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What is This?
Needle accumulation rate model-based reconstruction of palaeo-tree biomass in the western subalpine Alps

Olivier Blarquez,1,2 Christopher Carcaillet,1,2 Tasneem M Elzein1,2 and Paul Roiron2

Abstract
An appropriate bioproxy is required to decipher Holocene tree biomass dynamics from the stand scale in relation to local processes such as disturbance or global climate change. Here we used plant litter collected in traps placed in subalpine forests, and data on the surrounding stands, to develop calibration equations for converting the observed macroremain accumulation rates to tree biomass (basal area) values. The needle accumulation rate (NAR) was modeled for Larix decidua and Pinus cembra. We then used the calibration equation developed from the trapped macroremains to reconstruct past tree biomass for sedimentary Holocene series from two subalpine lakes in the Alps. Our data show that NAR is significantly correlated with basal area. We found a clear overrepresentation of L. decidua NAR compared with its real basal area. This distortion potentially masks the occurrence of P. cembra, another important functional species of subalpine ecosystems, when macroremains are not calibrated. Without calibration, the use of NAR to describe past plant biomass always leads to an overestimation of L. decidua biomass and an underestimation of P. cembra biomass. Several shifts between the dominance of the two species, which were masked when using unadjusted NAR, were apparent and occurred at both sites. By comparing the reconstructed basal areas with fire frequencies, we found that P. cembra biomass accumulation preceded the increase of fire frequency and that fire frequencies superior to 0.0085 fire/yr could induce a long-term loss of resilience of cembra pine forest to the benefit of larch. This results to a slight biomass accumulation preceded the increase of fire frequency and that fire the reconstructed basal areas with fire frequencies, we found that P. cembra biomass accumulation preceded the increase of fire frequency and that fire frequencies superior to 0.0085 fire/yr could induce a long-term loss of resilience of cembra pine forest to the benefit of larch. This results to a slight dominance of Larix biomass from 2500 to 2000 cal. BP until the present day at the two sites. Our results provide increased understanding of tree biomass dynamics associated with specific vegetation phases, and shifts in dominant species, and highlight the needs to understand the causes of these shifts and identify how such processes are related to local environmental conditions.

Keywords
biomass, calibration, fire, Larix decidua, macroremains, Pinus cembra, trees

Introduction
Reconstructions of past vegetation biomass patterns that incorporate aspects of ecosystem dynamics could provide greater insights into the processes (stresses or disturbances) involved in detected changes than simply using the relative abundance of bioproxies (e.g. pollen, needles, diatoms), or their apparent accumulation rates. Furthermore, reconstruction of past-biomass can help to determine the range and variability of ecological structure (Fulé et al., 1997) and are important for predicting the structure of future vegetation in a changing world (Jackson and Overpeck, 2000; Swetnam et al., 1999).

Pollen is the most widely used bioproxy to reconstruct palaeobiomass (Seppä et al., 2009). Although this proxy has many advantages, pollen-based biomass reconstructions have several limitations that have been widely discussed in the literature (e.g. regional versus local pollen representation, Prentice, 1985). This limits the accuracy of pollen analyses, especially in mountain areas (Markgraf, 1980). Recently, other bioproxies have been used with varying degrees of success; for example, sedimentary charcoal series have been used to estimate the palaeobiomass burning at a global scale (Marlon et al., 2008), phytoliths have been used to reconstruct forest structure, including Leaf Area Indices (Bremond et al., 2005), and satellite–pollen calibration has been used to reconstruct quantitatively palaeowood cover (Tarasov et al., 2007). However, although terrestrial plant macroremains (e.g. needles, leaves, flower organs , seeds and fruits) occur at most sites that provide pollen or charcoal records, this bioproxy is rarely used for quantitative vegetation reconstruction. This is surprising as plant macroremains have obvious advantages, such as high taxonomic resolution (Birks and Birks, 2000), suitability for spatially precise studies (Birks, 1973; Dunwiddie, 1987; Tinner and Kaltenrieder, 2005) and could be efficiently used to assess local taxa presence and past treeline dynamics (Birks and Bjune, 2010).

