Effects of host abundance on larch budmoth outbreaks in the European Alps

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Abstract

1 Outbreaks of the larch budmoth (LBM) in the European Alps are among the most documented population cycles and their historical occurrence has been reconstructed over 1200 years.

2 Causes and consequences of cyclic LBM outbreaks are poorly understood and little is known about populations near the margin of the host's distribution range.

3 In the present study, we quantify historical LBM outbreaks and associated growth reductions in host trees (European larch). Tree-ring data collected from 18 sites between approximately 500 and 1700 m a.s.l. in the Northern pre-Alps are compared with data from the Western Alps and Tatra Mountains, as well as with nonhost Norway spruce.

4 Highly synchronized host and nonhost growth in the Northern pre-Alps shows that periodic LBM outbreaks are largely absent near the distributional limit of larch. By contrast, growth patterns in the Western Alps LBM core region are indicative of LBM events. Although climatic conditions in the Northern pre-Alps and Tatra Mountains would allow LBM outbreaks, low host plant abundance is likely the key driver for the absence of cyclic outbreaks in these regions.

5 The results obtained in the present study suggest that, in addition to the climatic conditions, host-species abundance is critically important for the occurrence of periodic LBM outbreaks and the determination of the respective outbreak range.

Keywords Dendroecology, forest composition, forest entomology, *Larix decidua*, *Lepidoptera*, population ecology, tree rings, tri-trophic.

Introduction

One of the most frequent causes of local to large-scale forest disturbance is the occurrence of insect outbreaks (Schowalter & Lowman, 1999; Volney & Fleming, 2000; Logan *et al.*, 2003; Kurz *et al.*, 2008; Schowalter, 2012). The effects of insect outbreaks can be diverse, including economic losses from tree mortality and growth suppression, as well as effects on ecosystem services, such as carbon sequestration (Day & Leather, 1997; Ayres & Lombardero, 2000; Dale *et al.*, 2001; Logan *et al.*, 2003; Kurz *et al.*, 2008; Seidl *et al.*, 2008; Schowalter, 2012). Outbreaks of forest Lepidoptera are commonly characterized by periodic regularity and trophic level interactions play key roles as drivers of outbreak cycles (Berryman, 1996; Hunter &

Dwyer, 1998). The larch budmoth [*Zeiraphera diniana* (Gn.); LBM] is one of the most intensively investigated and probably best-documented cyclic forest Lepidoptera species (Berryman, 1996; Baltensweiler *et al.*, 2008). Outbreaks of LBM occur with a high degree of regularity every 8–10 years predominantly in subalpine forests of the European Alps (Baltensweiler & Rubli, 1999; Esper *et al.*, 2007).

Populations of this foliage-feeding insect are reported from the Pyrenees, Alps and Tatra Mountains, with trees in the genera *Larix*, *Pinus* and *Picea* utilized as hosts. Although occasional outbreaks occur on *Pinus* in the Alps, these are caused by a separate host race (Dormont *et al.*, 2006) and most periodic outbreaks occur on European larch (*Larix decidua* Mill.) in subalpine elevations of the European Alps (Baltensweiler *et al.*, 1977), with the optimal outbreak zone estimated at 1700 and 2000 m a.s.l. (Baltensweiler *et al.*, 2008; Johnson *et al.*, 2010).

