

Long-term effects of climate and land-use change on larch budmoth outbreaks in the French Alps

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ABSTRACT: The intensity of cyclic larch budmoth (*Zeiraphera diniana* Guenée; LBM) outbreaks across the European Alps has been reported to have weakened since the early 1980s. In addition to a warmer climate, changes in land-use cover over modern and historical times may have affected the LBM system. Here, we present tree-ring-based reconstructions of LBM outbreaks from a mixed subalpine larch–pine forest in the French Alps for the period 1700–2010. Temporal variation in LBM outbreak severity was mainly driven by land-use changes, including varying forest structure and species composition. Human population pressure and associated resource demands for fuel wood and construction timber not only resulted in a reduction of larch and subsequent suppression of pine, but also supported an overall grassland expansion for livestock. Superimposed on modern land abandonment and pine re-colonization is a strong warming trend, which may also contribute to the observed late 20th-century weakening of Alpine-wide cyclic LBM outbreaks. Our results suggest that a complex interplay of different factors triggered less synchronized LBM outbreaks at broader scales, with overall significantly lower intensities at local scales.

KEY WORDS: *Zeiraphera diniana* · Tree rings · Climate change · Land use/cover change · Forest structure · Tree composition

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1. INTRODUCTION

Biological disturbances are an integral component of plant communities (White & Pickett 1985, Johnson & Miyanishi 2007). In forest ecosystems, bio-disturbances, such as insect outbreaks, play an important role in shaping forest composition, structure and dynamics (Morin et al. 2007). Long-term records

of insect outbreaks show that the duration and severity of such events can be influenced by land management, together with aspects of fire suppression (Blais 1983, Mitchell 1990), as well as landscape fragmentation (Roland 1993, Radeloff et al. 2000, Wood et al. 2010). Furthermore, population outbreaks of the larch budmoth (*Zeiraphera diniana* Guenée; LBM) cause defoliation, and thus inhibit ring width forma-

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tion in the moth's main subalpine host tree, the European larch (*Larix decidua* Mill), widespread between ~800 and 2300 m a.s.l. (Bennetti 1998). The LBM is a Holarctic insect characterized by regular large-scale population outbreaks (Baltensweiler & Rubli 1999); such outbreaks seem to be closely related to the prevailing ecological site conditions and synoptic-scale climate fluctuations (Baltensweiler et al. 2008). Until the 1970s, LBM had mass outbreaks every 8–9 yr with a regularity that has not been adequately explained (Büntgen et al. 2009). Certain factors have been hypothesized, such as changes in density-dependent factors (Fischlin & Baltensweiler 1979, Bjornstad et al. 2002, Turchin et al. 2003, Johnson et al. 2004). A decline in the intensity of LBM outbreaks and a lack of spatial synchrony have been observed across the European Alps since 1981 (Baltensweiler 1993). A possible reason for this and comparable collapses of population cycles might indeed be direct and/or indirect effects of global warming (Esper et al. 2007, Kress et al. 2009, Johnson et al. 2010). However, it has been demonstrated that outbreaks of the same insect species may respond differently to warming and dryings trends in different parts of the insect geographic distribution range (Thomson et al. 1984, Swetnam & Lynch 1993), and that insect dynamics may be influenced by more than one environmental driver (Cappuccino & Price 1995, Simard et al. 2012). In this regard, possible effects on LBM dynamics and its outbreaks associated with land-use changes that alter the land cover have, to our knowledge, never been properly considered. The profound landscape transformation in the European Alps, particularly during the second half of the 20th century in France and Italy (Motta & Garbarino 2003, Tasser et al. 2009), has the potential to alter and may even disrupt the cyclic behavior of the LBM system on various spatiotemporal scales. Forest dynamics and composition have been severely influenced by societal activities (Motta & Nola 2001, Risch et al. 2003), with larch having been favored over Arolla pine (*Pinus cembra* L.) for several decades because it was more compatible with grazing activities and useful for domestic uses (i.e. fuel wood, building material). Recently, with land-use abandonment, *P. cembra* has begun to re-establish (Motta & Nola 2001, Holtmeier 2003) and larch regeneration has decreased (Chauchard et al. 2010).

Based on the fact that forest cover has changed in area, pattern and perhaps in composition, and that LBM is closely associated with certain trees, it would be useful to determine whether land-use abandonment might have influenced the dynamics

of LBM outbreaks. This would be of great importance for future decadal projections of land management and natural resources (Sala et al. 2000). Indeed, the direct effect of climate and land use on LBM and larch ecology is not yet understood, and interactions between them represent a large uncertainty in projections of future ecological change in the Alps. The influence of land-use change on ecological processes is a solidly established concept (Watt 1947), but quantification of those effects remains an issue, due to the complexity of the factors involved (Peterson & Parker 1998) and the difficulty of conducting large-scale experiments over long temporal scales. Thus, more research is clearly needed to make reliable predictions about not only the climate system and the insect biology, but also the interactions between climate change and land-use change, insect population dynamics and forest responses.

Here, we use tree-ring width (TRW) measurements to detect and reconstruct historical LBM outbreaks in 5 mixed forests of *L. decidua* (hereafter larch) and *P. cembra* (pine) all situated in a French Alpine valley. We aim to: (1) analyze changes in outbreak frequency over the last 3 centuries, and (2) understand how dynamics of the LBM system are related to changes in climate and/or land use. Reconstructed LBM outbreak patterns are therefore compared with temperature and precipitation variability during the past 3 centuries, as well as with modifications in both larch and pine forest structure and composition. Although based on a local-scale study, the complex interplay of natural and social drivers on the LBM system is presented and discussed with special emphasis on past, present and projected broader land-cover changes in the French Alps.

