Animal Conservation. Print ISSN 1367-9430

Does a set-aside conservation strategy help the restoration of old-growth forest attributes and recolonization by saproxylic beetles?

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Keywords
delayed harvesting; forest reserves; temperate deciduous forests; insect biodiversity; deadwood; tree microhabitats.

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Editor: Darren Evans
Associate Editor: Nick Isaac

Received 06 May 2013; accepted 28 November 2013

doi:10.1111/acv.12101

Abstract

The decline of many saproxylic species results from the decrease in old-growth structures in European harvested forests. Among conservation tools, protected reserves withdrawn from regular harvesting and extended rotations have been employed to restore old-growth attributes in structurally simplified managed forests, even if the effects of such management actions on forest habitats and biodiversity remain largely unknown.

In this study, we compared structural stand features and saproxylic beetle assemblages in two stand classes – recently harvested stands and long-established reserves, where less or more than 30 years had elapsed since last harvest. Habitat and saproxylic beetle data were collected according to standardized protocols in 153 plots in seven lowland deciduous forests.

Tangible contrasts in stand features were found between long-established reserves and recently harvested plots. Indeed, most higher-value densities and volumes were found in unharvested areas. The difference was weaker for microhabitat-bearing tree density than for deadwood; some deadwood features, such as volume of large downed and standing deadwood showed a very pronounced difference, thus indicating a marked deleterious effect of forest harvesting on these elements. Deadwood diversity, on the other hand, was only slightly affected and the level of stand openness did not change.

The response of saproxylic beetles to delayed harvesting was weaker than the structural changes in deadwood features. Nevertheless, long-established reserves showed higher species richness and slightly but significantly dissimilar species assemblages than recently harvested plots. Indeed even if only some guilds weakly increased in non-harvested plots, harvesting classes significantly affected the abundance of a quarter of the species tested.

Our results tend to question measures such as rotating and temporarily ageing patches. We argue in favor of permanent strict fixed-location reserves. Future work should examine how stands recover old-growth forest attributes and how the associated saproxylic fauna colonizes in the long term.

Introduction

European forest dynamics has been deeply affected by forestry and forest fragmentation for millennia (Peterken, 1996). Stand composition and structure have been greatly simplified by harvesting and other uses, even in remote areas. Several studies demonstrated the negative effects of conventional management practices on old-growth structures (e.g. Burrascano *et al.*, 2013; Green & Peterken, 1997; Lombardi *et al.*, 2008). Structural simplification has been shown to result in the decline of many associated saproxylic populations, but the issue has received more attention in

North America and northern Europe than in central and southern Europe (e.g. Martikainen *et al.*, 2000; Grove, 2002).

In forests subjected to structural simplification through harvesting, strategies to restore old-growth attributes may involve (1) setting aside forest plots, (2) extended rotations, (3) retention of structural features at the time of harvest and (Keeton, 2006) (4) man-made restoration of structural elements (Martikainen *et al.*, 2000). In the last 20 years, there has been an increasing focus on systematic conservation planning, that is how to select protected areas in a way that captures biodiversity as efficiently as possible (e.g. Margules & Pressey, 2000). Protected forests include different protection categories and surface areas (Schmitt *et al.*, 2009) and they are described worldwide in countless ways. Areas 'left for natural dynamics' can be found in several protection categories often as (so-called) strict forest reserves, where neither silvicultural intervention nor any other avoidable human impacts are allowed, but other denominations abound: wilderness areas, areas withdrawn from regular management, abandoned, unharvested, set-aside forest areas or unmanaged core areas in national parks. Among passive restoration strategies (Bauhus, Puettmann & Messier, 2009), small-scale management tools such as delaying harvesting, leaving unharvested patches or preserving habitat trees (Lachat & Bütler, 2009) have been employed to increase the number of old-growth structures in forests (Bauhus *et al.*, 2009). Other examples include woodland-key habitats, green-tree retention patches left in clearcuts as short-term refuges or lifeboats for many organisms during the regeneration phase in Scandinavia and North America (e.g. Vanha-Majamaa & Jalonen, 2001, Aubry *et al.*, 1999), ageing or old-growth patches kept as portions of management units in France (Lassauce *et al.*, 2013). Despite an increase in the number of empirical studies concerning the effects of forest abandonment on species diversity (see Paillet *et al.*, 2010), the relative efficiency of each management strategy in supporting biodiversity remains unknown. When harvesting activities are delayed for several decades, natural forest dynamics may bring about structural changes that restore old-growth attributes, depending on site potential (Vandekerkhove *et al.*, 2009): larger trees, heterogeneous vertical and horizontal structure with greater variations in tree size, age, spacing and species composition, increased supplies of deadwood, more large snags and fallen trees, multiple canopy layers, changes in disturbance regime, canopy gaps and understory patchiness. These structural changes have been recorded in several case studies (e.g. Lassauce *et al.*, 2012, 2013, Sitzia *et al.*, 2012) and may impact biodiversity.

In this study, we compared the habitat parameters and the diversity of saproxylic beetles (i.e. abundance, species richness and composition) in set-aside and harvested areas in seven lowland deciduous French forests. The issues were addressed in two steps: (1) How were saproxylic habitat parameters, such as the diversity and density of deadwood and tree microhabitats, affected in long-established set-aside plots compared with recently harvested plots? (2) Did saproxylic beetle assemblages (including rare species) respond to these habitat changes?