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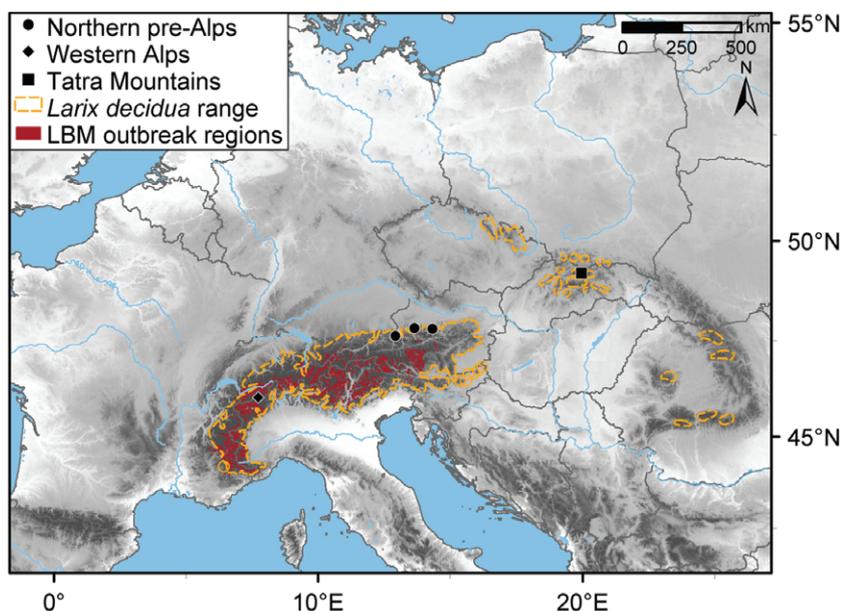
Figure 1 Natural distribution of *Larix decidua* and delimitation of larch budmoth (LBM) outbreak regions in Central Europe and tree-ring sampling sites. In the Northern pre-Alps, *L. decidua* (LBM host species) and *Picea abies* (nonhost species) were sampled at 18 sites. In the Western Alps and Tatra Mountains, only *L. decidua* was sampled. [Colour figure can be viewed at wileyonlinelibrary.com].

During outbreak years, LBM population densities may reach 30 000 larvae per tree (Baltensweiler & Rubli, 1999). Host trees foliage subsequently exhibit discolouration and trees may become completely defoliated, although this rarely results in tree mortality (Baltensweiler *et al.*, 1977; Esper *et al.*, 2007). Based on larval population census data and historical records of forest discolouration, Baltensweiler and Rubli (1999) have documented regional population cycles dating back to 1800 AD. Outbreak regions across the European Alps are divided into 22 sub-regions covering the 'Western', 'Central' and 'Eastern Alps' (see Supporting Information, Fig. S1). Areas where LBM defoliation is most frequent are concentrated at the centre of the Alps, with only occasional defoliation towards the edges of the Alpine arc (Fig. 1) (Baltensweiler & Rubli, 1999; Johnson *et al.*, 2004).

Dendrochronological reconstructions have been used to extend information on LBM oscillations beyond the historical period (i.e. prior to the time of the oldest written records) because tree defoliation significantly reduces radial growth and xylem cell wall development so that LBM outbreaks leave distinct signatures in tree rings (Schweingruber, 1979; Esper *et al.*, 2007; Baltensweiler *et al.*, 2008; Büntgen *et al.*, 2009; Johnson *et al.*, 2010). This signature was used to develop multicentury LBM reconstructions for timberline sites in the French Alps (Rolland *et al.*, 2001) and Swiss subalpine valleys (Weber, 1997). Esper *et al.* (2007) developed a 1200-year LBM outbreak reconstruction for subalpine regions in Switzerland and Büntgen *et al.* (2009) produced a 300-year spatial reconstruction covering the main outbreak regions of the Alpine arc.

Investigations of mechanisms driving LBM population dynamics include Fischlin and Baltensweiler (1979) who identified needle-quality as key factor linking host quality with LBM population growth. Anderson and May (1980) quantified host–pathogen dynamics impacting LBM population density fluctuations. Turchin *et al.* (2003) developed a tri-trophic model to show that interactions of LBM with both needle-quality and parasitoid populations could explain observed patterns of periodicity.

Bjørnstad *et al.* (2002) revealed the existence of outbreak waves travelling from west to east along the Alpine arc and Johnson *et al.* (2004) showed that these waves spread out from two distinct epicentres: one in the central and one in the south-western Alps; see also Price *et al.* (2006). Despite the high periodicity of historical LBM cycles, outbreaks have largely been absent from European Alps during the last three decades.