2. MATERIALS AND METHODS

2.1. Site characteristics and sampling design

The Maurienne Valley, Savoy, France, is a typical arc-shaped Alpine valley located along the border between France and Italy, and is dominated by mixed larch–Arolla pine forests in the subalpine. The treeline is located between 2350 and 2400 m a.s.l., depending on slope and aspect. We selected 5 sampling sites in order to cover the whole upper valley (from west to east): Orgère (ORG, 45° 13' 27" N, 6° 40' 33" E), on a south-facing slope, and on north-facing slopes, Avrieux-Arlette (ARL, 45° 13' 10" N, 6° 42' 55" E), Bramans val d'Ambin (AMB, 45° 13' 22" N,

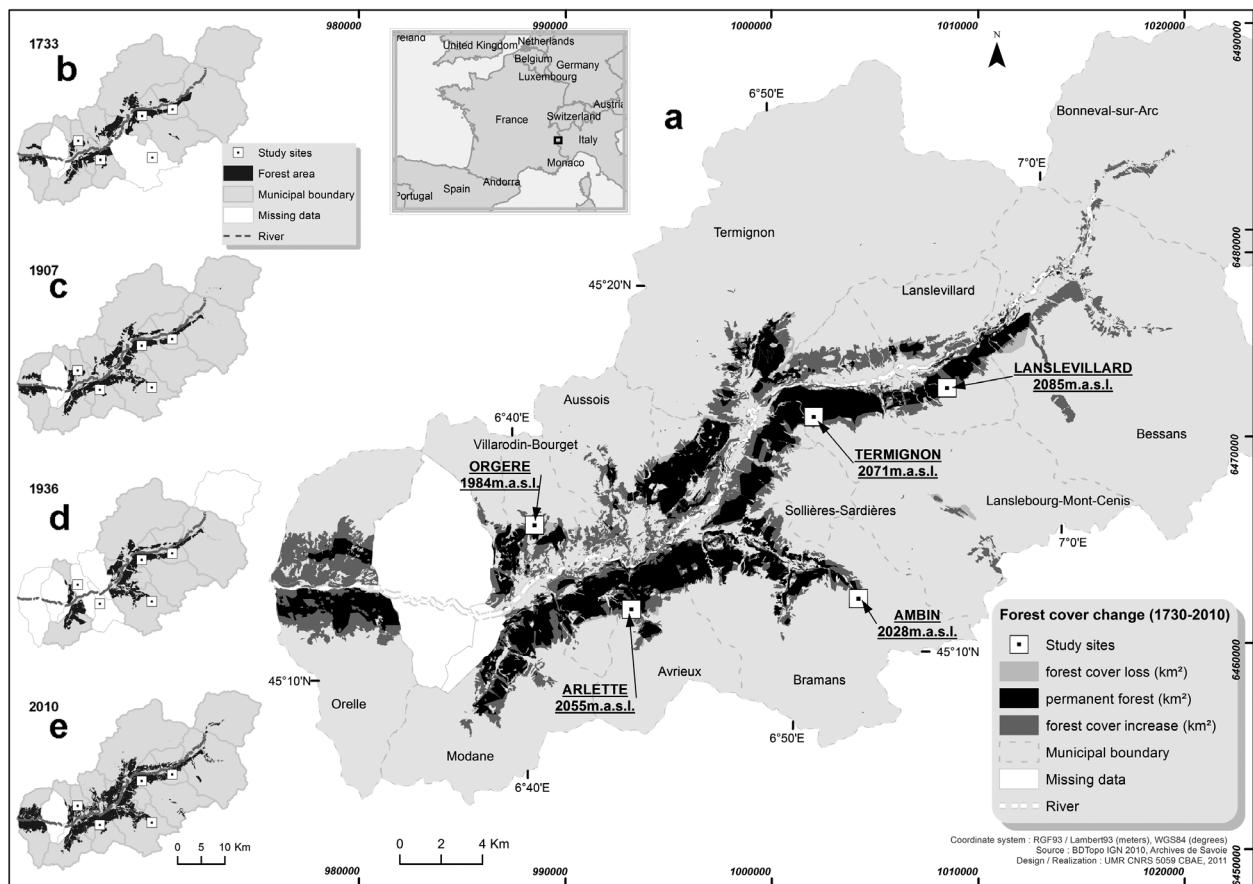


Fig. 1. (a) Upper Maurienne Valley with the sampling sites (white circles) and area of forest cover change (km^2) in the period 1728–2010. In particular, permanent forests (black area), forest cover loss (light gray area) and the increase in forest cover (mid-gray area) are reported: (b) forest area (km^2) in 1728–1738 (source Mappe Sarde), (c) forest area (km^2) in 1850–1895 (source Premier cadastre français), (d) forest area (km^2) in 1927–1939 (source Cadastre rénové) and (e) forest area (km^2) in 2010. White areas indicate that data are missing or not verified

$6^\circ 46' 35'' \text{ E}$, Termignon (TER, $45^\circ 16' 37'' \text{ N}$, $6^\circ 48' 59'' \text{ E}$) and Lanslevillard (LAN, $45^\circ 17' 25'' \text{ N}$, $6^\circ 54' 34'' \text{ E}$) (see Fig. 1 for details).

In fall 2009 and spring 2010, 10 mixed larch–pine plots (plot size = 400 m^2) were designed along an altitudinal gradient between 1700 and 2000 m a.s.l., in which all trees (pine and larch) were sampled to determine their individual growth rates and ages, as well as stand age structure and forest recruitment history. A tree was considered when its diameter (\varnothing) was $>5 \text{ cm}$ at 30 cm height (h); a sapling when $\varnothing < 5 \text{ cm}$ at $h = 30 \text{ cm}$; a seedling when $h \leq 30 \text{ cm}$. The age of trees, determined by taking one core per tree, was assessed after correction of the age-at-30 cm using an allometric equation providing the number of years to reach the coring height (Motta et al. 2006, Genries et al. 2009). This procedure is based on the assumption that the harvested saplings grew at the same rate as the initial growth rate of

the mature trees from which the cores were obtained. Based on height–age analysis, the age to reach coring height was estimated to be $10 \pm 3 \text{ yr}$ ($n = 665$, $r = 0.62$, $p < 0.001$) for larch, and $13 \pm 5 \text{ yr}$ ($n = 144$, $r = 0.65$, $p < 0.001$) for Arolla pine (Genries et al. 2009). Since the procedures used for age estimation can introduce errors into subsequent analyses, age structure was constructed for 10 yr classes to account for these errors.

Two cores per tree were taken at breast height ($\sim 1.3 \text{ m}$ above surface) from 20–27 individuals of larch and pine trees per site to guarantee the subsequent development of robust tree-ring chronologies. Pine is normally a non-host species for the common dark form of LBM (Baltensweiler 1993, Nola et al. 2006), which can be a valuable reference species to help disentangle the effect of insect defoliation on TRW from that of adverse climatic conditions (Dormont et al. 2006, Büntgen et al. 2009).

