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Biodiversity and structure in managed and unmanaged forests: a comparison based on the strict forest reserves network in France

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Abstract

In Western Europe, the long history of forest management over the past centuries has shaped both landscape- and local-scale forest structure. As a consequence, forest biodiversity has probably been impoverished and recovery is still ongoing. In France, the strict forest reserves network was created to serve as a reference for biodiversity conservation and close-to-nature forest management and currently includes around 200 sites. However, research comparing biodiversity in managed and unmanaged forests remains strikingly poor despite the relatively large number of candidate sites.

In order to close the gap in knowledge in the French context, we studied forest structure (living and dead wood amounts) and the biodiversity of 6 taxa (vascular plants, saproxylic fungi, birds, bats, carabids and saproxylic beetles) by comparing fifteen strict forest reserves with adjacent managed forests, on a total of 213 plots.

In terms of forest structure, we showed that deadwood was the most discriminant criterion between managed and unmanaged forests in France. In terms of biodiversity, we showed that only saproxylic fungi richness responded significantly to management abandonment. For the other groups, the results were less clear, and further analyses correlating forest structure with taxa or ecological groups are programmed in the forthcoming year.

This applied research closely associated managers and researchers and is a good example of research-action involving protected areas.

Keywords

Forest management, stand structure, saproxylic species.

Introduction

In Western Europe, the long history of forest management over the past centuries has shaped both landscape- and local-scale forest structure. Except for the most northern boreal locations, "real" primeval forests are virtually inexistent in Europe; all the forests have undergone more or less intensive management until a recent past (BENGTSSON et al. 2000). As a consequence, the network of strictly protected areas is made up of forests where harvesting has only quite recently stopped.

In France, the strict forest reserves network was created to serve as a reference for biodiversity conservation and close-to-nature forest management (GILG 2004); it currently covers up to 0.3% of the national territory (core areas of national parks excluded, www.inpn.mnhn.fr), distributed over 200 sites representative of the main forest types.

Despite the extent of this network, research comparing the biodiversity between these areas and adjacent managed forests remains strikingly poor (PAILLET et al. 2010). References for sustainable forest management (e.g. how much deadwood exists in French forest reserves?) as well as scientifically estimated levels of biodiversity are lacking. In this context, we sought to answer the following two questions:

- What stand structure features differ in managed forests and strict forest reserves (with a special focus on old-growth features: deadwood and large trees)?
- How does biodiversity respond to management abandonment?

This paper gives an overview of the significant results obtained to date. For forest stand structure, we focused on variables associated with old-growth forests (BOBIEC 1998; BONCINA 2000). Hence, we studied deadwood amount (volumes and densities), and basal areas and densities of (large) living trees. For biodiversity, we compared the total species richness of six taxa: saproxylic fungi, vascular plants, carabids, saproxylic beetles, birds and bats (further details on the project: http://gnb.irstea.fr, in French).

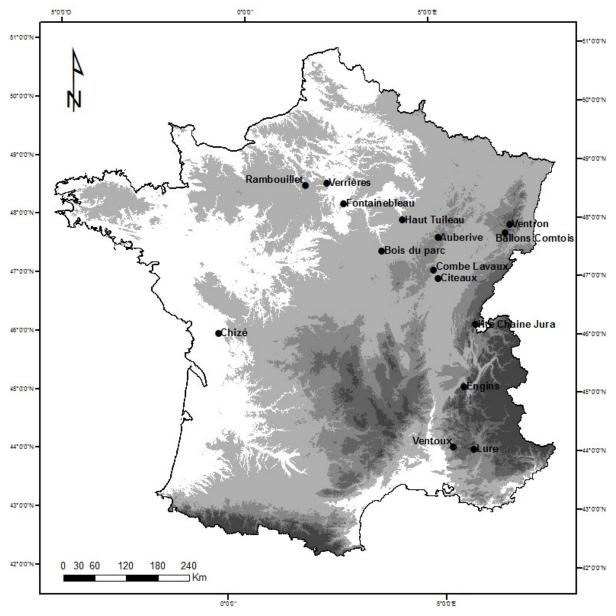


Figure 1: Map of the study sites

Materials and methods

Study sites

We compared fifteen strict forest reserves distributed across France (Figure 1) with adjacent managed forests in the same site conditions. The mean time since last harvesting was 46 years (min: 8, max: 147) for unmanaged reserves and nine years (min: 0, max: 76) for managed forests. We restricted our study to mixed lowland oak-beech-hornbeam forests and mountain beech-fir-spruce forests. These forest types represent around 40% of the total forested area in France (www.ign.fr).