Assessing past biomass requires a robust calibration of present-day relationships between the proxy and biomass, irrespective of the proxy used. Until now, the modern analogue technique (Overpeck and Webb, 1985) represents the only way to estimate past biomass when values are not directly measurable from palaeoassemblages (Davis et al., 1973; Jackson and Williams, 1985).

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Figure 1. Locations of the study sites for the biomass calibration of modern macroremain influx (black dots) and the palaeobiomass reconstruction inferred from macroremains (above: Lac du Loup; below: Lago Perso).

The present study aims to provide a method to calibrate plant macroremains that can be used for estimating plant biomass. We then applied this calibration to records of sedimentary palaeomacroremains in order to analyze the dynamics of subalpine forest biomass during the Holocene. The resulting dynamics are compared with fire reconstruction histories, based on the hypothesis that fire is one of the natural disturbances shaping forest communities in Alpine regions (Carcaillet et al., 2009; Tinner et al., 1999).

To test the capacity of macroremains to predict plant biomass, we used the current rates of plant particle fall, which we assumed represented the macroremain accumulation rate on that spot. This modern rain of plant fragments was recorded in 30 traps and calibrated against an easily available biomass descriptor, the tree basal area. We focused on subalpine forest ecosystems because: (i) these mountain-type ecosystems appear to be among the most sensitive to future global climate change (Thüller et al., 2005) or changes in land use (Dirmbock et al., 2003); and (ii) because understanding past biomass dynamics is critical for predicting future changes and formulating sustainable management policies (Botkin et al., 2007). We also focused on two key functional species of the modern subalpine belt: European larch (Larix decidua Mill.) and cembra pine (Pinus cembra L.). We hypothesized that (i) sedimentary macroremain records are biased by an overrepresentation of L. decidua because of the deciduous character of this conifer; and (ii) the relative biomass of co-occurring evergreen species, such as P. cembra, would be underrepresented relative to Larix if uncorrected needle fall rates are used to estimate species biomass. A deciduous tree rejuvenates its total leaf area each year, whereas an evergreen tree only replaces a fraction of its leaf area each year, depending on the lifetime of the leaves (or needles). P. cembra has a needle lifetime of approximately 3–7 years (Li et al., 2006), although needles may be retained for up to 12 years at higher altitudes (Nebel and Matile, 1992). Our study provides a valuable method to estimate plant biomass using macroremains and allows us to discuss the variability in biomass throughout the postglacial period and to contextualize these results in terms of the dynamics of fire-sensitive ecosystems.

Materials and methods

Study area

Our study area is in the dry western Alps at the boundary between the more Mediterranean Alps to the south (Queyras massif) and the more continental Alps to the north (Vanoise massif). Sites selected for macroremain traps are located in the Maurienne valley, in the area surrounding Lac du Loup (45°11′14″N; 6°32′16″E, Figure 1), while the sites selected for the palaeobiomass reconstructions are two subalpine lakes on north-facing slopes, Lac du Loup (France) and Lago Perso (44°54′21″N; 6°47′50″E, Italy).

Mixed stands of larch and cembra pine, with scattered mountain pines (Picea abies (L.) H. Karst.), form characteristic subalpine north-facing forests in the dry inner western Alps, with woody understoreys characterized by Ericaceae. Pastures in these areas are dominated by short grasses, Poaceae and Cyperaceae, which are also found in grazed woodlands or grasslands with isolated trees.