2.2. Sample preparation and chronology development

All core samples were air dried, glued onto wood supports, and sanded to enhance ring boundaries. Ring-width measurements were performed with a resolution of 0.01 mm, using LINTAB equipment (Frank Rinn, Heidelberg, Germany), and subsequently analyzed with the TSAP software package. After visual cross-dating to identify missing rings, common marker years and ring width patterns were assessed according to *Gleichläufigkeit*, a statistical measure of the year-to-year agreement between the interval trends of the chronologies based upon the sign of agreement (Schweingruber 1988), and a Student's *t*-test, which determines the degree of correlation between curves. Cross-dating of all the tree-ring series was then verified using the COFECHA program (Holmes 1993), which assesses the quality of cross-dating and measurement accuracy of tree-ring series using the segmented time-series correlation technique. To remove the biological age trend and facilitate examination of climatic extremes in the context of adjacent years and decades, the TRW data were detrended using first a negative exponential or linear function, and 30 yr cubic smoothing splines as a second option by means of ARSTAN software (Cook 1985). This rigorous detrending was previously used in papers to identify LBM outbreaks (Speer et al. 2001, Nola et al. 2006, Paritsis et al. 2009) and to emphasize high-frequency year-to-year variability in the remaining chronologies (Battipaglia et al. 2010). Afterwards, an autoregressive model was applied to remove the autocorrelation structure with the previous year ring width, resulting in white-noise time series (Biondi & Swetnam 1987). Individual series within each site were averaged with a robust (bi-weight) estimation of the mean. The expressed population signal (EPS) was calculated within each site to indicate the level of coherence of the constructed chronology, and how it portrays the hypothetical perfect population chronology.

2.3. Growth-climate response analyses and outbreak detection

Correlations between the TRW chronologies and climate variables were calculated for the period 1700–2000 to identify the dominant climate controls of ring formation. High-resolution $0.5^\circ \times 0.5^\circ$ grids (Casty et al. 2005) of monthly temperature means and precipitation were used for growth-climate re-

sponse analyses. Correlation coefficients were calculated separately between each month and season—winter (January, February, March), spring (April, May), summer (June, July, August), autumn (from September to December)—and temperature and precipitation, using bootstrapped correlation analyses for significance testing ($p < 0.05$; Guiot 1991). To quantify temporal changes in the relationship between climate and TRW, we additionally calculated moving correlations over 40 yr time windows, thus producing a time series of bootstrapped correlation coefficients on a monthly and seasonal basis (Biondi & Waikul 2004, Kress et al. 2009). However, only the significant correlations were discussed and displayed.

Three different methods were applied to identify LBM outbreaks: (1) the pointer year method, where each tentative outbreak year must be associated with a $>50\%$ growth reduction compared with the 6 neighboring rings (Paritsis et al. 2009); (2) comparisons of host (larch) and non-host species (pine), where the outbreaks were detected as a decrease in the growth of individual host trees without a corresponding decrease in the non-host species (Büntgen et al. 2009); and (3) identification of characteristic years or periods that meet or exceed some assigned parameter, such as ring-width index (RWI) ≥ 0.85 standard deviations (σ) below the mean RWI (ca. the smallest 20th percentile) and the RWI for the 1st year of the inferred outbreak $\leq 60\%$ of the previous year (Nola et al. 2006). An outbreak is identified when the 3 methods agree, in the case of larch chronology, and when methods (1) and (3) agree, in the case of pine chronology. Methods (2) and (3) were assessed using the OUTBREAK program (R. L. Holmes and T. W. Swetnam, unpubl. manual [on file at Laboratory of Tree-Ring Research, University of Arizona]; see also Speer et al. 2001). This program generally compares the host chronologies with non-host chronologies; the climate signals are removed through subtraction of the non-host index chronology and the occurrence of outbreaks events is recorded. For Method (3), we ran OUTBREAK separately for larch and pine, and considered them both to be possible host species. In this case, the individual chronologies were analyzed to identify the growth reduction corresponding to the following parameters: (1) RWI $\geq 0.85\sigma$ below the mean RWI and (2) RWI for the first year of the inferred outbreak $\leq 60\%$ of the previous year.

LBM outbreak reconstruction was initially performed at the site level. The site chronologies were then aggregated into a regional composite time series of outbreak events for the whole study area. To avoid spurious interpretation of past outbreak frequency

due to the low sample size, we started our analysis of the composite time series in 1700 (when at least 50 % of the total sampled trees were included in the total chronology). Only years at each site with >25 % of affected series were regarded as outbreaks (Nola et al. 2006, Büntgen et al. 2009). See Table 1 for the characteristics of reconstructed LBM attacks of larch and pine. Frequency, percentage of affected trees and growth reduction distribution were transformed and fitted by locally weighted polynomial regression (LOWESS; Cleveland 1979) smoothing with a 50 yr time window. The statistical significance of switches in event frequencies was determined where trends exceed 2 σ away from the long-term mean.

Superposed epoch analysis (SEA; Swetnam & Betancourt 1990) was further applied to test the statistical significance of the associations between environmental events (outbreaks or climate) and tree-ring growth. SEA was conducted by taking into account, for each outbreak, the first year of the attack and the 3 years before and after the selected year; it was performed using the EVENT program (R. L. Holmes and T. W. Swetnam, on file at the Laboratory of Tree-Ring Research, University of Arizona). Statistical significance was determined by a bootstrap method in which years are selected randomly, and expected mean values of climate conditions are calculated for the entire period of analysis. We performed SEA for climate data by 1, 2 and 3 month seasons, and annual time periods, but only results that are statistically significant and consistent across different data arrangements are shown. Moreover, we used singular spectrum analysis (SSA) to assess possible oscillatory behavior and changing temporal patterns of reconstructed LBM along the chronology for different periods. It is a nonparametric method for analyzing time series similar to principal components analysis (Vautard & Ghil 1989). SSA enables the user to evaluate changing periodic behavior in a single time series by extracting pairs of 'reconstructed components' or 'waveforms', which represent the dominant periodic modes of the time series. SSA was applied to the tree growth increment data and was performed using the SSA program (J. A. Boninsegna and R. L. Holmes, on file at the Laboratory of Tree-Ring Research, University of Arizona).

2.4. Historical information

Antique maps, along with additional GIS data and reports, were used to estimate the change in forest cover between different time periods. In particular,

we used Mappe Sarde, first land register of the Duchy of Savoy, Kingdom of Sardinia (established in 1728–1738), Premier cadastre français (est. 1850–1895), Cadastre rénové (est. 1927–1939), the phytosociological map (Bartoli 1996), Corine Land Cover (2000) and the database BD topo IGN (2010).

The antique maps (data source: www.archinoe.net/cg73v2/cadastre.php) were scanned, rasterized, georeferenced and vectorized into a GIS system (ESRI ArcInfo 9.3). The maps were further enhanced by rubber sheeting, which spatially warps the data to fit with more accurate modern maps (Balletti 2000, Niederoest 2002). See Table 2 for details on the maps; original map photos are available in Figs. S1 and S2 in the Supplement at www.int-res.com/articles/suppl/c062p001_supp.pdf.

