a comparison in managed and unmanaged ancient forests of the southern French Alps. *Annals of Forest Science*, **62**, 135–142.

Mc Carthy, B.C. & Bailey, R.R. (1994) Distribution and abundance of coarse woody debris in a managed forest landscape of the central Appalachians. *Canadian Journal of Forest Research*, **24**, 1317–1329.

McComb, W. & Lindenmayer, D. (1999) Dying, dead, and down trees. *Maintaining Biodiversity in Forest Ecosystems* (ed. by M.L. Hunter), pp. 335–361. Cambridge University Press, Cambridge, UK.

Norden, B. & Appelqvist, T. (2001) Conceptual problems of Ecological Continuity and its bioindicators. *Biodiversity and Conservation*, **10**, 779–791.

Økland, R.H. (1996) Are ordination and constrained ordination alternative or complementary strategies in general ecological studies? *Journal of Vegetation Science*, **7**, 289–292.

Økland, R.H. (1999) On the variation explained by ordination and constrained ordination axes. *Journal of Vegetation Science*, **10**, 131–136.

Økland, R.H. & Eilertsen, O. (1994) Canonical correspondence analysis with variation partitioning: some comments and an application. *Journal of Vegetation Science*, **5**, 117–126.

Oldeman, R.A.A. (1990) *Forest, Elements of Sylvology*. Springer-Verlag, Berlin, Germany.

Peterken, G.F. (1996) *Natural Woodland, Ecology and Conservation in Northern Temperate Regions*. Cambridge University Press, Cambridge, UK.

Prodon, R. & Lebreton, J.D. (1994) Analyses multivariées des relations espèces-milieu: structure et interprétation cologique. *Vie et Milieu*, **44**, 69–91.

Rameau, J.C. (1992) Dynamique de la végétation à l'étage montagnard dans les Alpes du sud. Première approche des hêtraie-sapinières. Les applications possibles au niveau de la gestion. *Revue Forestiere Francaise*, **44**, 393–413.

Sabatier, R., Lebreton, J.D. & Chessel, D. (1989) Principal component analysis with instrumental variables as a tool for modelling composition data. *Multiway Data Analysis* (ed. by R. Coppi and S. Bolasco), pp. 341–352. Elsevier, Amsterdam.

Samuelsson, J., Gustafsson, L. & Ingelög, T. (1994) *Dying and Dead Trees: A Review of Their Importance for Biodiversity*. Swedish Threatened Species Unit, Uppsala, Sweden.

Schnitzler, A. & Borlea, F. (1998) Lessons from natural forests as keys for sustainable management and improvement of naturalness in managed broadleaved forests. *Forest Ecology and Management*, **109**, 293–303.

Spagarino, C., Pastur, G.M. & Peri, P.L. (2001) Changes in Nothofagus pumilio forest biodiversity during the forest management cycle. 1. Insects. *Biodiversity and Conservation*, **10**, 2077–2092.

Speight, M.R. & Wainhouse, D. (1989) *Ecology and Management of Forest Insects*. Clarendon Press, Oxford, UK.

Thioulouse, J., Chessel, D., Dolédec, S. & Olivier, J.M. (1997) ADE-4: a multivariate analysis and graphical display software. *Statistics and Computing*, **7**, 75–83.

Thomas, J.W. (1979) *Wildlife Habitats in Managed Forests in the Blue Mountains of Oregon and Washington*. USDA Forest Service Pacific NW Region, Portland, Oregon.

Yoccoz, N. & Chessel, D. (1988) Ordination sous contrainte de relevés d'avifaune: limination d'effets dans un plan d'observation deux facteurs. *Compte Rendus Académie Science*, **307**, 189–194.

Accepted 17 March 2010
First published online 28 April 2010

Editor: Simon R. Leather
Associate editor: Donald Quicke