Tree-ring studies revealed that this absence of LBM outbreaks from the late 20th Century onward has been unique over the past 1000 years (Esper *et al.*, 2007). However, the drivers of this phenomenon and ecological factors influencing the occurrence and/or interruption of cyclic LBM outbreaks are still not fully understood (Johnson *et al.*, 2010). Battipaglia *et al.* (2014) argued that land-use changes and forest composition might affect the LBM system. Changes in climate and host-plant availability may profoundly affect the success of insect herbivores (Bale *et al.*, 2002). Although most studies focus on LBM outbreak cycles and focal areas, little is known about LBM dynamics near distributional limits and it remains unclear why cycles develop in specific regions and not in others. Considering that the geographical range of European larch extends well beyond the LBM cyclic outbreak range (Fig. 1), it is still uncertain what factors constrain the geographical distribution of the outbreak region. Although the natural range of larch is disjunct (McComb, 1955; Bauer, 2012; Wagner, 2013), a major and continuous distribution area is found in subalpine elevations (with an additional prevalence over a wide elevational range) in the European Alps. Besides this core habitat, larch is indigenous in some disjunct parts of the Carpathian arc (Wagner, 2013), including the Tatra Mountains where a recent study revealed the absence of cyclic LBM outbreaks (Konter *et al.*, 2015). Little information exists at the edge of the hosts' main distribution range and the identification of factors limiting species at their range edges can provide information critical for understanding the drivers of a species interactions within ecological systems (Holt & Keitt, 2005; Bahn *et al.*, 2006; Sexton *et al.*, 2009).

Table 1 Characteristics of larch (L) and spruce (S) chronologies in the Northern pre-Alps sorted by elevation

Site #	Latitude	Longitude	m a.s.l.	Period L	S	MSL L	S	AGR L	S	Lag-1 L	S	$Rbar_s$ L	S	EPS L	S
1	47°47′	13°33′	527	1828–2010	1826–2010	174	174	1.24	1.02	0.89	0.79	0.63	0.55	0.98	0.94
2	47°40′	13°01′	760	1850–2008	1857–2008	149	128	1.11	1.36	0.85	0.81	0.57	0.51	0.96	0.88
3	47°50′	14°27′	894	1914–2010	1917–2010	93	88	1.91	2.03	0.87	0.68	0.57	0.50	0.98	0.89
4	47°50′	14°26′	901	1916–2010	1838–2010	92	117	2.00	1.74	0.88	0.82	0.63	0.48	0.99	0.93
5	47°45′	14°21′	950	1830–2009	1827–2009	172	168	1.08	1.22	0.84	0.80	0.60	0.54	0.97	0.92
6	47°38′	12°51′	1040	1838–2008	1885–2008	163	111	1.21	1.83	0.84	0.71	0.60	0.52	0.95	0.87
7	47°31′	12°47′	1080	1889–2008	1879–2008	110	102	1.57	1.92	0.79	0.83	0.64	0.54	0.96	0.95
8	47°45′	14°26′	1150	1829–2009	1792–2009	173	189	1.05	0.99	0.84	0.83	0.59	0.53	0.97	0.92
9	47°31′	12°47′	1250	1803–2008	1871–2008	183	125	1.22	1.73	0.87	0.74	0.55	0.59	0.94	0.85
10	47°33′	12°48′	1310	1832–2008	1794–2008	164	191	1.16	1.04	0.81	0.80	0.60	0.58	0.96	0.84
11	47°35′	12°53′	1330	1806–2008	1849–2008	185	139	1.09	1.70	0.84	0.76	0.58	0.54	0.97	0.84
12	47°46′	14°25′	1350	1855–2009	1865–2009	144	132	1.37	1.65	0.85	0.88	0.54	0.57	0.97	0.97
13	47°46′	14°25′	1460	1847–2009	1845–2009	145	150	1.21	1.31	0.79	0.84	0.58	0.62	0.94	0.96
14	47°49′	13°35′	1500	1785–2010	1798–2010	193	197	0.89	0.84	0.71	0.73	0.73	0.54	0.95	0.87
15	47°33′	12°48′	1560	1780–2008	1879–2008	165	100	1.28	2.20	0.74	0.69	0.61	0.56	0.93	0.85
16	47°34′	12°49′	1600	1706–2008	1683–2008	271	266	0.72	0.87	0.74	0.79	0.74	0.55	0.97	0.83
17	47°34′	12°49′	1620	1747–2008	1848–2008	244	138	0.85	1.48	0.81	0.71	0.65	0.60	0.96	0.89
18	47°31′	13°01′	1670	1781–2008	1836–2008	193	160	1.18	1.51	0.82	0.78	0.66	0.65	0.97	0.96