The rubber sheeting process aims to: (1) identify control points on historical maps and on the present-day one (we used as a reference the BD topo IGN 2010; the unmoved temporal geo-features are set as the control points, such as important settlements, rivers and mountains); (2) perform quality control checks on the spatialized database (metadata are loaded into GIS from the database software program Access); and (3) obtain an affine transformation to change the coordinate system origin and to remove possible geometric distortion (Ghilani & Wolf 2006).

The digital plot maps were merged into a master coverage illustrating the subdivision history across the study area. The plots were used to calculate the area covered by permanent forests during the different map periods and the possible spatial error due to differences in map scales and the georeferencing methods used. The quality of the historical maps, in terms of completeness, integrity and correctness, was high for all the municipalities except Bramans, where the control points did not perfectly overlap (white zone in Fig. 1). Further, because it is well known that altitude plays an important role in the interaction between climate and LBM outbreak patterns (Baltensweiler & Rubli 1999, Johnson et al. 2010, Daux et al. 2011), we verified that most of the change in forest cover occurred in subalpine forest at an altitude between 1700 and 2000 m a.s.l. (Fig. S3 in the Supplement at www.int-res.com/articles/suppl/c062p001_supp.pdf), which is considered the optimal zone for larch defoliation (Baltensweiler et al. 2008).

Human population and livestock inventories were obtained for each municipality over the last 260 yr. The numbers of permanent inhabitants in the villages closest to the study site were obtained from demographic databases (<http://cassini.ehess.fr>), from the Archives Départementales de Savoie (www.

savoie-archives.fr/), combined with documentary data (Rambaud & Vincienne 1964, Jail 1969). Numbers of cattle and sheep + goats in the upper Maurienne Valley were obtained from the Archives Départementales de Savoie, from the agricultural census (recensements généraux agricoles) and from the literature (Rambaud & Vincienne 1964, Jail 1969).

Finally, we used redundancy analysis (RDA), a constrained ordination method (Rao 1964), to investigate the proportion of variability explained by predictor variables relating to anthropogenic influences and historical forest cover, and their correlation with LBM outbreak frequency and severity. A 6×9 matrix was created, associating the 6 time periods classified by the maps (see Table 2) with the corresponding historical predictors (i.e. inhabitant or animal numbers, forest cover or structure) and LBM variables (i.e. outbreak frequency or severity). RDA is a technique used for 2 sets of variables, one set being dependent on the other. Its aim is to maximize the explained variance of the dependent variables by a linear combination of the explanatory variables. The analysis was performed using the package XLSTAT 2010 (Microsoft).

3. RESULTS

3.1. LBM outbreak characteristics: frequency, population and individual severity

A high EPS value for all sites (>0.85) indicates that TRW chronologies were representative of radial growth variation of the whole tree population (Wigley et al. 1984). However, the mean larch TRW chronology (Fig. 2a) revealed several ring width reductions, interpreted as the consequence of LBM outbreaks because these depressions did not correspond to similar events in the pine non-host reference chronology (Fig. 2b). We thus found a low correlation between the TRW of the 2 species ($r = 0.32$, $p < 0.05$). Between 1700 and 2010, 23 LBM outbreaks (orange crosses, Fig. 2a) were detected. The date and characteristics of each event are summarized in Table 1, which also highlights the data common to our reconstructed LBM events and the historical evidence. The same

method was applied to the pine tree-ring series to detect any LBM attacks on this species and to identify any climate effect in the growth reduction of both species. The length of each larch outbreak varied between 2 and 5 yr and the events occurred with a mean \pm SD LBM interval of 13 ± 5 yr. That said, almost half of the LBM events (44 %) occurred during the 19th century. Only 6 events were identified within the pine series (green crosses, Fig. 2b), characterized by a short duration and a more limited number of affected trees and less growth reduction as compared with larch (Table 1). The comparison between our reconstruction of LBM outbreaks and the historical defoliation events observed during the period 1800–2000 in the same area (Baltensweiler & Rubli 1999) showed 60% agreement between the reconstructed and observed events (common events: 1813, 1819, 1854–1856, 1953, 1961 and 1971).

The 310-yr reconstructed outbreak history showed a clear change in the frequency (outbreaks 100 yr^{-1}) between 1810 and 1850, when the frequency reached its highest value (Fig. 2c), but no cyclic recurrence of outbreaks was found. Another period of elevated frequency was recorded between 1730 and 1750, while during the entire 18th century the frequency distribution was characterized by periodic LBM events with significant wavelengths of 8 and 17 yr (Fig. 2c, inset). Together, the 8- and 17-yr cycles accounted for almost 60% of variance during this time period. From 1860 to 2010, a slight decrease in the outbreak frequency was observed, and no significant wavelength was recorded in the LBM events.

Outbreak severity can be measured at the population level and expressed in terms of the percentage of affected trees (Fig. 2d), or at the individual level, expressed as radial growth reduction (Fig. 2e). The severity pattern at both population and individual levels followed a similar trend to the frequency, with 3 statistically significant switches over the same time period, although the exact dates of maxima were not synchronous. However, the percentage of affected trees (Fig. 2d) was higher during the first half of the 18th century than during the period of maximal outbreak frequency from 1810 to 1850. During the 19th century, the period between 1815 and 1835 appears

Fig. 2. Reconstruction of larch budmoth (LBM) outbreak regime. (a) Mean *Larix decidua* tree-ring indexed chronology (orange line) and number of samples (black line). Orange crosses indicate LBM outbreaks. (b) *Pinus cembra* tree-ring width (TRW) chronology (green line) and number of samples (black line). Green crosses indicate LBM outbreaks. (c) Frequency of LBM outbreaks, (d) percentage of affected trees (population severity) and (e) percentage of growth reduction (individual severity) transformed and fitted by LOWESS smoothing with a 50 yr time window. Dashed lines: 99% confidence range; the mean value of each distribution (μ) and the standard deviation (2σ) are reported; gray shading: changes in outbreak characteristics. The inset in (c) shows singular spectral analysis over the period 1700–1799; the periods are given in years for each significant peak