Material and methods

Study areas

The plots were located in seven lowland beech, *Fagus sylvatica* L., and oak, *Quercus robur* L and *Q. petraea* (Mattus.) Liebl., forests (Table 1) in the Atlantic or Continental biogeographic domain. Each forest was several hundred kilometers from the others: one in western France (Chize), three in eastern France (Auberive, Citeaux, Combe-Lavaux), one in central France (Troncais) and two in northern France (Rambouillet, Fontainebleau). The plots in each forest were several hundred meters apart. A design of 153 plots was set up in managed stands (98) and in recently (16) or long-established (39) forest reserves. Managed forests were coppice-with-standards under conversion to high forest (33), even-aged (54) or uneven-aged (11) high forests (see Supporting Information Table S1). All plots were located in mature stands before regeneration felling or final cut. Last harvests consist of thinning operations in even-aged high forests and single tree removals in coppice-with-standards stands under conversion and uneven-aged high forests. The time elapsed from last harvest was postulated

Table 1 Sampling design layout. Among long-established reserves (L-UNH), old (> 30 years) and very old reserves (> 100 years) were not tested separately due to the small number of replicates available in the latter category. Managed plots and recently established reserves are grouped in R-HAR. Sampling year between brackets

	Beech			Oak			
		L-UNH > 30 yrs			L-UNH > 30 yrs		
	R-HAR < 30 years	30–100 years	> 100 years	R-HAR < 30 years	30–100 years	> 100 years	Total
Auberive [2009]	11	4		7	2		24
Chize [2010]	10	2		12			24
Citeaux [2010]				6	6		12
Combe-Lavaux [2010]	3	2		1	2		8
Fontainebleau [2008]	5	3	9	7			24
Rambouillet [2007]				24	6		30
Troncais [2009]				28	3		31
Total	29	11	9	85	19	0	153

for each plot based on management plans, reports or information from local managers. Unlike Christensen *et al.* (2005), we did not derive the number of years since last harvest from the official establishment date of the reserves as these do not necessarily coincide. Because the time since last harvest was not precisely known in several cases, we classified the plots into two harvesting classes based on the best estimate of the length of time without harvesting or removal of trees and deadwood (Table 1): 'recently harvested' (R-HAR < 30 years ago, $n = 114$), including harvested plots ($n = 98$) and recently established reserves ($n = 16$); or long-established reserves (L-UNH > 30 years, $n = 39$), including old (> 30 years and < 100 years, $n = 30$) and very old reserves (> 100 years, $n = 9$). Very old reserves were found in the Fontainebleau state forest only. We collected environmental and entomological data following standardized protocols.

Beetle sampling and identification, species characterization

Flying saproxylic beetles were sampled by two cross-vane flight interception traps (Polytrap™, E.I. Purpan, Toulouse, France) per plot, set about 20 m from each other, for a total number of 306 traps. The unbaited traps were suspended roughly 1.5 m above ground. Active insects were collected from April to August during 1 year. For each species in all the taxa from the ±50 families recorded, we characterized degree of geographic rarity in France according to the FRISBEE database (http://frisbee.nogent.cemagref.fr/index.php/en/) and distinguished common (abundant and/or widely distributed) and rare (not abundant and only locally distributed) species. All species were assigned to one saproxylic trophic group, but only the four main guilds were studied (xylomycetophagous, xylophagous, saproxylophagous and zoophagous).

Stand and deadwood variables

We used a combination of fixed-area and fixed-angle techniques to estimate (1) wood volumes for live trees, snags, logs and stumps, and (2) the basal area of live trees on 0.15 ha (Fontainebleau, Auberive, Chize, Citeaux, Combe-Lavaux) or 0.30 ha (Rambouillet, Troncais) plots. We set a minimum diameter of 7.5 cm for live trees, snags and logs.

Four variables were used to describe the deadwood: tree species, diameter (six classes: 5, 10–15, 20–25, 30–40, 50–65, > 70 cm), position (log, snag, stump), decay stage [nine classes adapted from Sippola, Siitonen & Kallio (1998) and Larjavaara & Muller-Landau (2010) and crossing three classes of remaining bark cover (from 95% of the stem still covered by attached bark to missing bark over the whole stem) and three classes of inner wood hardness assessed by 'knife penetration test' (from hard outer wood to deeply disintegrated and soft inner wood)]. A deadwood diversity index was calculated as the number of observed deadwood types, that is the number of combinations of the above four variables (tree species × diameter class × decay class × position), as suggested by Siitonen *et al.* (2000). The volume of live trees was calculated using wood volume tables based on the dbh variable, and used to estimate the deadwood volume ratio (= dead wood/(live + dead wood)), accounting for site productivity (Hahn & Christensen, 2004). Based on the deadwood surveys, we selected seven deadwood variables for analysis: (1) deadwood volume, (2) deadwood volume ratio, (3) number of deadwood types, (4) standing deadwood volume, (5) large standing deadwood (diameter > 40 cm) volume, (6) downed deadwood volume, and (7) large downed deadwood (diameter > 40 cm) volume. The thresholds defining large deadwood, large and very large trees were inspired by results in Nilsson *et al.* (2003) and Larrieu & Cabanettes (2012).