MSL, mean series length (years); AGR, average growth rate (mm/year); Lag-1, first-order autocorrelation; $Rbar_s$, inter-series correlation; EPS, expressed population signal. Lag-1, $Rbar_s$ and EPS were calculated for raw (nondetrended) chronologies.

The present study aims to assess the historical occurrence of LBM outbreaks near the distributional limit of host European larch and to analyze the environmental factors causing the delimitation of LBM outbreaks to specific regions. We search for LBM signatures in larch tree-ring width chronologies from the edge of the hosts' core habitat in the Northern pre-Alps. We compare findings from this range edge with findings from the LBM core region in the Swiss Alps, as well as a disjunct larch habitat in the Tatra Mountains where LBM does not incur outbreaks. Studying the geographical distribution of LBM outbreaks relative to climatic conditions, as well as host species abundance, will provide insights into the environmental drivers of the presence of cyclic LBM outbreaks.

Materials and methods

Study design and tree-ring data

Tree-ring data from three different regions within the range of European larch were used for the present study (Fig. 1). The Northern pre-Alps represent the edge of larch's core habitat, the Swiss Alps represent the core distribution of larch and the Tatra Mountains represent a disjunct habitat where larch is a minor forest species and LBM does not incur outbreaks.

For reconstructing potential historical LBM outbreaks towards the distribution limits of European larch, tree-ring samples were collected at 18 stands in the Northern pre-Alps from 527–1670 m a.s.l. (Table 1). In each stand, 10 dominant host trees (European larch) were cored twice with a 5-mm increment borer at breast height (approximately 130 cm) parallel to the slope. Norway spruce (*Picea abies* [L.] Karst.) was considered as nonhost species and sampled in the same stands and in the same manner to differentiate between climate- and insect-related growth variations. Additional larch tree-ring data with the same

sampling procedure were used (i) from 11 sites within the core distribution of larch in the Western Alps covering an elevational transect from 985–2200 m a.s.l. and (ii) from two sites outside the core larch range in 950 and 1500 m a.s.l. in the Tatra Mountains (Table 2). The three regions are referred to as N-Alps for the sites in the Northern pre-Alps, W-Alps for the sites in the Western Alps and Tatra for the sites in the Tatra Mountains.

Tree-ring widths were measured to an accuracy of 0.01 mm using TSAP-WIN scientific software and a LINTAB 6 measurement device (RINNTECH, Germany) (Rinn, 2003). Cross-dating accuracy was confirmed statistically using COFECHA (Holmes, 1983). Descriptive statistics of raw chronologies include mean series length (i.e. an estimate of mean tree age at breast height within a site), average growth rate and first-order autocorrelation (lag-1) (Tables 1 and 2). Inter-series correlation ($Rbar_s$) and the expressed population signal (Wigley *et al.*, 1984) were calculated to estimate the internal coherence of the chronologies.

Age and size related growth trends were removed from individual series by transforming raw ring width data into ring width indices (RWI). Two different detrending techniques were applied: (i) a cubic smoothing spline with a frequency cut-off of 50% at 30 years (RWI_{30}) to emphasize high-frequency variability for LBM detection analyses and (ii) a stiffer spline with a frequency cut-off of 50% at 200 years (RWI_{200}) to maintain low-frequency, inter-decadal scale variability for growth/climate response analyses (Cook & Peters, 1981). After truncation at a minimum replication of five series, the detrended single series were averaged to site- and species-specific chronologies using a bi-weight robust mean (Mosteller & Tukey, 1977).