At each of the fifteen locations, sample plots were randomly selected and matched according to site conditions: edaphic and topographic conditions were checked in the field so that each plot within the forest reserve had its equivalent outside the reserve. The managed plots were selected within a radius of 5km around the forest reserve boundaries and in stands composed exclusively of native tree species. The final sample had 213 plots (Table 1).

Stand structure characterisation

Forest stand structure was characterised using a combination of two sampling techniques. On each plot, for all living trees with a diameter at breast height (DBH) of more than 20cm in lowland forests and 30cm in mountain forests, we used a fixed angle plot technique to measure the trees comprised within a fixed relascopic angle of 2% (resp. 3%). Practically, this means that, in lowlands, trees with a DBH of 60cm within a maximum distance of 30m from the centre of the plot (resp. 20m in mountains) were included in the sample and accounted for a basal area of 1m²/ha (resp. 2.25m²/ha in mountains).

All other variables were measured using a fixed area plot technique. Within a fixed 10m ($314m^2$) radius, we measured (i) the diameter of all living trees from 7.5 to 20cm DBH (resp. \leq 30cm in mountains) and (ii) the

volume of snags and stumps with a diameter \leq 30cm. Within a 20m radius, we recorded the volume of downed deadwood (logs > 30cm) and standing dead trees (stumps with a height \leq 1m and snags with a diameter > 30cm).

Finally, logs with a diameter < 30cm were measured using Line Intersect Sampling (LIS, Woodall & Williams 2005) on a total length of 60m.

We then used the measurements to infer densities and basal area of living trees (including very large trees with DBH ≥ 67.5 cm) and deadwood densities and volumes at the plot level.

Table 1: Number of plots comparing unmanaged strict reserves and adjacent managed forests.

| | Sites | Managed forests | Unmanaged strict reserves | |
|----------|----------------------|-----------------|---------------------------------|--|
| Lowland | Auberive | 12 | 12 | |
| | Bois du Parc | 5 | 5 | |
| | Chizé | 12 | 12 | |
| | Citeaux | 6 | 6 | |
| | Combe-Lavaux | 4 | 4 | |
| | Fontainebleau | 16 | 13 | |
| | Haut-Tuileau | 7 | 7 | |
| | Rambouillet | 8 | 8 | |
| | Verrières | 4 | 4 | |
| | Total Lowland | 74 | 71 | |
| | Ballons Comtois | 8 | 8 | |
| | Engins | 5 | 5 | |
| Mountain | Haute Chaine Jura | 8 | 8 | |
| | Lure | 4 | 4 | |
| | Ventron | 4 | 4 | |
| | Ventoux | 5 | 5 | |
| | Total Mountain | 34 | 34 | |
| | Total | 108 | 105 | |

Biodiversity protocols

Due to differences in sampling dates for each taxon, all data were not available at the time of writing.

Fungi

Saproxylic fungi (i.e. species for which the sporophore grows on wood) were sampled once in autumn. We searched for fungi on all living trees and large dead trees (snags, stumps and logs with a diameter > 30cm) retained for stand structure characterization (see above), and recorded and identified all sporophores occurring to a height of 3m. In addition, six small logs intersecting the transects mentioned above were surveyed.

Vascular plants

We used the Braun-Blanquet (1932) abundance-dominance method to inventory all vascular plants within a 1000-m² circular plot once in spring. All censuses were performed by two observers. Sampling effort was limited to 35min (+/- 5min) per plot.

Saproxylic and carabid beetles

Saproxylic beetles were sampled using multidirectional PolytrapsTM (EIP, Toulouse, France; BRUSTEL 2004) placed at a height of about 1 m. Two traps were located approximately 30 m apart on each plot.

Ground beetles were sampled using pitfall traps. In each plot, three traps were set 10m from the centre point along lines radiating out in three different directions (zero, 120 and 240 degrees) to ensure the independence of the traps (see Toïgo et al. 2013 for further details).

Sampling of all traps was carried out monthly over a three-month period. All beetles were identified to species level. Total richness per plot was calculated by pooling all the species caught in all the traps during the entire sampling period.