The basal area of large trees (67.5 < dbh ≤ 87.5 cm) and very large trees (dbh > 87.5 cm) were measured on 0.15–0.3 ha plots; the density of large trees was also inventoried in 1-ha circular plots. Tree microhabitat densities were inventoried during leaf-burst in 1-ha circular plots centered around the two flight traps. We recorded seven microhabitat types borne by live trees (Larrieu & Cabanettes, 2012): (1) 'empty' cavities, (2) cavities with mould, (3) fruiting bodies of saproxylic fungi, (4) sap runs, (5) dead branches, (6) tree crown deadwood, and (7) missing bark [i.e. hard patches of wood with no bark > 600 cm^2] (see Table 2 for further details on predictors). Microhabitats other than crown deadwood were only recorded when visible on the trunk beneath and within the tree crown. Trees with more than one microhabitat of the same type were counted only once, but trees bearing more than one microhabitat type were counted once for each microhabitat type. The total density of microhabitats, the number of microhabitat types (among the seven observed types) and the individual densities of four microhabitat types ('empty' and mould cavities pooled, dead branches and tree crown deadwood pooled, sporocarps of saproxylic fungi and sap runs) were considered for analysis. Stand openness was assessed as the total proportion of open areas (clearings, edges, stand surface with a well-developed herb layer composed of flowering plants) in a 1 ha plot. For further details on how the environmental variables were measured, see Bouget *et al.* (2013).

Data analysis

Our main objectives were to compare (1) stand structural characteristics and (2) saproxylic beetle assemblages in the two stand classes (R-HAR and L-UNH) based on the amount of time elapsed since last harvest. Because the same set of environmental variables was used for both traps in the same plot, the catches of the two traps were combined prior to analyses carried out at the plot level.

The differences in mean values of structural stand features between recently harvested and long-established reserves were analyzed with a Generalized Gaussian or Poisson Linear Mixed Model where 'forest' was a spatially implicit random effect on the intercept (lmer function in lme4 R-package).

Table 2 Effect of the harvesting class on stand characteristics (deadwood, microhabitat, large trees, openness)

	Factor	Detail	Signif	Est R-HAR	Est L-UNH	Ratio	Error distribution family
Stand features	Basal area of large trees	Basal area of large trees in a 0.3 ha plot (67.5 < dbh ≤ 87.5 cm) (m^2 ha^{-1})	***	2.957 (1.579)	7.198 (1.663)	2.43	Gaussian
	Basal area of very large trees	Basal area of the very large trees in a 0.3 ha plot (dbh > 87.5 cm) (m^2 ha^{-1})	***	0.501 (0.591)	2.405 (0.628)	4.80	Gaussian
	Density of large trees	Number of large trees in a 1 ha plot (dbh > 67. 5 cm)	***	1.389 (0.487)	2.116 (0.487)	1.52	Poisson
	Openness	Proportion in cumulative area of open areas (clearings, edges, areas with a well-developed herb layer composed of flowering plants) (%) in a circular 1 ha plot	NS	12.490 (5.188)	11.667 (5.962)		Gaussian
MH features	Density of microhabitat-bearing trees	Total density of microhabitat-bearing trees in a 1 ha plot	***	2.647 (0.129)	3.046 (0.131)	1.15	Poisson
	Number of microhabitat types	Number of microhabitat types in a 1 ha plot	**	1.468 (0.061)	1.702 (0.070)	1.16	Poisson
	Density of cavity-bearing trees	Density of cavity-bearing trees in a 1 ha plot: 'empty' cavities with an entrance above 3 cm in width, woodpecker breeding and feeding holes, deep cavities formed between roots, cavities with mould with an entrance above 10 cm in width	***	1.620 (0.093)	2.208 (0.098)	1.36	Poisson
	Density of fungus-bearing trees	Density of fungus-bearing trees in a 1 ha plot: fruiting bodies of tough or pulpy saproxylic fungi, > 5 cm in diameter	***	0.397 (0.203)	0.458 (0.208)	1.15	Poisson
	Density of deadwood-bearing trees	Density of deadwood-bearing trees a 1 ha plot: crown deadwood in (large dead branches > 20 cm in diameter and > 1 m in length, crown deadwood volume > 20% of the total crown wood volume)	**	1.624 (0.276)	1.824 (0.278)	1.12	Poisson
	Density of sap-run-bearing trees	Density of sap-run-bearing trees: sap runs > 10 cm in length in a 1 ha plot	NS	−1.142 (0.327)	−1.359 (0.394)		Poisson
DW features	Deadwood volume	Total volume of deadwood in a 0.3 ha plot (m^3 ha^{-1})	***	22.677 (9.539)	79.976 (10.992)	3.53	Gaussian
	Deadwood ratio	Volume ratio = deadwood /(Live trees+deadwood)	***	0.099 (0.025)	0.225 (0.030)	2.27	Gaussian
	Large downed deadwood volume	Volume of large downed deadwood (> 40 cm in diameter) in a 0.3 ha plot (m^3 ha^{-1})	***	3.052 (4.029)	27.387 (4.875)	8.97	Gaussian
	Large standing deadwood volume	Volume of large standing deadwood (> 40 cm in diameter)) in a 0.3 ha plot (m^3 ha^{-1})	***	2.123 (3.067)	18.658 (3.701)	8.79	Gaussian
	Standing deadwood volume	Volume of standing deadwood (> 10 cm in diameter) in a 0.3 ha plot (m^3 ha^{-1})	***	4.529 (2.811)	21.910 (3.572)	4.84	Gaussian
	Downed deadwood volume	Volume of downed deadwood (> 10 cm in diameter) in a 0.3 ha plot (m^3 ha^{-1})	***	16.791 (7.487)	57.373 (8.684)	3.42	Gaussian
	Number of deadwood types	Nb deadwood types (tree species*diameter*decay*position)	**	2.400 (0.243)	2.559 (0.245)	1.07	Poisson

