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Snags and large trees drive higher tree microhabitat densities in strict forest reserves

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ABSTRACT

Tree microhabitats (cavities, conks of fungi, bark features) play an important role for both rare and specialized species biodiversity; their preservation should therefore be targeted by biodiversity-friendly forest practices. However, when compared to other old-growth characteristics like deadwood or large trees, tree microhabitats have only recently been studied so related scientific knowledge is still relatively limited. Defining target values for microhabitat densities in managed forests is mostly based on expert knowledge rather than quantitative empirical data.

We compared the densities of microhabitat-bearing trees between managed forests, where wood is still harvested, and strictly protected forest reserves, where harvesting has been abandoned, in 17 French forests (222 plots) located in both lowlands and mountain regions. We found that microhabitat densities are generally higher in strict forest reserves than in managed forests and that this difference is mainly driven by standing dead and large living trees. Though scarce, standing dead trees over-contribute to the difference observed while large trees played a lesser but significant role. In addition, contrary to results obtained for other old-growth characteristics (such as deadwood volumes), the difference between managed and strict forest reserves was higher in mountain than in lowland forests. For individual microhabitats, five out of eleven microhabitats in mountains and only one in lowland (woodpecker cavities) were significantly more numerous in strict forest reserves than in managed forests. Finally, total microhabitat density and density of specific microhabitats such as cavities and bark features increased with time since the last harvest. This increase was also mainly supported by standing dead microhabitat-bearing trees. Compared to previous studies in comparable contexts, the densities we estimated were generally higher; however, such comparisons could only be made for the most documented microhabitat types.

Our results support the idea that management abandonment favours the abundance and diversity of microhabitats. However, microhabitat dynamics remain poorly known and only long-term monitoring will help understand underlying mechanisms of recruitment. In the meantime, our results may inspire forest managers in their application of daily biodiversity-friendly practices.

1. Introduction

The pressure on forest ecosystems to provide goods and services, such as wood, is increasing worldwide (Millenium Ecosystem Assessment, 2005) while the surface area concerned by retention measures (i.e. set-aside areas) is likely to be too small to sustain forest biodiversity efficiently (Parviainen et al., 2000). Preserving biodiversity in managed forests is thus a challenge, and numerous methods for implementing biodiversity-friendly forest management have been documented. Among other methods, several ones aim to promote the presence of structural elements known, or assumed, to be important for biodiversity but which are usually rare in managed forests. Such structural features include lying and standing deadwood (Christensen et al., 2005; Lombardi et al., 2012), habitat trees (Bütler et al., 2013; Bouget et al., 2014a) or more generally structural legacies issued of natural disturbances and structural heterogeneity (Franklin et al., 2002;

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Zellweger et al., 2013). Various approaches comprise silviculture for old-growth attributes (Bauhus et al., 2009), integrative approaches (Bollmann and Braunisch, 2013; Kraus and Krumm, 2013), management for naturalness (Winter, 2012), retention forestry (Drapeau et al., 2009; Gustafsson et al., 2013) but they all share the same objective. Among the structural attributes targeted by these types of management, tree microhabitats (hereafter "microhabitats") are typically cited but most of the time overlooked due to the absence of a consensual definition or a lack of knowledge; this situation persists despite a recent gain in interest and a convergence towards standardization of census procedures (Vuidot et al., 2011; Larrieu et al., 2014b; Winter et al., 2015). By "tree microhabitats", we mean peculiarities that are not borne by all trees including cavities, cracks, conks of fungi or bark features, and that potentially provide a necessary substratum for certain taxa during at least a part of their life cycle (Winter and Möller, 2008; Vuidot et al., 2011; Siitonen, 2012; Larrieu et al., 2014b).

The most often studied microhabitats to date are cavities, both excavated and decayed, for which a worldwide review has recently been published (Remm and Lõhmus, 2011). The authors point out the lack of publications in Western Europe. In France, recent studies are rare and restricted to specific forest ecosystems like mountain beech-fir forests (Larrieu and Cabanettes, 2012; Larrieu et al., 2012, 2014a) and Mediterranean forests (Regnery et al., 2013). This review also underlines that nationwide assessments of the main microhabitat types are still lacking, or are poorly implemented, in national forest inventories (see e.g. Tinner et al., 2012 for Switzerland; and Gao et al., 2015 for a broader scope).