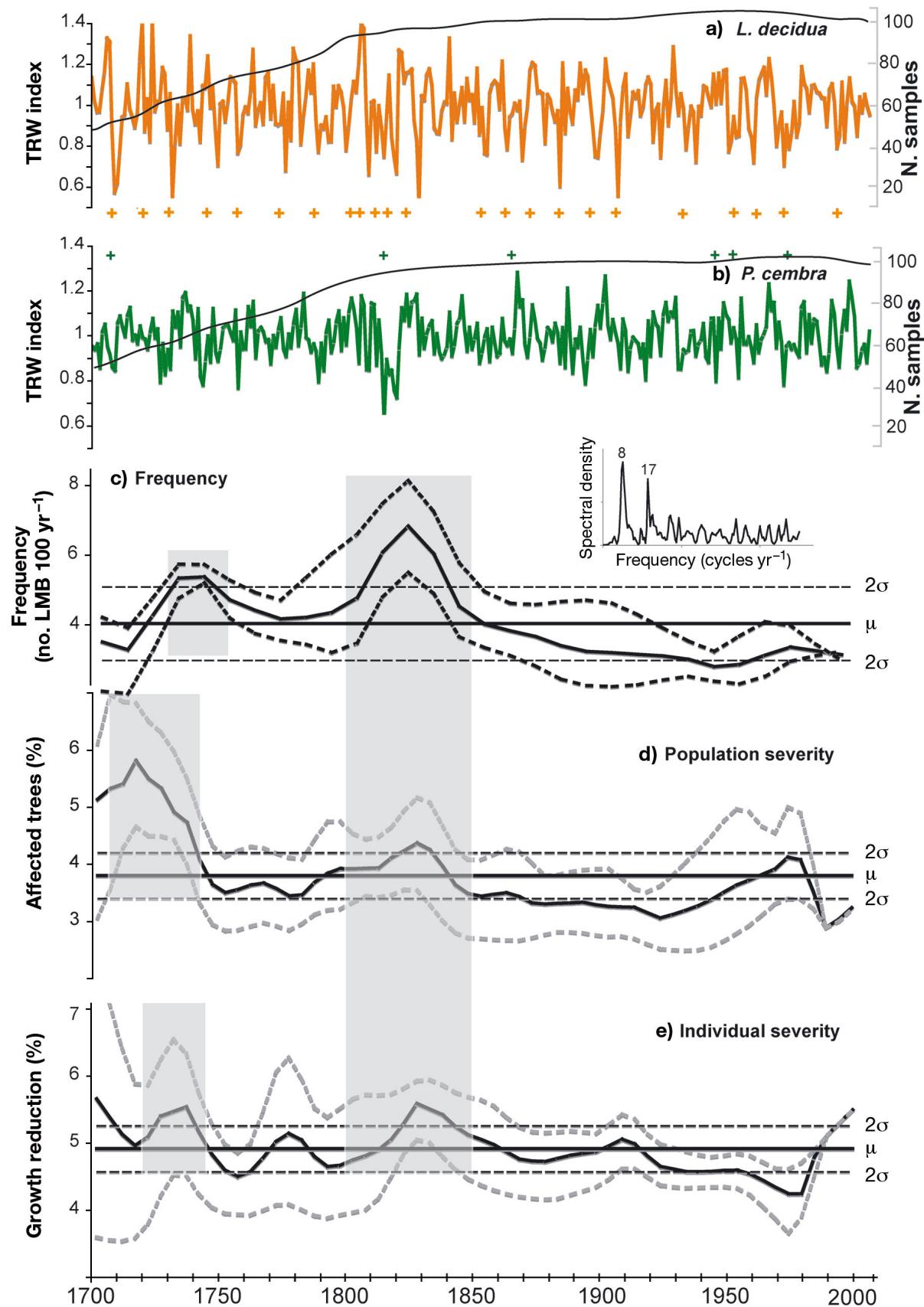


Table 1. Characteristics of reconstructed larch budmoth (LBM) attacks on *Larix decidua* and *Pinus cembra*. The percentage of growth reduction is calculated as follows: $100 - (\text{growth in the first year of the outbreaks/growth in the previous year}) \times 100$

No. outbreaks	Initial year	Length (yr)	Affected trees (%)	Growth reduction (%)
<i>Larix decidua</i>				
1	1708	2	45	78
2	1721	4	32	76
3	1730	2	34	75
4	1747	3	25	60
5	1758	4	33	60
6	1775	3	28	75
7	1789	4	39	50
8	1801	2	30	85
9	1809	4	37	98
10	1813 ^a	2	30	95
11	1819 ^a	2	27	75
12	1829	2	35	96
13	1854 ^a	4	30	60
14	1864	4	25	68
15	1877	3	25	65
16	1884	5	28	69
17	1898	5	25	85
18	1908	3	30	90
19	1933 ^a	4	25	60
20	1953 ^a	2	39	50
21	1961 ^a	3	25	40
22	1975 ^a	5	30	60
23	1996	3	25	75
<i>Pinus cembra</i>				
1	1708	2	25	35
2	1816	1	25	37
3	1866	1	27	30
4	1944	1	26	33
5	1953	2	25	28
6	1976	1	27	31

^aCorrespondence between reconstructed LBM events and those observed during the period 1800–2000 by Baltensweiler & Rubli (1999)

to have been the most important for both frequency (Fig. 2c) and the 2 components of severity (Fig. 2d,e). The trends for both population and individual severities were generally lower than the average value recorded for the entire record, particularly during the 1850–1940 and 1950–1980 time periods, when the trends were within the $<2\sigma$ range.

3.2. Forest recruitment and land uses

Forest dynamics were assessed through tree recruitment data (Fig. 3a), showing that over the past 310 yr the forest has experienced almost continuous regeneration. Larch largely dominated the recruitment ($58 \pm 10\%$) during the 18th and 19th centuries,

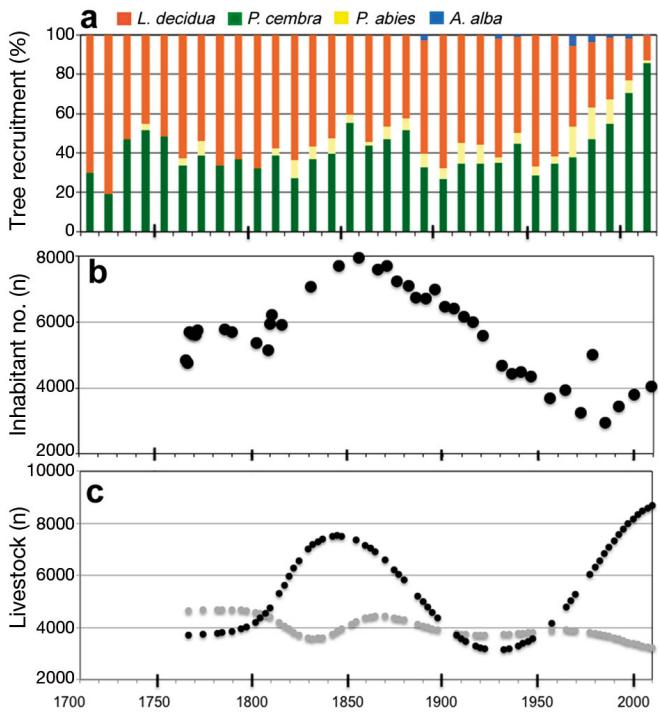


Fig. 3. (a) Relative recruitment per decade and per canopy species for *Larix decidua* (orange), *Pinus cembra* (green), *Abies alba* (blue) and *Picea abies* (yellow). (b) Number of local human inhabitants in the municipalities surrounding the study sites. (c) Number of resident sheep and goats (black circles) and cattle (gray circles)