Stands were classified as recently managed (R-HAR < 30 years ago) or long-established reserves (L-UNH > 30 years ago). Differences in stand features between the two harvesting classes were tested with a linear mixed model (NS = not significant; *$0.05 > P > 0.01$; **$0.05 > P > 0.001$; ***$P < 0.001$). Ratio = ratio dividing estimates of L-UNH by R-HAR (see Material and Methods) (SE between parentheses).

To rank the effect of the harvesting variable among structural predictors of variations in common or rare species richness, we assessed the multimodel-averaged estimates (Burnham & Anderson, 2002) determining the response of species richness to stand features. As colinearity among predictor variables may lead to unreliable parameter estimates, we implemented the strategy suggested by Zuur, Ieno & Elphick (2010) to address multicolinearity before model averaging. We sequentially dropped the covariate with the highest variance inflation factor (VIF), then recalculated the VIFs and repeated this process until all VIFs were below a preselected threshold (Zuur *et al.*, 2010 suggest a cut off at 3). We used the 'vif.mer' function to calculate VIFs for linear mixed-effects models built using the lmer function in the 'lme4' package (Table 2). As the relationship between species richness and deadwood volumes is better described by semi-log models (Martikainen *et al.*, 2000), we used (log x+1)-transformed values for deadwood volumes. The selected variables with VIF < 3 were: harvesting class, openness, basal area of very large trees (dbh > 87.5 cm), large tree 1 ha density, density of sap-run-bearing trees, density of fungus-bearing trees, density of cavity-bearing trees, density of crown deadwood-bearing trees, number of microhabitat types, total deadwood volume, deadwood ratio, log10 (large downed deadwood volume), log10 (large standing deadwood volume). For each response variable, we generated the null model and generalized linear mixed models (Poisson error structure) with all the combinations of two explanatory variables. Using the differences in the Akaike information criterion (AICc) scores between each model and the best model (ΔAICc) as well as the Akaike weights for each model, we calculated the model-averaged estimates. Only significant variables ($P < 0.10$ across all the models) were displayed (lme4, MuMIn, arm; R-packages).

To rank the effect of the harvesting variable among structural predictors on variations in species composition (including singletons), we performed a Canonical Analysis of Principal coordinates (vegan R-package, CAP, Anderson & Willis, 2003). Based on Jaccard distance matrices, we carried out inertia partitioning on all explanatory environmental variables, as colinearity among predictor variables is not considered to be a problem in CAP. We calculated total constrained inertia, the marginal (intrinsic) inertia explained by each variable (with all other variables partialled out before analysis), the latter's statistical significance (permutation tests – 100 runs) and the relative contribution of each set of variables (deadwood, microhabitat, stand, forest, harvesting class) to constrained inertia. In addition, we used a pairwise ANOSIM procedure based on Jaccard distance matrices to test for differences in assemblage composition among predefined groups with spatially constrained permutation tests (Clarke, 1993); the grouping factor was the harvesting treatment and the spatial constraint the forest.

We also used a generalized linear mixed model, with a spatially implicit variable (forest) as a random factor on the intercept and a Poisson error distribution, to analyze the differences between the two harvesting classes in (1) mean abundance and richness per plot of rare or common species and trophic groups, and (2) mean abundance of selected species (more than 20 individuals caught and occurring in at least 10 out of the 153 plots in our data set). Since we found a close correlation between total abundance and the number of beetle species recorded on a plot, we used the number of individuals as a covariate in the richness models (Gotelli & Colwell, 2001) to separate the effects on the number of individuals from species effects. To analyze differences in occurrence per plot of selected beetle species between the two harvesting classes, we used a generalized linear mixed model with a binomial error structure and 'forest' as a spatial random effect (lmer function in lme4 R-package). In order to quantify the magnitude of significant differences between R-HAR and L-UNH treatments, we computed an index by dividing model estimates for each of the harvesting treatments (estimate L-UNH/ estimate R-HAR) with 'forest' as a random factor.

All analyses were conducted using R v2.12.0. All R-packages used are available online at http://cran.r-project.org/web/packages/available_packages_by_name.html. The 'vif.mer' function is available online at https://github.com/aufrank/R-hacks/blob/master/mer-utils.R.