The climate is continental-type, characterized at Lago Perso by a mean precipitation (rain and snow) of ~880 mm/yr (Motta and Lingua, 2005). More precise climate data collected at St Michel-de-Maurienne (1360 m a.s.l., ~2 km from Lac du Loup and at the macroremain trap sites) indicate a mean precipitation of 947 ±184 mm/yr and a mean annual temperature of 7.1 ± 0.6°C (January, −0.2 ± 2.2°C; July, 15.5 ± 1.6°C). The bedrock of the area is composed of Permocarboniferous schists and sandstones (Lac du Loup, macroremain trap sites) or calcareous schists (Lago Perso, Motta and Lingua, 2005) with acidic soils and podzols occurring under mature forests (Mourier et al., 2008).

Macroremain trap design

We used the term macroremains to describe all particles >500 µm produced by plants that were captured in the traps. The macroremains included needles, leaves, flowers, seeds, stems, and cones, which were identifiable to the species or genus level using simple ocular observations or a stereomicroscope (6.3–50×).

Thirty (30) traps were randomly placed in forest openings within the mixed larch × cembra pine forests of the subalpine belt between 2000 and 2100 m a.s.l. (Figures 1 and 2). The sites selected for macroremain collection were north-facing (Figure 1). The traps were made from 5 l food containers (ø = 22.4 cm, i.e. a surface of 363 cm²) stacked on three 1 m metal rods driven into the ground (Figure 2). To avoid the plant remains rotting, small holes (ø = 1 cm) were made at the bottom of containers to allow water to enter. Bottom-holes were covered by a mesh (0.5 mm) to trap the plant remains. Macroremains were collected in the 30 traps twice per year (June and October) from June 2008 until June 2011 corresponding to 3 years of trapping. The material collected was identified and counted in order to calculate the macroremain accumulation rate, subsequently termed Needle Accumulation Rate (NAR: #/cm² per yr), totally 210 066 and 9198 needles were counted for L. decidua and P. cembra during the three years of trapping, respectively. The macroremain traps used in this study
are not appropriate for collecting remains of dwarf shrubs and herbs, therefore we only focused on the main tree remains, the needles of *P. cembra* and *L. decidua* that largely dominated the litter fall. The other tree species or tall shrubs present in the plots were scarce and their remains were rarely found in the traps, these species included *Abies alba*, *Picea abies*, *Alnus viridis*, *Betula pubescens*, *Sorbus aucuparia*, and *Salix caprea*.

To calibrate NAR in terms of plant biomass, we used the most robust biomass descriptor available, the basal area (m²/ha). Each macroremain trap was placed in the center of a 12 m radius plot (450 m² per sample-unit), and the basal area of all trees within these 12 m radius plots was measured. This 450 m² area was assumed to be sufficiently large to estimate the tree biomass that produced the macroremains we collected in the traps (Bray and Gorham, 1964; Spain, 1984). Basal areas expressed in m² per 12 m radius plot were converted into m²/ha. In total, 1.35 ha (30 × 450 = 13 500 m²) of subalpine forests was sampled.

**Palaeoecological study design**

The two lakes, Lac du Loup and Lago Perso, were cored using a Russian corer and a Kajak-Brinkurst sampler (details given in Blarquez et al., 2010b). Lac du Loup (1400 m², 0.65 km² watershed) is situated at 2035 m a.s.l. within the municipality of Orelle in the Maurienne Valley, France (Figure 1), whereas Lago Perso (408 m², 0.27 km² watershed) is at 2000 m a.s.l. within the municipality of Cesana Torinese in the Susa Valley, Italy (Figure 1).

Plant remains were retrieved at high resolution (1 cm) by soaking and sieving sediments, then macroremains were identified and counted. Between 10 and 20 cm³ of sediment were sieved per sample. In the present study we focused solely on needles of the two dominant tree species, *L. decidua* and *P. cembra*, whose needles were both abundantly recorded in the lake sediments and macroremain traps. Their abundances were subsequently expressed as the NAR (#/cm² per yr) using solid age–depth models based on a total of 21 calibrated ^14C datings of plant macroremains and ^210Pb measurements (details given in Blarquez et al., 2010a, b). Calibrated ages before present are denoted as ‘cal. BP’.