Statistical analysis

To analyze similarities in year-to-year variability within elevational belts in the N-Alps, the inter-chronology correlation

Table 2 Characteristics of larch chronologies in the Western Alps and Tatra Mountains sorted by elevation

Region	Latitude	Longitude	m a.s.l.	Period	MSL	AGR	Lag-1	Rbar$_s$	EPS
W-Alps	46°18′	8°00′	985	1924–2011	83	1.30	0.80	0.74	0.97
	46°18′	8°00′	1100	1907–2010	87	1.47	0.75	0.67	0.93
	46°12′	8°04′	1400	1928–2010	78	1.56	0.66	0.62	0.96
	46°12′	8°03′	1575	1875–2011	131	1.13	0.79	0.60	0.97
	46°12′	8°03′	1712	1898–2011	108	1.33	0.79	0.67	0.97
	46°12′	8°03′	1713	1879–2010	105	1.09	0.75	0.61	0.95
	46°11′	8°03′	1900	1847–2010	118	1.19	0.69	0.69	0.93
	46°13′	8°03′	2020	1844–2010	130	0.93	0.76	0.66	0.96
	46°13′	8°04′	2150	1771–2009	167	0.67	0.70	0.65	0.93
	46°00′	7°45′	2200	1816–2011	135	1.39	0.66	0.71	0.94
	46°01′	7°46′	2200	1762–2011	216	0.91	0.73	0.73	0.96
Tatra	48°55′	20°15′	950	1767–2012	230	0.57	0.68	0.71	0.97
	49°09′	20°04′	1500	1770–2012	232	0.76	0.67	0.77	0.98

MSL, mean series length (years); AGR, average growth rate (mm/year); Lag-1, first-order autocorrelation; Rbar$_s$, inter-series correlation; EPS, expressed population signal. Lag-1, Rbar$_s$ and EPS were calculated for raw (nondetrended) chronologies.

(Rbar$_c$) (i.e. the average correlation among RWI$_{30}$ chronologies) was determined. The influence of temperature on tree growth in the high frequency domain was evaluated using Pearson's correlation coefficients based on the RWI$_{30}$ N-Alps larch and spruce chronologies and 30-year spline filtered June/July/August (JJA) temperatures over the 1850–2000 period. The JJA season was selected because this is the most important season for tree growth in this region (see below).

Potential LBM signatures in the N-Alps larch trees were analyzed via two independent methods. First, potential outbreaks were identified by detecting negative growth variations in the N-Alps RWI$_{30}$ larch chronologies exceeding 2 SDs. To separate LBM-induced growth anomalies in the host from other environmental factors that could also lead to growth suppressions in specific years, negative growth anomalies were also detected in the nonhost species (i.e. in the N-Alps RWI$_{30}$ spruce chronologies). These anomalies were then compared with historical reports of LBM outbreaks in the Central and Eastern Alps, which are based on historical defoliation observations, near our study sites (Baltensweiler & Rubli, 1999).

Second, we used known 20th Century LBM outbreaks reported by Baltensweiler and Rubli (1999) and evaluate N-Alps larch growth deviations subsequent to these specific events with superposed epoch analysis (SEA) (Panofsky & Brier, 1958). Within the SEA, we aligned RWI$_{30}$ chronologies with respect to known LBM events (= year 0 in SEA) over the 20th Century and analyzed growth deviations 5 years before and after these events. Thereby, tree growth is expressed as scaled anomalies with respect to the mean of the 5 years preceding an event (years −5 to −1). Event years were derived from Baltensweiler and Rubli (1999) and outbreak regions in the 'Central Alps' and 'Eastern Alps' were selected because these are closest to our N-Alps sampling sites (see Supporting Information, Fig. S1). Accordingly, LBM outbreak events include 1906, 1921, 1946, 1954, 1963, 1972 and 1982 for the 'Central Alps' and 1947, 1957, 1965 and 1982 for the 'Eastern Alps'. The same procedure was applied to the N-Alps spruce chronologies for cross-comparison with the response pattern of a nonhost species. Finally, the SEA was applied to the W-Alps larch chronologies using the respective events representative of this region in 1900, 1908, 1915, 1923,