Results

Overall, the compiled dataset included 99 383 individuals in 476 beetle species (25 taxa identified at the genus level only), among which 377 common, 69 rare (15% of the total number) and 30 species with an undefined rarity status were recorded.

Habitat parameters in R-HAR plots versus L-UNH

Significant differences in stand features (deadwood, microhabitat, large trees, openness) were measured between L-UNH and R-HAR (Table 2). Values for deadwood (deadwood volume, deadwood ratio, number of deadwood types, downed deadwood volume, large standing deadwood volume, standing deadwood volume, large standing deadwood volume), microhabitats (density of microhabitat-bearing trees, number of microhabitat types, density of cavity-bearing trees, density of deadwood-bearing trees, density of fungus-bearing trees) and large tree characteristics (basal area of large trees and very large trees, density of large trees) were always considerably higher in L-UNH than in R-HAR plots. Deadwood diversity was only slightly, although significantly, higher in L-UNH. Only the density of sap-run-bearing trees and openness values remained significantly unaffected by the harvesting class.

The magnitude of the differences between R-HAR and L-UNH plots was even more pronounced with respect to certain deadwood features. These differences were characterized by a high relative increase from R-HAR to L-UNH that is the ratio dividing estimates in L-UNH by R-HAR for four variables: large downed deadwood volume

(estimate ratio = 8.97), large standing deadwood volume (estimate ratio = 8.79), standing deadwood volume (estimate ratio = 4.84) and basal area of very large trees (estimate ratio = 4.80). This indicates a strong negative effect of forest harvesting on those attributes. According to the estimate ratio, the differences measured between L-UNH and R-HAR plots were even more pronounced for large deadwood volumes than for large tree characteristics. Microhabitat features were not as impacted as were deadwood and stand features by the harvesting class (Table 2).

Saproxylic beetle diversity in R-HAR plots versus L-UNH

Species composition

Variations in total inertia of saproxylic beetle assemblages were explained by geographical (35.0%), deadwood (9.0%), microhabitats (8.8%) and stand structural characteristics (7.0%) (Table 3). Only openness, microhabitat diversity, deadwood ratio and deadwood diversity had a significant ($P < 0.05$), although marginal, contribution to variations in species composition. As along with the density of fungus-bearing trees and large standing deadwood volume, the class of time elapsed since harvesting showed a non-significant trend ($P < 0.1$), accounting for only 1.7% of the constrained inertia. A spatially constrained ANOSIM test also showed slightly, but significantly, dissimilar species assemblages between the harvesting classes (1000 permutations, R: 0.168; significance: 0.002).

Species richness

The class of time elapsed since harvesting was not a key variable for saproxylic beetle species richness; it ranked fifth in explanatory value among the 12 structural stand features and was only slightly significant (Table 4). L-UNH, however, showed a higher saproxylic beetle species richness than R-HAR plots (Table 4). The best models for both rare and common species were the number of deadwood types and openness, and the best for common species was deadwood volume ratio.

Table 3 Ranked effect of the harvesting class among structural and spatial predictors on variations in species composition

	Predictors	Cumulated marginal inertia	%CI
Spatial	Forest**	7.348	34.97%
Set-aside	Harvesting class°	0.357	1.699%
Stand	Basal area of large trees, basal area of very large trees, density of large trees, openness**	1.475	7.019%
MH	Total density of microhabitats, number of microhabitat types*, density of cavity-bearing trees, of fungus-bearing trees°, of deadwood-bearing trees, of sap-run-bearing trees	1.863	8.866%
DW	log10 (Total volume deadwood), Deadwood ratio*, log10 (large downed deadwood volume), log10 (large standing deadwood volume)°, log10 (downed deadwood volume), log10 (standing deadwood volume), Number of deadwood types*	1.899	9.041%

Canonical Analysis of Principal coordinates (CAP) used to partition the variation in the response species-plot matrix with respect to the combination of explanatory stand features (deadwood, microhabitat, large trees, openness); %CI: relative contribution to constrained inertia. Significance of marginal contribution to inertia: °0.1 > P > 0.05; *0.05 > P > 0.01; **0.01 > P > 0.001.

Table 4 Ranked effect of the harvesting class among structural predictors on variations in species richness. Multimodel averaged estimates for structural stand features (deadwood, microhabitats, large trees, openness) and harvesting class determining the response of saproxylic beetle species richness (rare, common). Relative importance is the weight of evidence for each parameter across all the best models combining several variables (mixed-effect models, with forest as a random effect)

species richness	variable	Variable Model-averaged estimate (significance)	Relative contribution	Best models (DeltaAICc < 3)	
Rare	1. Number of deadwood types	1.48***	0.93	divDW+open	AICc = 596.8
	2. Openness	0.81**	0.65		
Common	1. Openness	10.02***	1.00	open+ratio	AICc = 1166.7
	2. Deadwood ratio	6.53***	0.51	divDW +open	AICc = 1167.0
	3. Number of deadwood types	10.81***	0.45		
	4. Harvesting class	3.92°	0.01		
	5. Density of cavity-bearing trees	3.70°	0.01		
	6. log10 (Volume of large downed deadwood)	3.70°	0.01		

Only significant variables (°0.1 > P > 0.05; *0.05 > P > 0.01; **0.01 > P > 0.001; ***P < 0.001) were selected.