**Statistical analyses**

We used inverse parametric non-linear regressions:

\[
BA_{t} = \frac{a \cdot \text{NAR}_{t}}{\text{NAR}_{t} + b}
\]

(1)

to calibrate the NAR collected in the traps (NARₜ) for *L. decidua* and *P. cembra*, and to model their basal area around the traps (BAₜ). This Michaelis-Menten type equation form permits to introduce an asymptotic term, which is required to fit the biological assumption stating that BAₜ cannot tend to infinity and remains straightforward to be extended to further studies. Following our study design, each macroremain trap displays different NARₜ each year, we thus choose to perform our inverse non-linear regressions on averaged NARₜ. In order to keep the variability of NAR in the model, we used weighted non-linear least square method, assigning inverse standard deviation weight \(1/\sigma_{\text{NAR}_{t}}\) at each NARₜ value. Consequently traps recording regular NARₜ have more weight in the model, and this method prevents traps from recording anomalous NARₜ a given year to bias the model. We chose to force models through the origin to avoid basal area reconstruction errors when applied to the sedimentary NAR series, which often display very low NAR values. Residuals from the models were tested to verify if they were normally distributed, had homogeneity of variance and were independent, by applying the Shapiro, Breusch-Pagan and Durbin-Watson tests, respectively. Spearman’s correlation coefficients (\(\rho\)) were calculated between the fitted basal area values (BA_{sim}) estimated by the regression models and the measured values (BAₜ). Spearman’s
correlation coefficients between the measured values and the fitted values simulated by the non-linear models were used to confirm the validity of the calibration. Leave-one-out cross-validation was used to calculate the coefficient of variation of the root mean square errors (CV(RMSE) in %) of the models to further illustrate the stability of the models and the validity of the calibration. Then, we used the transfer function \((a \text{ and } b)\) to transform fossil NAR from sediments (\(NAR_f\)) into reconstructed basal areas (\(BA_f\)):

\[
BA_f = \frac{a \cdot NAR_f}{NAR_f + b}
\]  

(2)

This transformation provided an overview of the biomass dynamics of \(P. cembra\) and \(L. decidua\) since 11 700 and 7500 years ago for Lac du Loup and Lago Perso, respectively. To explore the relationships between species, simulated basal areas were converted into percentages. To highlight the main trends in the records, we used locally weighted polynomial regressions (LOWESS, with \(a=0.05)\).

To compare reconstructed basal area percentages to fire regimes at the two lakes, we used the dates of fire events retrieved from a statistical analysis of the sedimentary charcoal series from the two lakes (Blarquez et al., 2010a, b). We reconstructed fire frequency using a non-parametric kernel smoothing regression and estimated 95% confidence intervals using bootstrap procedures (Mudelsee et al., 2004). We defined periods of high fire frequency probability as periods when it was \(\geq 1\) standard deviation (1σ) higher than the mean for the whole record (Carcaillet et al., 2007).

**Results**

**Needle Accumulation Rate (NAR) – basal area calibration**

The calibration equations of both \(L. decidua\) and \(P. cembra\) showed that \(NAR\) could be used to describe more than 64% (adjusted \(R^2 > 0.64)\) of the measured basal areas (\(BA_f\)), and displayed a good stability (CV(RMSE)<6.5% ; Table 1, Figure 3A, B) indicating that our model is robust. However, there was a marked between-species difference in \(NAR\)-basal area ratio. For instance, a basal area of 30 m\(^2\)/ha (an expected mean value in subalpine old forests, Chauchard et al., 2010; Motta and Lingua, 2005) corresponds to c. 12 needles/cm\(^2\) per yr for \(L. decidua\) and 0.5 needles/cm\(^2\) per yr for \(P. cembra\). Thus, \(Larix\) stands released substantially more needles than \(Pinus\) stands with equivalent basal areas.