Bats

Bats were inventoried using 30min ultrasonic point-counts. Two observers listened to bat echolocation calls during the first four hours of the night. In all, three censuses were carried out by the same observers: one in spring

and two in summer. All bats were determined to species level whenever possible. All sampling periods were pooled to calculate species richness.

Birds

Breeding birds were surveyed using a standardized monitoring methodology (JIGUET et al. 2012): five-minute censuses were carried out by skilled observers during two sampling periods in spring (before and after May 8 with a 4–6 week gap in between). Every individual seen or heard was recorded. Total species richness was calculated as the sum of all species detected during the two sampling periods.

Statistical analyses

Analyses were processed in R v.2.5.1 (R Development Core Team 2007). Management type, i.e. managed forest vs. unmanaged strict reserve, was used as the explanatory variable.

For stand structure characteristics, we considered basal area, deadwood volume and living and dead tree densities. We used non-linear mixed effects models (nlme function, nlme package) with an exponential link. In practice, we obtained a multiplication coefficient between managed and unmanaged forests for each explanatory variable. This allowed us to take into account the initial values of stand characteristics. We then re-estimated coefficients using bias-corrected bootstrap confidence intervals calculated with 9999 iterations (library boot). The significance of these results was assessed using a Bayesian posterior p-value (Gosselin 2011).

For biodiversity data, total species richness per plot of each taxa was used as the response variable. We used generalised mixed effects models (Imer function, Ime4 library) with a Poisson error distribution with site as a random effect to analyse the response of biodiversity to forest management. We also added a plot random effect to account for potential over-dispersion of the data (Elston et al. 2001).

Table 2: Dendrometric data comparing unmanaged (UNM) forest reserves (n = 105 plots) to adjacent managed (MAN) forests (n = 108 plots). Coef = multiplication coefficient between MAN and UNM data, Bca- and Bca+ = lower and upper values of bias-corrected bootstrap confidence intervals calculated with 9999 iterations. N = number, V = volume, DBH = Diameter at Breast Height. p = sampled posterior Bayesian p-value. ***p<0.001; **p<0.01; *p<0.05; (*) p<0.1; ns: non-significant result.

| Variable | Coef | р | Mean MAN | Bca- | Bca+ | Mean UNM | Bca- | Bca+ |
|---|------------|-----|-------------|-------|-------|-------------|------|-------|
| N living trees / ha | 1,225 | * | 508,8 | 447,6 | 580,6 | 623,3 | 555 | 703,5 |
| N very large trees / ha (DBH>67.5cm) | 2,052 | ** | 3,4 | 2 | 5 | 7 | 6 | 8,5 |
| Total basal area (m²/ha) | 1,166 | *** | 22,9 | 21,6 | 24,2 | 26,7 | 25,2 | 28,3 |
| Total basal area of large trees (m²/ha) | 2,467 | ** | 1,4 | 0,8 | 2,3 | 3,5 | 3 | 4,2 |
| N standing deadwood / ha | 0,932 | ns | 84,8 | 62,7 | 108,1 | 79,1 | 55,3 | 115 |
| N stumps / ha | - 0,301 | *** | 62,6 | 53,3 | 80,3 | 18,8 | 12 | 31,8 |
| V standing deadwood | 4,591 | *** | 4,6 | 2,9 | 9,3 | 21,2 | 17,9 | 27,5 |
| V lying deadwood | 4,759 | *** | 6,2 | 3,6 | 9,9 | 29,6 | 25,2 | 36,1 |
| Total deadwood V | 4,595 | *** | 11,1 | 7,1 | 17,4 | 50,9 | 44,7 | 60,9 |

Results

Forest stand structure (Table 2)

Living trees

Living trees were significantly more numerous (by 22%) in strict reserves (623 trees/ha) than in managed forest (509 trees/ha). In particular, there were twice as many very large trees (DBH \geq 67.5 cm) in strict reserves (7 trees/ha) than in managed forests (3.4 trees/ha). Basal area was also significantly higher (by 16%) in unmanaged reserves (26,7m²/ha) than in managed forests (22.9m²/ha). Similarly, the basal area of very large trees was 2.46 times higher in the reserves (3.5 vs. 1.4m²/ha in managed sites), which indicates that very large trees are both more numerous and larger in the reserves.