Table 5 Values of the estimates (s.e. between parentheses) from generalized linear mixed effect models with a Poisson error distribution for abundance and richness of ecological groups of saproxylic beetles species in 'recently harvested (R-HAR < 30 years ago) or 'long-established reserves' (L-UNH > 30 years ago)

		Abundance		Species richness	
		Estimate R-HAR	Estimate L-UNH	Estimate R-HAR	Estimate L-UNH
Feeding guilds	Mycophagous	4.066 (0.306)	4.201 (0.306)***	2.25 (0.099)	2.395 (0.106)*
	Saproxylophagous	2.345 (0.340)	2.533 (0.341)***	1.339 (0.172)	1.415 (0.180) NS
	Zoophagous	4.029 (0.154)	4.038 (0.155) NS	2.099 (0.119)	2.233 (0.124)*
	Xylophagous	5.056 (0.457)	4.745 (0.457)***	2.65 (0.077)	2.601 (0.084) NS
Rarity groups	Common	5.773 (0.341)	5.572 (0.341)***	3.682 (0.001)	3.776 (0.001)**
	Rare	2.073 (0.431)	2.27 (0.432)***	0.744 (0.184)	0.919 (0.1985) NS
	Total	5.859 (0.326)	5.672 (0.326)***	3.786 (0.001)	3.889 (0.001)***

Probability (*P*) of a significant difference between mean values is indicated by: NS = not significant. $*P < 0.05$, $**P < 0.01$, $***P < 0.001$. We used the abundance of a covariate in species richness models.

Guild composition

The abundance of common and xylophagous species was significantly lower in L-UNH than in R-HAR plots. Zoophagous species abundance was not sensitive to the harvesting class. In contrast, mycophagous, saproxylophagous and rare species were more abundant in L-UNH. The number of mycophagous, zoophagous and common species per plot, after accounting for abundance, was slightly, but significantly, higher in L-UNH. For saproxylophagous, xylophagous and rare species, no significant difference in species richness was observed between harvesting classes (Table 5).

Individual species responses

At the individual species level, about 25% ($n = 39$.) of the tested species had a significant response in abundance to the harvesting class. The same proportion of significantly responding species occurred in both harvesting classes: half of the species were significantly more abundant in R-HAR plots, and half were significantly more abundant in L-UNH. Two rare taxa were included among the species responding positively to L-UNH (none were found in R-HAR plots; Table 6).

Table 6 Difference in abundance per plot of selected species between 'recently harvested' (R-HAR < 30 years ago) or 'long-established reserves' (L-UNH > 30 years ago) plots

Abundance > in R-HAR	Abundance > in L-UNH
Ampedus quercicola	*Anaspis flava*
Anaglyptus mysticus	***Anaspis melanopa***
Anostirus purpureus	*Cis boleti*
Aulonothroscus brevicollis	*Clerus mutillarius*
Cyclorhipidion bodoanus	*Corticeus unicolor*
Ernoporicus fagi	*Cryptarcha undata*
Hemicoelus fulvicornis	*Dasytes plumbeus*
Hylecoetus dermestoides	*Dryocoetes villosus*
Leiopus femoratus	*Hylis olexai*
Litargus connexus	*Mycetochara maura*
Megatoma undata	*Mycetophagus ater*(*)
Phymatodes testaceus	*Oxylaemus cylindricus*
Platycerus caraboides	***Paromalus parallelepipedus***
Stenocorus meridianus	*Ptilinus fuscus*(*)
Taphrorychus bicolor	*Rhagium bifasciatum*
Tetratoma ancora	*Scolytus rugulosus*
Vincenzellus ruficollis	*Thanasimus formicarius*
Xyleborinus saxesenii	*Tritoma bipustulata*
Xyleborus dispar	*Trypodendron signatum*
	Xyleborus dryographus

Only significant differences are shown (*P*-value < 0.001 after a Bonferroni correction for 150 tests). Only species sampled in at least 10 plots and with more than 20 individuals were analyzed, with generalized linear mixed-effect models and a binomial error distribution; 'forest' was a random factor. Bold indicates significant in occurrence, (*) indicates rare species.

Discussion

Changes in stand structure induced by non-harvesting

In L-UNH (i.e. plots set-aside for at least 30 years) originating from managed stands, we measured tangible contrasts in stand characteristics compared with R-HAR plots. Indeed, most of the stand characteristics we studied displayed higher volume and density values in long-established set-asides than in R-HAR areas.

More than 30 years without harvesting allowed the deadwood volumes to increase significantly. Vandekerkhove *et al.* (2005) already showed that deadwood can accumulate quite fast in forest reserves, especially in terms of density. In abandoned beech forests in Germany, Meyer & Schmidt (2011) indicated a rather fast relative increase in deadwood volume: total deadwood doubled in about 9 years (standing deadwood in 7 years). Such figures are probably dependent on dominant tree species, soil fertility and the silvicultural stage of the stand at the time it was set aside. Several other studies found a similarly significant increase in deadwood volume in long-unharvested stands compared with managed ones (Kirby, Webster & Antczak, 1991; Sippola *et al.*, 1998; Motta *et al.*, 2010; Calamini *et al.*, 2011), or at least for coarse woody debris (Boncina, 2000; Marage & Lemperiere, 2005; Sitzia *et al.*, 2012). Timonen *et al.* (2011) also

demonstrated that deadwood volumes are higher in woodland key habitats than in managed stands.