The simulated basal areas inferred from the calibration equations were tested against measured values using Spearman \(\rho\) correlation tests. The results showed highly significant correlation coefficients \((p < 0.001)\) for both \(L. decidua\) (\(\rho = 0.66)\; \text{Figure 3C}\) and \(P. cembra\) (\(\rho = 0.82)\; \text{Figure 3D}\). As a consequence of our choice to constrain the linear models to pass through the origin, our reconstruction appears to slightly underestimate the basal areas for low values (< 10 m\(^2\)/ha, Figure 3C, D). However, the statistics are assumed to be sufficiently reliable to provide realistic reconstructed basal areas, at least when the reconstructed basal areas are < 50 m\(^2\)/ha.

**Basal area reconstruction**

The fossil needle accumulation rates (\(NAR_f\)) of \(L. decidua\) were higher than those of \(P. cembra\) (Figure 4A, B) at both sites. The resulting percentage pattern (Figure 4C, D) suggests that \(L. decidua\) has been largely dominant since the Younger Dryas–Holocene transition, i.e. since 11 700 cal. BP at Lac du Loup (Figure 4C) and 7500 cal. BP at Lago Perso (Figure 4D).

Figure 4E and F shows the reconstructed basal areas for Lac du Loup and Lago Perso, respectively (\(BA_f\)). Although \(L. decidua\) largely made the greatest contribution to the needle records (and hence \(NAR_f\)), the reconstructed basal areas suggest that the dynamics of the two species have varied at the two sites. The mean (±SE) reconstructed basal areas over the last 7500 years at Lago Perso are 8.0±0.6 and 3.7±0.3 m\(^2\)/ha for \(Larix\) and \(Pinus\), respectively, while at Lac du Loup, the mean Holocene (last 11 750 years) reconstructed basal areas are lower for \(L. decidua\) (2.8±0.1 m\(^2\)/ha, Figure 4F) and higher for \(Pinus\) (13.5±0.9 m\(^2\)/ha, Figure 4F). The mean (±SE) cumulative basal area for the last 7500 years is 11.8±0.6 m\(^2\)/ha at Lago Perso and 16.3±1.0 m\(^2\)/ha at Lac du Loup (Figure 4E, F).

At Lac du Loup, despite the consistent dominance of the \(NAR_f\) of \(L. decidua\) since 11 700 cal. BP, the reconstruction showed that the basal areas have changed over time (Figure 4E and G). The basal area of both species was extremely low from 11 700 to 8200 cal. BP (Figure 4E). However, the reconstructed basal area before 8000 cal. BP is probably not very informative because of the very low \(NAR_f\) values, at the boundary of acceptable values for the model (Figure 3). The basal area percentage values showed that \(Pinus\) clearly dominated from 7800 to 3500 cal. BP (Figure 4G). From 3500 to 2000 cal. BP, the percentage basal area of \(Pinus\) remained greater than the basal area of \(Larix\). A clear shift occurred at ~2000 cal. BP, when the \(Larix\) basal area became dominant, a pattern that has persisted until the present day (Figure 4G).

At Lac du Loup, in contrast to Lac du Loup, \(L. decidua\) dominated the record in terms of both \(NAR_f\) and basal area from the beginning of the record (7500 cal. BP and until 3700 cal. BP; Figure 4F, H). The percentage basal area of \(P. cembra\) began to dominate the record from 3700 cal. BP, until a shifted occurred at 2500 cal. BP in favor of a greater basal area of \(Larix\); this lasted until the present day, except for a 200 yr period around 1000 cal. BP when \(Pinus\) dominated (Figure 4H).