while the 20th century was characterized by an increase in pine, spruce (*Picea abies* [L.] Karst) and silver fir (*Abies alba* Mill.) recruitment and a decrease in larch starting in the 1940s and peaking after 1960, when pine represented $59 \pm 19\%$ of the recruitment on average, and larch only $28 \pm 11\%$. Based on the Kingdom of Savoy tax census from the 18th to 19th centuries and on the French census during the 19th to 20th centuries, the total inhabitant numbers in the 10 municipalities of the upper Maurienne Valley increased from 1800 and reached a maximum in 1846. After the mid-19th century, the human population started to decrease gradually until 1975, when the lowest population was recorded (2931 inhabitants), i.e. almost 65% less than the maximum recorded in 1846 (Fig. 3b). Until the 1950s, the inhabitant numbers correlated well with the number of domestic animals that were the economic basis of the mountain society, in particular with the total number of sheep and goats (Fig. 3c). However, during the 1980s and 1990s, the local sheep economy became more pronounced in the area, thanks to economic funding from the French government and EU agricultural policies, which supported the breeding of rare sheep and coincided with the increase in pine recruitment.

The total cover of subalpine forests was estimated using the 6 historical maps (Table 2). We observed a decrease of 38% (from 35.6 to 22.2 km²) between the 18th (Mappe Sarde) and the late 19th centuries (Premier cadastre français), and a huge increase of 136% (22.2 to 52.5 km²) in forest cover during the 20th century.

The relationships between LBM frequency and severity and anthropogenic factors were assessed through RDA (Fig. 4). The first and second axes accounted for 83.7 and 15.8% of the total variance, respectively. The LBM frequency (LBMf) and the

percentage of growth reduction (Gr) were positively associated with the number of inhabitants (I) and number of cattle (C), while an opposite cluster was revealed with forest cover (FC). The percentage of affected trees (At) was positively linked to the percentage of larch (LADE) and negatively associated with pine (PICE), the latter related to the number of sheep and goats (SG).

3.3. Radial growth and climatic interaction

SEA applied on larch TRW series (Fig. 5a) showed a significant tree growth decrease during outbreak years (given as 0 in Fig. 5) and in the 3 following years, whereas the relationship was highly positive during the 3 yr prior to the LBM outbreak. For pine, in contrast, there were no significant departures in tree-ring growth with the SEA over the 7-yr window before, during or after outbreaks, although a slight TRW decrease was recorded during the year after each reconstructed event (Fig. 5b).

The correlation between TRW of both tree species with climate features (Fig. S4 in the Supplement at www.int-res.com/articles/suppl/c062p001_supp.pdf), as well as the 40 yr running correlations (data not shown) performed to test temporal stability of climate-growth relationships, showed no correlation with precipitation, and a correlation only with summer temperature (larch, $r = 0.30$, $p < 0.05$; pine, $r = 0.49$, $p < 0.01$), and no temporal shift was observed. Moreover, SEA between TRW and climate features revealed that there was no linkage between LBM outbreaks, as reconstructed from larch, with the instrumental temper-

Table 2. Source and characteristics of the historical maps used for forest cover reconstruction. Forest cover is expressed as mean \pm SD

Source ^a	Years	Scale	Forest cover (km ²)
Mappe Sarde	1728–1738	1:2372	35.6 \pm 3.4
Premier cadastre français	1850–1895	1:500; 1:50000	22.2 \pm 3.1
Cadastre rénové	1927–1939	1:20000	35.2 \pm 2.9
Phytosociological map	1996	1:50000	36.8 \pm 1.7
Corine Land Cover	2000	1:100000	50.1 \pm 1.6
BD topo IGN	2010	1:25000	52.5 \pm 1.3

^aSee <http://ddaf73.agriculture.gouv.fr/Observatoire/>

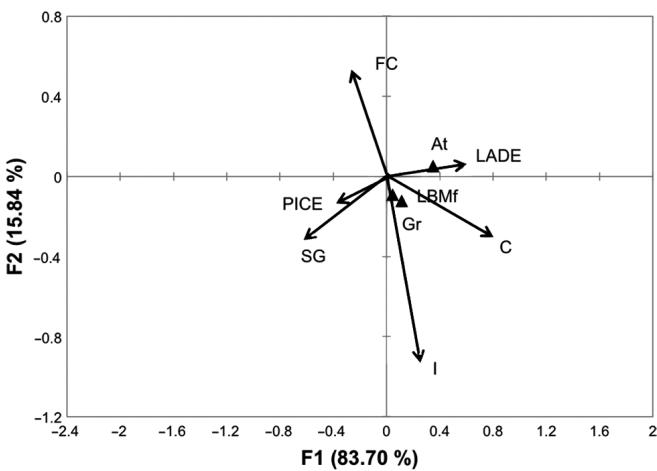


Fig. 4. Redundancy analysis (RDA) of larch budmoth (LBM) outbreak frequency and severity in relation to anthropogenic factors and historical land uses. The first and second axes are displayed and they accounted for 99.5% of the total variance. Arrows represent the number of inhabitants (I), number of cattle (C), number of sheep and goats (SG), forest cover (FC), percentage of *Larix decidua* (LADE) and percentage of *Pinus cembra* (PICE). Triangles: LBM frequency (LBMf), the percentage of growth reduction (Gr) and the percentage of affected trees (At)

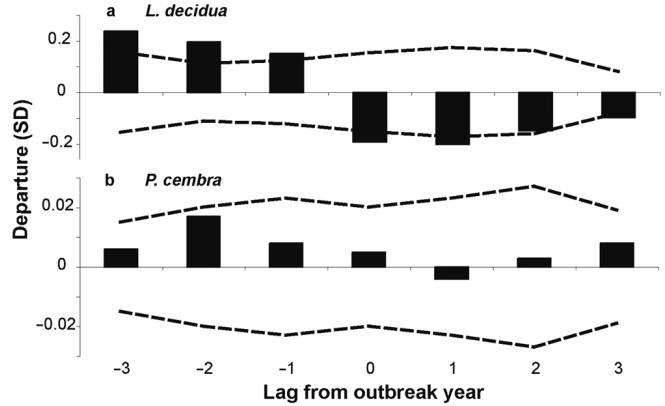


Fig. 5. Relationship between local tree-ring width index and larch budmoth outbreaks determined by superposed epoch analysis for (a) larch *Larix decidua* and (b) Arolla pine *Pinus cembra* stand chronologies. Bars represent deviation from normal conditions based on 1000 simulations. The 99% confidence limits are plotted as dashed lines