1929, 1937, 1945, 1954, 1963, 1972 and 1981 (Baltensweiler & Rubli, 1999; Esper *et al.*, 2007) (see Supporting Information, Fig. S1) to evaluate the typical post-LBM growth pattern in the infestation core region, which typically shows a strong growth suppression during LBM events and up to 3 years after the outbreaks (Baltensweiler *et al.*, 2008; Battipaglia *et al.*, 2014).

To evaluate the long-term growth/climate relationships along elevational transects and among regions, bootstrapped correlations were calculated using the RWI$_{200}$ chronologies together with temperature means and precipitation sums of different warm seasons (May/June/July = MJJ; June/July/August = JJA; May/June/July/August = MJJA) over the period 1901–2000. Climate data were obtained from the HISTALP database (Auer *et al.*, 2007) for the Alpine regions. We used the grid points N47°30′ E13°30′ for the N-Alps, N46°10′ E7°50′ for the W-Alps and, from the CRU TS3.21 dataset (Harris *et al.*, 2014), N49°15′ E19°45′ for the Tatra. All statistical procedures were performed using ʀ, version 3.1.1 (R Development Core Team, 2014) and the packages 'dplR' (Bunn *et al.*, 2012) and 'treeclim' (Zang & Biondi, 2015).

The bioclimatic envelope of the three regions was characterized (i) using instrumental JJA (and December/January/February = DJF) temperature data from stations representative of the regions and elevations (see Supporting Information, Table S1) and (ii) with estimates of larch proportion from inventory data of the respective regions. The study regions comprise different countries such that homogenous inventory data are unavailable, although percentage data were compiled that were representative of the regions. For the N-Alps, larch proportion data were provided by the 'Nationalpark Kalkalpen' based on canopy cover; for the Tatra basal area, data were provided by the National Forest Centre Zvolen; and, in the W-Alps, larch proportion data were obtained from Brändli (1998) based on stem numbers.