**Basal area–fire frequency relationship**

The fire frequency (fires/yr) increased at both sites from the beginning of the sequences until 2000 cal. BP when the fire frequency was maximal (Figure 5A, B, modified from Blarquez et al., 2010a, b). The fire frequency was maximal (fires/yr) increased at both sites from the beginning of the sequences until 2000 cal. BP when the fire frequency was maximal (Figure 5A, B, modified from Blarquez et al., 2010a, b).

<table>
<thead>
<tr>
<th>Species</th>
<th>Calibration equation</th>
<th>(a) [95% CI]</th>
<th>(b) [95% CI]</th>
<th>(BA_f) (m(^2)/ha) (min; max)</th>
<th>(NAR_f) (#./cm(^2) per yr) (min; max)</th>
<th>Adjusted (R^2)</th>
<th>CV (RMSE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Larix)</td>
<td>(BA_f=(a \cdot NAR_f) / (NAR_f+b))</td>
<td>176.7 (-333.9; 687.4)</td>
<td>57.77 (-135; 250.6)</td>
<td>(0; 40.37)</td>
<td>(1.77; 14.77)</td>
<td>0.64</td>
<td>0.036</td>
</tr>
<tr>
<td>(Pinus)</td>
<td>(BA_f=(a \cdot NAR_f) / (NAR_f+b))</td>
<td>71.97 (7.49; 136.5)</td>
<td>0.673 (-0.1789; 1.526)</td>
<td>(0.43; 0.29)</td>
<td>(0.074)</td>
<td>0.66</td>
<td>0.065</td>
</tr>
</tbody>
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Figure 3. Inverse non-linear regressions between measured basal areas ($BA_t$) and needle accumulation rates ($NAR_t$) for $Larix decidua$ (A) and $Pinus cembra$ (B), horizontal bars indicate the standard deviation of each $NAR_t$ value for the three consecutive sampling years (see materials and methods). Measured basal areas against fitted values ($BA_{sim}$) simulated by the linear models for $Larix decidua$ (C) and $Pinus cembra$ (D).

Figure 4. Macrolest remain accumulation rate to biomass reconstruction after bio-proxy calibration. Raw sedimentary needle accumulation rate ($NAR$) for Lac du Loup (A) and Lago Perso (B) and percentages of $NAR$ (C, D) for $Larix decidua$ (grey curve) and $Pinus cembra$ (black). Reconstructed basal areas ($BA_s$) for Lac du Loup (E) and Lago Perso (F) and their relative basal areas (G, H).
The Holocene: 22 (5): 583–595

Discussion

We have provided the first subalpine reconstruction for the European Alps of tree biomass dynamics using calibrated equations linking needle accumulation rate (NAR) to tree basal area, which is a very robust descriptor of tree biomass (Whittaker, 1966). Although macroremains are a commonly used proxy in palaeoecology (Birks, 2007), very few studies have used long-term plant macroremain records to reconstruct tree biomass (Birks and Meentemeyer, 2001; Hennessey et al., 1992). Our models based on inverse non-linear regression showed that NAR is related to basal area, in accordance with previous litter fall studies, indicating that needle abundance is a good descriptor of tree biomass (Birks, 1973; Dunwiddie, 1987). Our models based on inverse non-linear regression showed that NAR is related to basal area, in accordance with previous litter fall studies, indicating that needle abundance is a good descriptor of tree biomass (Birks, 1973; Dunwiddie, 1987).

Calibrated NAR: a biomass proxy?