However, we showed that deadwood diversity only increased slightly in L-UNH (partly due to the lack of large-diameter logs in late decay stages). Nonetheless, in the data compiled by Timonen *et al.* (2011), deadwood diversity was much higher in woodland key habitats compared with managed stands, probably partly because of an initial selection effect, that is deadwood in the selected plots when they were selected as set-asides or as key habitats.

The difference between L-UNH and recently managed plots may be more pronounced with respect to certain deadwood qualities, as suggested by Siitonen *et al.* (2000). In their Finnish study in spruce forests, large dead coniferous and deciduous trees were respectively 25 and 35 times more abundant on average, in unharvested plots than in R-HAR stands. Accordingly, we found a strong impact of harvesting on large dead wood (downed and standing), with a ninefold increase in large deadwood when harvesting is delayed for at least 30 years. This increase in large deadwood was twice as high as for total deadwood volume. Boncina (2000) and Meyer & Schmidt (2011) also found a rapid accumulation of standing deadwood from unmanaged to managed stands.

Nonetheless, more deadwood was found in longer-established beech reserves (Christensen *et al.*, 2005) and in 60-year-old over-mature French coppices compared with 20-year-old mature coppice (Lassauce *et al.*, 2012). Vandekerkhove *et al.* (2009) argued that full natural restoration of deadwood characteristics (with virgin forests in Central Europe as a reference) may be quite long. Furthermore, Larrieu, Cabanettes & Delarue (2012) showed that a 50-year period of non-intervention was too short to develop complete stand maturity in beech-fir stands, even in highly productivity contexts.

Like Bauhus *et al.* (2009), we were able to detect a list of structural elements (deadwood, microhabitats, large trees) which become significantly more frequent in unharvested stands. We also showed, in accordance with the results simulated by Ball, Lindenmayer & Possingham (1999), that the increase in microhabitat-bearing tree density was weaker than the increase in deadwood density. Reaching high levels of microhabitat density requires time, since the probability of microhabitat occurrence or the number of microhabitat types increases with tree diameter (e.g. Larrieu *et al.*, 2012). In a simulation model, Ranius, Niklasson & Berg (2009) pointed out the importance of tree age for cavity formation on trees (see also empirical data in Gibbons, McElhinny & Lindenmayer, 2010). Furthermore, Fan *et al.* (2003; 2005) showed a higher frequency of cavity trees in 120-year-old forests than in younger stands, and in old-growth than in managed stands (like Bauhus *et al.*, 2009). In our results, a slightly higher density of cavity-bearing trees was measured in L-UNH than in R-HAR plots.

Across our sampling design, L-UNH and R-HAR forests did not differ in terms of stand openness, as the stands were too young to be significantly impacted by canopy gap dynamics. Gap dynamics is known to increase average sun exposure in old-growth forests compared with managed stands (Rugani, Diaci & Hladnik, 2013), and open forest habitats are required by a large number of specialized saproxylic species (Vodka, Konvicka & Cizek, 2009).

Effect of non-harvesting on saproxylic beetle assemblages

In our study, the effect of non-harvesting on biodiversity was slightly significant. The class of time elapsed since harvesting seemed to be important for 25% of the tested species, but was not as important a variable as structural parameters for saproxylic beetle assemblages in our data. Some guilds and groups were positively influenced by non-harvesting (mycophagous abundance and richness, saproxylophagous and rare species abundance), but the relationship was weak and clearly had less impact than deadwood features (see Table 2 and Table 4). Many saproxylic species may simply require a small amount of dead wood that is also available in managed forests. Or structural changes in stand characteristics may occur more quickly than the response of saproxylic organisms. Delayed responses by saproxylic beetle communities may be due to the limited ability, at least for old-growth forest specialists, to colonize favorable substrates (dispersal, habitat detection, etc.) and their density-dependence in the colonization process. Local assemblages may be deeply affected over the long term by historical deadwood supplies (Hanski & Ovaskainen, 2002). Furthermore, population levels must reach minimum thresholds for species to be detected. This interpretation is reflected in our study: the two most typically influential variables for saproxylic beetle richness – deadwood diversity and openness – did not respond strongly to more than 30 years without harvesting. Yet, deadwood diversity has been recognized as a key factor for saproxylic beetle diversity in temperate deciduous forests (Bouget *et al.*, 2013) and other studies based on similar time frames have demonstrated significant responses of saproxylic beetle diversity to setting aside forest areas (Timonen *et al.*, 2011; Lassauce *et al.*, 2013). However, Horák, Chobot & Horáková (2012) raised the question of the status of the rare species pool, deeply affected by commercial forestry in European multisecular managed forests. In our study (Table 5), rare species were more abundant (but not more species-rich) in forest reserves than in managed plots (in agreement with previous results by Lassauce *et al.*, 2013 and Hardersen, 2003 in Germany). We therefore hypothesize (1) that set-aside areas may act as incubators for rare species found in neighboring managed areas, or (2) that forest management reduces the amount of habitats available to rare species and therefore their populations, without leading them to disappear or (3) that most rare species have disappeared and only populations of a few surviving species increase with the amount of dead wood. To address these questions, it would be helpful to use very old reserves as references for species distribution and abundance. Considering the short set-aside period in our study, saproxylic beetle assemblages were probably strongly influenced by both initial forest conditions (pre-existing large trees, beetle assemblages, etc.) and the spatial isolation of

the plots. The comparison between managed stands and set-asides should be deepened and a long-term monitoring strategy put in place (Djupström, Weslien & Schroeder, 2008).