As a result, management recommendations concerning microhabitats and habitat trees have been largely based on intrinsic expert knowledge and clearly lack established scientific guidelines for close-to-nature forest management. For example, deciding which habitat trees to conserve for supporting forest biodiversity in managed forests may rely on the presence of certain microhabitats (Bütler et al., 2013). Yet, little is known about their occurrence in forests. To fill this gap in knowledge, we need reference values covering a large spectrum of microhabitat types and biogeographical regions as well as various management situations. Such references for old-growth attributes like deadwood and large trees have recently been published for France (e.g. Bouget et al., 2014b; Paillet et al., 2015b), but data on microhabitats are less common (Larrieu et al., 2014b). Values based on measurements taken in forests that have remained unmanaged, i.e. unharvested and without any forestry operations for a certain amount of time and that are under natural disturbance dynamics since last harvesting, may help forest managers define target values and prioritize actions. The respective roles of living and dead standing trees as sources of microhabitats at the stand level are not quantified, despite clues indicating that snags and large trees generally bear more microhabitats (e.g. Vuidot et al., 2011). In addition, the effects of forest management abandonment on microhabitat densities may vary with context and should account for biogeographical parameters, in particular when lowland and mountain forests are compared.

We analysed the response of several microhabitat density indices to management abandonment by comparing seventeen French forests located in lowland and mountain regions containing strict forest reserves with adjacent managed forests. We also analysed the effect of time since last harvesting on the same indices. We hypothesized that:

(i) as for other old growth attributes, the total microhabitat density should be higher in strict reserves than in managed forests;
(ii) higher densities in strict forest reserves should be primarily attributed to snags and large trees, in spite of their modest contribution to the overall microhabitat density;
(iii) the density of individual microhabitat types should differ between managed forests and strict reserves, some types being more present in managed areas (e.g. bark loss), and others being more present in abandoned areas (e.g. woodpecker cavities);
(iv) the total and individual microhabitat densities associated with strict forest reserves should increase with time since the last harvesting; and conversely, densities for microhabitats dependent on managed forests should decrease with time since the last harvesting.

Ultimately, our aim was to provide forest practitioners with values for biodiversity-friendly management and to document the dynamics of different microhabitat types with respect to management abandonment.

2. Materials and methods

2.1. Study sites

We compared seventeen strict forest reserves distributed across France with adjacent managed forests under the same site conditions (the sampling design is detailed in Paillet et al., 2015b, and only the main points are reminded here). In a nutshell, management types roughly correspond to harvesting recommendations in French managed forest that vary locally but could be summarised as follows: tree selection and felling occur generally every 5–10 years in the lowlands, and every 10–20 years in the mountains (see below). We restricted our study to mixed lowland oak-beech-hornbeam forests (*Quercus robur* L. and *Q. petraea* (Mattus.) Liebl., *Fagus sylvatica* L. and *Carpinus betulus* L., elevation $\leqslant$ 800 m) and mountain beech-fir-spruce forests (*Fagus sylvatica* L., *Abies alba* Mill. and *Picea abies* (L.) Karst., elevation > 800 m).

At each of the seventeen study sites, sampling locations were randomly pre-selected on a regular 100×100 m grid, then plots were selected according to site conditions observed in the field. Edaphic conditions (soil texture, depth, hydromorphy and reaction to HCl) and topography (elevation, aspect and slope) were checked in the field so that each plot within the forest reserve had its paired equivalent outside the reserve. The managed plots were selected within 5 km of the forest reserve boundaries and in stands composed exclusively of native tree species of the same forest type (oak-beech-hornbeam in lowlands, beech-fir-spruce in mountains). The majority of the plots were located in mature forests (see Paillet et al., 2015b) but, for the present study, plots without trees with a Diameter at Breast Height (DBH) higher than 30 cm were excluded from the analysis (which reduces the sample size compared to Paillet et al., 2015b). Due to field constraints and posterior plot selection, the final sample comprised a total of 222 plots but was not fully balanced (Table 1).

For 187 plots, the time since last harvesting was recorded from management plans or wood sales data. Stand age was generally unavailable. The mean time since last harvesting for the strict forest reserves was 48 years (46 ±SD 42 years in lowlands, and 50 ±SD 38 years in mountains) and for managed forests, 9 years (7 ±SD 5 years in lowlands and 12 ±SD 10 years in mountains). Twenty-five plots in the strict reserves had experienced harvesting during the last 20 years before designation, while five plots in managed forests had not been harvested for more than 20 years.

Silvicultural treatments were also recorded even though they were strongly biased by elevation: 78% of the uneven-aged forests (continuous cover) were located in mountain beech-fir-spruce forests whereas all the even-aged high forests (selective cutting followed by clearcutting and natural regeneration) were located in lowland beech-oak dominated forests. No other type of manage-