Our calibration model between macroremains from traps and surrounding tree basal areas, which assumes a non-linear relationship, allowed the reconstruction of Holocene total basal areas that are within the range of both observed basal areas around the traps (this study) and in other subalpine mixed larch-cembra pine forests (Genries et al., 2009b; Lingua et al., 2008; Motta and Edouard, 2005). Another way to calibrate NAR for estimating basal areas would have been to use correlations between NAR of the topmost lake sediments and the basal area of trees in the vicinity of the lakes (Birks, 1973; Dunwiddie, 1987). However, although this method has been used for pollen calibration studies (Davis et al., 1973; Seppä et al., 2009), some problems remain unsolved, e.g. it is difficult to define a sampling area for basal area measurement that is representative of the bioproxy accumulation rate recorded in the sediments (Prentice, 1985; Sugita, 1994). Moreover this method requires the inclusion of a large number of lakes to be statistically sound, which was not feasible in the context of our study. Furthermore, most subalpine lakes in the Pinus cembra × Larix decidua area of the western Alps are generally surrounded by pastured grasslands or grasslands with isolated trees. Hence, the number of samples would be too small to develop a reliable model. Our protocol that used many macroremain traps within a limited sampling area for measuring tree basal areas has the advantage of ensuring a locally precise representation of the relationship between NAR and basal area (Bray and Gorham, 1964; Spain, 1984). However, both methods provide complementary data.

Taphonomic issues arise when calibration equations are used to calibrate NAR from lake sediments. Indeed, the accumulation rate of plant particles in traps is not directly comparable with the NAR from sediments because of their own taphonomic processes that are lake-dependent (Hanlon, 1981). To control for this type of bias Birks and Bjune (2010) used NAR from traps located at water–sediment interface and considered taphonomic bias constant in time (Allison and Bottjer, 2011). If taphonomic conditions vary in time which is most probably the case, both methods (raised and immerged traps) may fail at reconstructing past biomass until taphonomic bias is precisely quantified (Allison and Bottjer, 2011).
Consequently, the initial assumption that taphonomic conditions are constant over time and between lakes is unavoidable. In addition, basin size, which strongly influences taphonomic conditions, was also assumed to be constant and not considered in the model (Hanlon, 1981; Jacobson and Bradshaw, 1981; Prentice, 1985). However, such bias is likely to have been minimal here, and the macrofossil fall likely to have been largely local, because of the limited surface area and basin size of the lakes we considered (Figure 1). Importantly, even if the reconstructed basa areas (Figure 4E and F) are within a realistic range for the type of ecosystem we studied, they must be regarded as indices of the past real tree basal area. In contrast to absolute basal area estimations, the transformation into percentages was able to describe the long-term specific biomass co-dynamics (relative contributions of the species).

**Overestimation of Larix decidua abundance based on NAR**

Uncalibrated palaeoproxies are commonly influenced by biases that are constrained by the bioproxy production rate of the different species, which may depend on the intrinsic functional traits of the species, age structure, stand vegetation structure and environmental factors (Dunwiddie, 1987; Jackson and Williams, 2004). For example, _Pinus_ pollen is always highly overrepresented in pollen records, since all pine species are wind dispersed and produce large amounts of pollen, and _Larix_ species are always underestimated in pollen records since they are poor pollen producers and dispersers (Birks and Birks, 1980).

This problem also arises in uncalibrated macroremains analyses, but the NAR of our two study species, _L. decidua_ and _P. cembra_, exhibit an opposite pattern to their usual pollen accumulation rates. Larch is a deciduous needleleaf tree that produces huge amounts of needles, which fall to the ground and are completely renewed annually. In contrast, _P. cembra_ is an evergreen conifer with a needle turnover of 2 to 12 years (Li et al., 2006; Nebel and Matile, 1992), and more generally 3–7 years. Thus, _L. decidua_ releases approximately three to seven times more needles to the ground than _P. cembra_ (in area or number) and its needles are comparatively overrepresented in both traps (Figure 3) and sediments (Figure 4). Consequently, uncorrected needle-based estimates will not accurately represent the relative biomass of the species. We thus stress the need for better characterization of the relationship between NAR and tree biomass, particularly when NARs are used to confirm long-term biomass estimations from model simulations (Heiri et al., 2006; Henne et al., 2011).