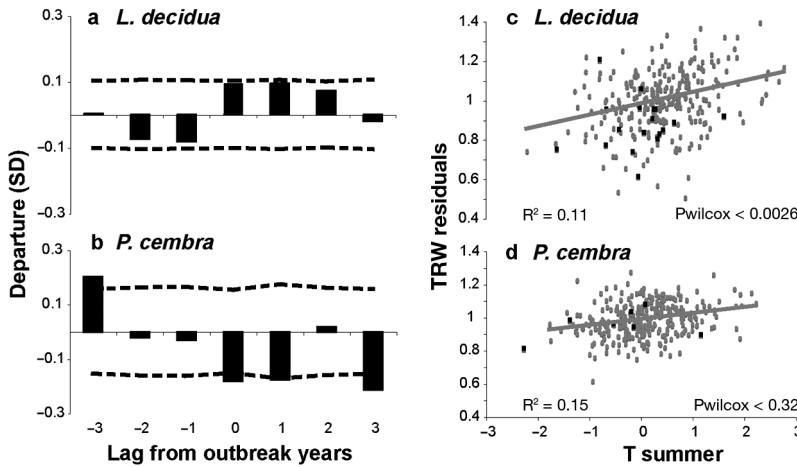


Fig. 6. (a,b) Mean departures for the summer temperature index for years before, during and after outbreak events for (a) larch *Larix decidua* and (b) Arolla pine *Pinus cembra*. The 99 % confidence limit is plotted as a dashed line. (c,d) Analysis of residuals of tree-ring width (TRW) for (c) *L. decidua* and (d) *P. cembra* with summer temperatures for the period 1900–2010. Black squares: larch budmoth events. p -values <0.05 (Wilcoxon-Mann-Whitney rank sum test) indicate significant differences between groups

ature record (Fig. 6a), while the reconstructed outbreaks events from pine were associated with cold summer temperatures (Fig. 6b). To determine the influence of LBM outbreaks on TRW without a climate bias, we calculated the residuals between TRW of both species and summer temperature by plotting the tree-ring parameters against summer temperature and fitting them with a regression line. While for larch (Fig. 6c) the TRW residuals for LBM outbreak events are clearly outliers compared with the whole chronology ($p < 0.05$), for pine, LBM residual TRW values are not different from the whole climate data set (Fig. 6d). Together, these results suggest there is less of an effect of climate than LBM outbreaks on larch TRW.

4. DISCUSSION

Forest insect outbreaks leave distinct and quantifiable signals in tree rings because defoliation significantly reduces radial growth during and after an outbreak year (Weber 1997), allowing LBM outbreak reconstruction over exceptional temporal (Esper et al. 2007) and spatial scales (Büntgen et al. 2009). The present study comprises the longest record of LBM outbreaks in the western Alps. Further, to our knowledge, it is the first study to link the effects of both climate and land-use change with insect outbreaks, providing relevant information for forest managers to counteract or mitigate the possible negative consequences on the forest ecosystems.

4.1. LBM outbreaks and climate

Distinctive growth depressions in the ring-width signature attributed to LBM outbreaks were found in our larch chronologies. Our reconstructed years of outbreak events were compared with previous reports (Weber 1995, 1997, Rolland et al. 2001, Nola et al. 2006, Daux et al. 2011) in order to verify the effectiveness of our LBM reconstruction. Some events recorded in our reconstruction presented a 1- or 2-yr shift in the initial date compared with other studies (Table 3). For example, Rolland et al. (2001) and Daux et al. (2011) referred to a 1811 outbreak and Nola et al. (2006) to 1810, whereas we found 2 outbreaks in 1809 and 1813, each lasting for a couple of years. Furthermore, these studies reported different numbers of outbreaks events

during the 19th and the 20th centuries in comparison with our findings: Rolland et al. (2001) found 22 outbreaks from 1801 to 1987, Nola et al. (2006) found 16 from 1802 to 1996, and Daux et al. (2011) reported 12 outbreaks from 1811 to 1996 (Table 3). These apparent differences could be due to 2 factors: first, the dispersion mechanisms of this insect and the traveling velocity of the LBM waves throughout the Alps (Bjornstad et al. 2002) and, second, the statistical criteria used in our outbreak analysis were based on a very conservative approach in order to reduce errors in LBM identification. In fact, although these studies were carried out in western Alpine valleys (Maurienne, Tarentaise, Susa, Névache), each of these valleys are separated by important mountains at the north (Vanoise Massif) and the south (Thabor Massif and mounts Ambin and Cenis). However, when comparing our LBM outbreak reconstruction with historical defoliation patterns observed by Baltensweiler & Rubli (1999) during the period 1800–2000, we have 60 % agreement between the outbreaks reconstructed and the observed (Table 1).

Among the 6 events recorded within the pine chronology, only 2 (1708, 1953) matched the LBM outbreaks reconstructed from larch TRW. Furthermore, the reconstructed pine outbreaks affected a limited number of individuals and growth reduction was less pronounced. These findings indicate that LBM population activity did not significantly alter pine growth. Moreover, 3 events identified as possible outbreaks on pine, i.e. 1816, 1944 and 1976, have

Table 3. Synthesis of larch budmoth (LBM) outbreak years on *Larix decidua* in the Maurienne Valley and the surroundings in the north (Tarentaise Valley) and south (Susa and Névache Valleys). X: event reported; empty cell: no reported event

LBM year(s)	Present study Maurienne	Rolland et al. (2001) Maurienne and Tarentaise	Nola et al. (2006) Susa	Daux et al. (2011) Névache
1708	X			
1721	X			
1730	X			
1747	X			
1758	X			
1766			X	
1775	X		X	
1789	X			
1792			X	
1801–1802	1802	1801	1802	
1809–1811	1809	1811	1810	1811
1813	X			
1819–1820	1819	1820	1820	1819
1829–1930	1829	1830	1829	
1837–1838		1838	1837	
1846		X	X	
1854	X			
1856–1857		1857	1856	1856
1864	1864		1865	
1867		X		
1875		X		
1877	X			
1883–1884	1884	1884	1884	1883
1892		X		
1898–1900	1898	1901	1899	1900
1908–1909	1908	1909	1908	
1918		X		
1926		X		
1933	X			
1935–1936		1936	1935	1935
1943				X
1945		X		
1953	X	X	X	X
1961–1963	1961	1963	1962	1962
1971–1972		1972	1971	1972
1975	X			
1979–1980		1980		1979
1987		X		
1996	X		X	X

also been recognized as extreme climate years in the Alps (Beniston et al. 2007, Battipaglia et al. 2010), thus suggesting that the growth reduction recorded in the pines might not be the result of insect attacks, but may simply be the result of extreme climate years. Indeed, for pine we found no significant relationships between TRW and the outbreak occurrence using the SEA approach (Fig. 5b) and, when climate variation was removed by calculating residuals, no statistical difference between pine TRW and summer temperature was found (Fig. 6d), whereas for larch

the difference remained significant (Fig. 6c). This assessment does not completely rule out the possible effect of climate stressors on LBM dynamics and outbreaks, but argues in favor of other environmental mechanisms regulating LBM outbreak dynamics, as well as the modification in vegetation cover and landscape structure triggered by land-use changes during the last few centuries.