Implications for forest management

Extended rotations, harvesting delays and reserves as conservation tools

In French forests, temporarily setting aside overmature stands before final harvesting, that is creating ageing and rotating islands (Lassauce *et al.*, 2013), is one of the management tools proposed to maintain saproxylic biodiversity associated with old successional stages. This approach aims to conciliate both timber production and biodiversity conservation goals. Larger trees generally have higher economic value while older stands have higher ecological value. We have shown that even a short delay in harvesting (minimum 30 years) induced significant changes in habitat conditions for saproxylic beetles, but only slightly affected saproxylic beetle assemblages. Further studies with longer harvesting delays would be necessary to analyze biodiversity responses. If longer-term habitat continuity is necessary for saproxylic beetle conservation, our results suggest that definitive strict fixed-location reserves should be favored over rotating and temporary set-asides. Moreover, the efficiency of ageing patches as temporary ecological sinks or sources has yet to be properly investigated.

Limits of management relinquishment and non-intervention: toward active restoration techniques?

Passive self-restoration of old-growth features through the abandonment of forest activities in harvestable deciduous stands takes time, at least for some features crucial for species conservation (large deadwood, tree microhabitats, etc.). Therefore, complementary active restoration techniques may be suggested to enhance the recruitment and accumulation of new substrates in conservation areas. Keeton (2006) showed that, in conventional silvicultural systems, active restoration is more successful in creating old-growth features than is delaying harvesting. For instance, standing dead trees, large downed deadwood and tree cavities can be artificially generated using cost-effective techniques like girdling trees, felling or pulling down large trees to be left on the forest floor and mechanically damaging tree trunks (with or without fungus inoculation). Costlier experiments with extreme habitat restoration have even been carried out in Italy (e.g. Cavalli & Donini, 2005). Active restoration requires an in-depth understanding of natural habitats to avoid structures inappropriate to local biodiversity; Jonsell, Nittérus & Stighäll (2004), for example, have underlined the differences between man-made and natural deadwood habitats. In any case, since most endangered saproxylic species have limited dispersal ability (e.g. Buse, 2012), the proper spatial distribution of created substrates is a prerequisite for effective restoration programs. The ecological impacts of active restoration techniques on biodiversity, but also on potential bark beetle outbreaks, should be monitored (Toivanen & Kotiaho, 2010). Thus said, active techniques should at least be considered when the restoration process must achieve the desired forest state within a relatively short time or when the species at stake are threatened by external factors.

Conclusions

Our results did not strongly support recommendations about extended rotations and reserve conservation in favor of saproxylic biodiversity. The rationale behind it would probably benefit from further studies in very old forest reserves, although they are scarce in Western Europe. In one of the study forests (Fontainebleau), despite a limited and unbalanced sampling design, we divided the class of L-UNH into old (> 30 years, $n = 3$) and very old (> 100 years, $n = 9$) reserves. From our exploratory analysis, the deadwood volume and diversity, the total beetle species richness, the rare species richness or abundance were not significantly higher in the older class. This trend deserves to be assessed by other case studies.

Forest areas left unharvested for more than 30 years show an accumulation of old-growth structures related to deadwood volumes and microhabitat diversity, but not deep changes in saproxylic beetle diversity. Restoring the old-growth-dependent community as a whole seems even slower than restoring these structural features. As suggested by Paillet *et al.* (2010), future work should examine the temporal effect of delayed harvesting at multiple time points on the same study area in order to evaluate, using a regression approach with the detailed time elapsed since harvesting, (1) how stands recover old-growth forest attributes and (2) how the associated saproxylic fauna colonize these set-asides in the long-term.

Acknowledgments

We are grateful to A. Lassauce, C. Moliard (Irstea), T. Barnouin, F. Soldati (ONF), N. Debaive (RNF) and all the local forest managers for field and laboratory work. We are indebted to Vicki Moore who reviewed the English manuscript, and to three anonymous reviewers whose constructive comments on an earlier version improved the manuscript. This research was granted by the French ministry in charge of the Ecology through the 'Biodiversité, Gestion Forestière et Politiques Publiques' (BGF) program (convention RESINE CVOJ 000 150, convention 10-MBGD-BGF-1-CVS-092, n°CHORUS 2100 214 651) and the National Forestry Board ('Office National des Forets', convention ONF-Cemagref, Action 5, 2008). This work was also partly funded by the French Environment and Energy Management Agency (ADEME).

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Bouget *et al.* ACV-05–13-OM-091. Supplementary Material