**Holocene biomass dynamics of the larch-cembra pine community**

Before c. 3500 cal. BP, the reconstructed biomass dynamics differed between the sites (Figure 4G and H). Previous studies, based solely on NAR, hypothesized that mixed forests at these sites were dominated by larch (Blarquez et al., 2010a, b). In contrast, our needle/biomass calibration indicates that forest biomass around Lac du Loup was dominated by _P. cembra_, while _L. decidua_ dominated the forest biomass around Lago Perso. Lac du Loup is in a valley influenced by western oceanic air-masses, while Lago Perso is influenced by the more eastern Adriatic air-masses. Consequently climatic conditions substantially differ at the two sites. The Gams-Michälet continentality index of mountain climate (Michälet, 1991) gives an _a_-angle < 60° for Lac du Loup and > 60° for Lago Perso, clearly indicating that the climate at Lago Perso is more continental (drier internal Alps) than at Lac du Loup (wetter intermediate Alps). We hypothesize that differences in tree dominance may also be linked to site-dependent processes and features such as slope and bedrock. For example, bedrocks formed acidic soils at Lac du Loup that evolved to podzol during the Holocene (Mourrier et al., 2008), whereas at Lago Perso soils are calcareous (Motta and Edouard, 2005).

Pollen records in the western Alps have indicated that larch has been abundant since only c. 2000 years ago (see Nakagawa et al., 2000). This could be explained by the fact that a certain threshold in larch biomass must be reached in order for its pollen to be recorded in sediments. This is supported by diverse types of macrofossil studies (e.g. based on imprints in tufa or macroremains in peat and lakes) that have already recorded the presence of this species for a long time, sometimes since the Lateglacial or late Dryas periods (Ali et al., 2006; Blarquez et al., 2010b; Gobet et al., 2005), showing the relative expansion of _Larix_ macrofossil abundance since c. 3500 cal. BP (Ali et al., 2004). Records of _Larix_ pollen in sediments can only show its presence, but cannot provide reliable indications of _Larix_ frequencies or biomass unless this poor pollen producer accounts for at least 50% of the biomass in the vicinity of sedimentary sites (Figure 4G, H).

**Vulnerability of the cembra pine forest to fire**

It appears from our biomass and fire frequency reconstructions that the same forest dynamics scenario happens at both sites synchronously and independently (Figure 5). Before 3000 cal. BP _Pinus cembra_ biomass is either high at Lac du Loup or increasing at Lago Perso, during the subsequent period that matches the period of maximal fire frequency (_Blarquez and Carcaillet, 2010; Genries et al., 2009a_). A threshold in the resilience of cembra pine forest seems attained during the 3000–1500 cal. BP period, this threshold was first estimated as 150 yr/fire fire return interval, corresponding to c. 0.0067 fire/yr by Blarquez and Carcaillet (2010) and resulting in long-term loss of resilience of the cembra pine forest. Our present study highlight that high fire frequencies, i.e. >0.0085 and >0.0105 fire/yr at Lac du Loup and Lago Perso, respectively, yielded a long-term decrease of cembra pine biomass to the benefit of larch.

**Conclusion**

Tree biomass indices can be reconstructed using calibrated needle fall rates. We found that _L. decidua_ biomass is greatly overestimated compared with _P. cembra_ biomass if uncorrected needle fall rates are used, highlighting the importance of proxy calibrations. Reconstructions generated by applying our calibrated needle/biomass model to sedimentary needle accumulation rates indicate that different species dominated at the two study sites, while the classical approach (without calibration) indicated that the vegetation structure at both sites was very similar. Late-Holocene synchronous larch biomass dominance at both sites was detected, driven by fire-induced loss of resilience of cembra pine forest probably caused by changes in land use and human-induced fire ignitions, because no known significant climate change occurred during the 3000–1500 cal. BP period that could explain such an ecological shift. However, long-lasting larch biomass dominance at Lago Perso during periods when human impact is considered to have been negligible (i.e. from 7500 to 3700 cal. BP) highlights the natural nature of this type of subalpine forest in the driest areas of the western Alps.

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