4.2. Variation in LBM outbreak intensity and land-use cover change

Our reconstruction of LBM outbreaks indicates that a broad range of severities and frequencies has occurred over the last 3 centuries, and that 3 different phases (Fig. 2c) in LBM frequency follow local forest patterns and changes in human society. The first phase of the frequency distribution is characterized by periodic LBM events, with wavelengths varying between 8 and 17 yr (Fig. 2c, inset), as well as the highest number of trees affected and the most important reduction in tree growth (Fig. 2d,e) and forest regeneration mainly dominated by larch recruitment (Fig. 3a). At the beginning of the industrial era, during the first half of the 19th century, an increase in local population (Fig. 3b) and military garrisons, sent to protect the nearby boundaries between France and the Kingdom of Savoy, created a major human demand for food, firewood and timber, and grazing areas for military mules and horses. This historical process triggered (1) an increase in livestock density (mostly sheep and goats), which certainly increased the effect of grazing on subalpine forests, and (2) a preferential selection of larch for timber and firewood, excluding other species, i.e. Arolla pine, silver fir and European spruce. Furthermore,

the reduction in Arolla pine cover, which occurred during the preceding Kingdom of Savoy era, had been achieved through selective tree harvesting and/or seedling/sapling suppression. People using the forest to graze their animals periodically removed the pine seedlings that were not browsed or trampled by cattle or sheep (Motta et al. 2006). All of these land uses and behavioral changes are involved in the observed changes in forest structure and composition. The general decrease in forest cover observed

from the historical maps (Table 2) and the enhancement of the proportion of larch coincided with the increase in LBM outbreak frequency and severity (Fig. 4). Indeed, outbreaks have been shown to be more common and pronounced in areas with a more homogeneous canopy as compared with those with a mixed composition (Roland 2005). Low pine and high larch densities seemed to explain the increase in frequency and severity of LBM outbreaks recorded between the periods described in the Premier cadastre français and Cadastre rénové historical maps. Later, the observed increase in forest cover, reported in recent maps (Table 2), seems to have contributed to the establishment of new dynamics, transforming the forest shape, and hence influencing the LBM regime once again. Progressive land abandonment, which started in ~1870 (Fig. 3b), but became more marked after 1950, resulted in an important recruitment of pine and other woody species including silver fir and European spruce (Fig. 3a) (Genries et al. 2009, Chauchard et al. 2010), and coincided with the decrease in LBM outbreak intensity. Indeed, while the 18th and 19th centuries were dominated by traditional agriculture, the 20th century recorded a rural mutation with a net disappearance of agricultural activities. This social change impacted the use of forest for timber, fuel wood or grazing, and thus the forest cover and the composition in favor of pine, to the detriment of larch cover.

Johnson et al. (2010) stated that the change in frequency of LBM observed in the last few centuries has been due to the elevational shifts of LBM populations in response to winter temperature fluctuations. We believe that LBM dynamics is related to the long-term changes in both climate and forestland uses. If it has been shown that higher temperatures increase LBM egg mortality (Büntgen et al. 2009), thus we hypothesize that land use should play a key role in the fragmentation and composition of the forested landscape by influencing the frequency of insect outbreaks that is itself a product of population connectivity. Forest cover decreased by 45% during the early 19th century between 1700 and 2000 m a.s.l., resulting in a fragmentation of the LBM habitat during the 18th century, although larch recruitment increased during the 19th century (Fig. 3a) because it was favored for several domestic uses. In contrast, the late 20th century experienced a net change in forest extent due to 136% forest expansion by tree colonization of grass parcels formerly grazed or used for hay production. However, the tree colonization in grassland as well as the recruitment in forest is mostly due to Arolla pine but not larch (Genries et al.

2009, Chauchard et al. 2010; Fig. 3a). Further, timber exploitation mostly used larch and not the other tree species. Consequently, the changes in forest composition based on pine and the current timber exploitation based on larch does not favor the development of LBM habitat. This change in forest composition despite an apparent change in forest defragmentation probably helps to explain why the late 20th century frequency of LBM outbreaks decreased since the mid-19th century and did not match the 18th century regime, which was more severe and more frequent.

It has been widely demonstrated that habitat fragmentation can have several effects on insect population dynamics (Pichancourt et al. 2006), including altering the fluctuation and speed of traveling waves (Kinezaki et al. 2003, Lecomte et al. 2004). For instance, Roland (1993) noted that outbreak frequencies of the tent caterpillar in North America were greater in highly fragmented habitats. However, results from Johnson et al. (2004) on the dynamics of LBM showed that when the level of forest fragmentation surpassed an upper threshold, the insect outbreaks in those highly fragmented habitats were less frequent. While the forest in the Maurienne Valley is currently less fragmented than in the previous centuries, the progressive reduction in larch regeneration since the 1950s is strongly linked to a decrease in LBM frequency.

Our findings indicate that, without ignoring the role of climate, the changes in LBM frequencies over the past 3 centuries coincide with the changes in local societies and the changing patterns of the subalpine landscape. The period of maximum LBM frequency and elevated individual and population severity was associated with the rise in human population levels and their highest density, the increase in grazing and larch recruitment in the valley (Fig. 4). The current reduction in the frequency and severity of LBM outbreaks is occurring during a period of rapid reforestation as a result of land-use abandonment, and is characterized by an important recruitment rate of Arolla pine that is progressively transforming canopy composition.

Although our findings are particularly relevant within a local context, they demonstrate the importance of extending historical data sources coupled with dendroecological studies to the entire Alpine arc in order to recognize and quantify the role of human impact and climate change on species distribution and forest dynamics. Indeed, understanding insect dynamics and their drivers is a prerequisite to simulating and predicting distribution patterns of their population outbreaks across space and time.

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