Deadwood

The combined number of snags and stumps (standing deadwood) did not differ significantly between strict forest reserves and managed forests. However, the number of stumps in the reserves represented only 30% of the number in the managed forests (p<0.001). For deadwood volumes, there was 4.5 times more standing (21.2 vs. $4.6 \, \text{m}^3/\text{ha}$), lying (29.6 vs. $6.2 \, \text{m}^3/\text{ha}$) and total deadwood (50.9 vs. $11.1 \, \text{m}^3/\text{ha}$) in the reserves, and all these results were significant.

Total species richness (Table 3)

Among the 6 taxa analysed, only saproxylic fungi displayed significantly higher total species richness in unmanaged reserves than in managed forests (12.3 vs. 8.6 species). Birds showed marginally higher total species richness in unmanaged (11.9 sp.) than in managed forests (11.1 sp.). For all the other groups, the total species richness did not differ.

Table 3: Total species richness comparisons between unmanaged strict forest reserves and adjacent managed forests. The results were derived from a generalised mixed model with Poisson error distribution. The estimated mean values have been back-transformed. Please note that the number of plots differ from one taxon to another. n = number of plots, SE = estimated standard errors. ***p<0.001; **p<0.01; *p<0.05; (*) p<0.1; ns: non-significant result.

| | _ | Managed forests | | Unmanaged reserves | | |
|--------------------|-----|-------------------|-------|--------------------|-------|-----|
| Taxa | n | Estimated Mean | SE | Estimated Mean | SE | р |
| Fungi | 99 | 8,6 | 1,192 | 12,3 | 1,19 | *** |
| Flora | 197 | 32,5 | 1,1 | 32,7 | 1,1 | ns |
| Carabids | 121 | 3,3 | 1,293 | 3,1 | 1,294 | ns |
| Saproxylic beetles | 169 | 26 | 2,032 | 24,2 | 2,032 | ns |
| Birds | 185 | 11,1 | 1,075 | 11,9 | 1,075 | (*) |
| Bats | 101 | 4,8 | 1,352 | 5,7 | 1,351 | ns |

Discussion

Strict forest reserves and managed forests differ in structure

We found that unmanaged strict forest reserves differed significantly from adjacent managed stands in terms of stem and stump number, total basal area, large tree and deadwood volumes. These latter two features are generally used as indicators of old-growth unmanaged forests (BOBIEC 1998; BONCINA 2000; GILG 2004). These results highlight the fact that forest management tends to shorten the silvigenetic cycle by eliminating the aged and senescent phases (PAILLET et al. 2010). Compared to the results obtained by BURRASCANO et al. (2013), our results showed higher differences in terms of basal area and density, but comparable results in terms of deadwood. However, BURRASCANO et al. (2013) found median deadwood volumes for old-growth forests that were much higher (157.3m³/ha) than those we obtained in the French forest reserves; this indicates that recovery in the French reserves is still an on-going process.

Small differences in terms of biodiversity

Our multitaxa analysis revealed that only saproxylic fungi had higher species richness in the reserves than in managed forests, thus confirming the results previously observed (Paillet et al. 2010). Birds tended to display the same pattern, but for all the other groups, forest management had no effect on species richness. Most surprisingly, saproxylic beetle species richness did not differ significantly between managed and unmanaged forests in our study, despite the differences in deadwood volumes. This supports the hypothesis that deadwood volume is probably not the main driver of saproxylic beetle richness in temperate forests (Lassauce et al. 2011). However, this lack of difference may also be due to several other factors, or their combination:

- the French forest reserves are probably too recent, and biodiversity is still recovering from past forest management;
- an extinction debt, notably due to centuries of deforestation in western Europe, has already been paid and potential sources of recolonisation for species have disappeared;
- current forest management in the surrounding forests is sufficiently sustainable to maintain the typical forest species;
- other factors at other time and spatial scales (especially at the landscape scale) play a greater role in biodiversity than forest management per se (see Toïgo et al. 2013 for a comparison with structural factors).

Conclusions

Although established quite recently, the French forest reserves showed higher stem densities, basal areas (especially for very large trees) and deadwood volumes. However, these structural differences were only partially reflected in terms of biodiversity. This study constitutes a first reference for French forests since research comparing structural attributes and biodiversity between managed and unmanaged temperate forests remains spectacularly scarce, and will undoubtedly serve as a basis for many other forest programs.

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