Results

Characteristics of the tree-ring data

Descriptive chronology statistics indicate comparable datasets between host and nonhost species, as well as among the larch
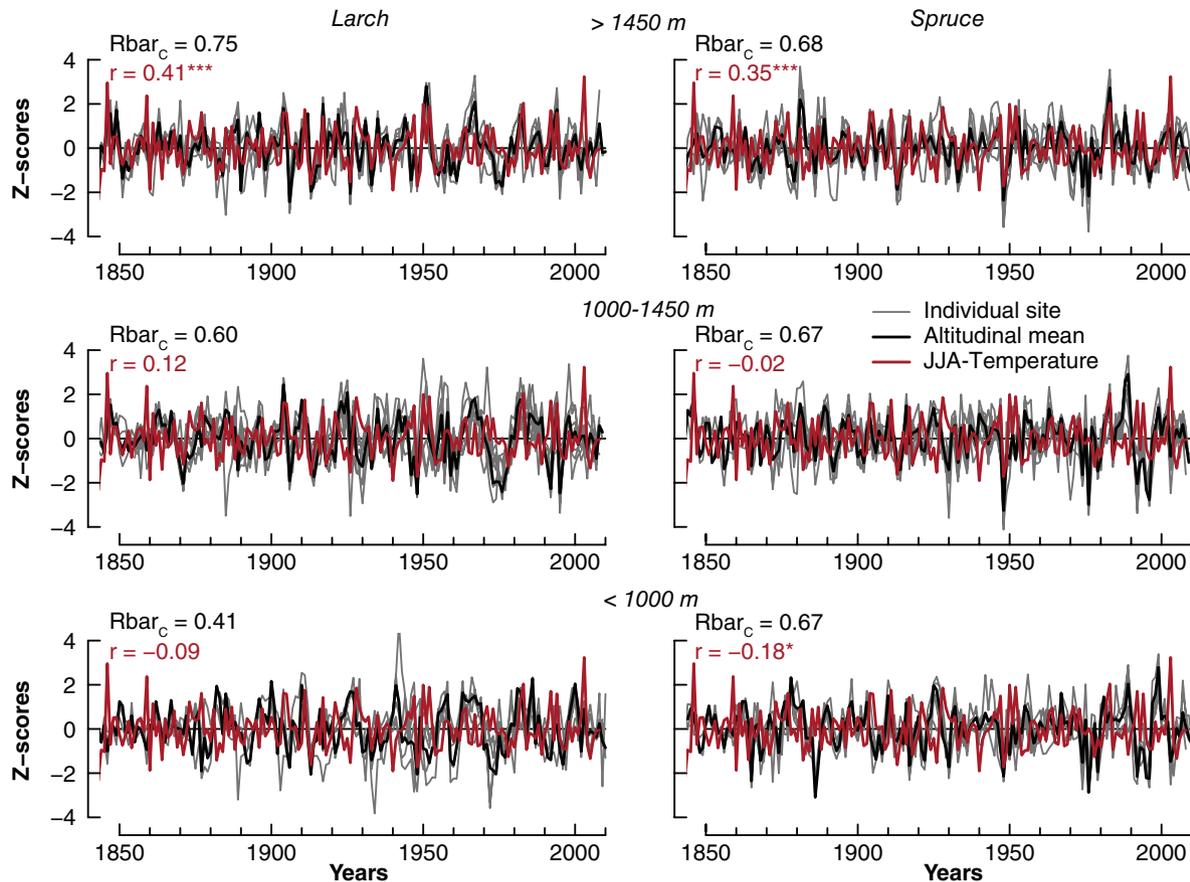
Figure 2 Larch and spruce chronologies from 18 locations in the Northern pre-Alps compared with local summer temperatures. All records were high-pass filtered (30-year spline) and normalized. $Rbar_c$ is the inter-chronology correlation within an elevational belt, and r is the correlation coefficient between temperatures and elevational mean chronologies over the period 1850–2000 (*$P < 0.05$, ***$P < 0.0001$). [Colour figure can be viewed at wileyonlinelibrary.com].

habitats (Tables 1 and 2). Mean series length of larch (spruce) chronologies varies between 92 and 271 (88 and 266) years in the N-Alps, and between 78 and 216 years in the W-Alps. Larch trees in the Tatra are older, with a mean series length of approximately 230 years. Average larch growth rates in the N-Alps (0.72–2.00 mm/year) are slightly higher than in the W-Alps (0.67–1.56 mm/year) and are lowest in the Tatra (0.57–0.76 mm/year). Lag-1 autocorrelation of larch growth is high in all regions, ranging between 0.67 and 0.89. $Rbar_s$ values show distinct coherency among individual ring width series for all chronologies and fluctuate between 0.54 and 0.74 in the N-Alps (0.48–0.65 for spruce), 0.60 and 0.74 in the W-Alps, and 0.71 and 0.77 in the Tatra, demonstrating highest internal coherence in the Tatra. Expressed population signal values of all larch sites exceed the widely accepted threshold of 0.85 (Wigley *et al.*, 1984), indicating sufficient internal signal strength for all sites. For spruce chronologies, three sites show only slightly lower values (0.83 and 0.84).

Host and nonhost growth variability in the N-Alps

By comparing the RWI_{30}-chronologies (Fig. 2; see also see Supporting Information, Table S2) (i.e. the growth variations in

the high frequency domain), it is obvious that the year-to-year variability is very similar within comparable elevations for both spruce and larch, at least in the higher elevations (see below). Interestingly, the correlation between host and nonhost species within a stand is high as well (see Supporting Information, Table S2). Summarized for all sites, the mean correlation between larch and spruce chronologies is $r = 0.40$, indicating that the environmental factors influencing growth are the same for both species at one site.

As noted above, annual larch growth patterns are very similar among sites at higher elevations, and they are characterized by a fairly high $Rbar_c$ value of approximately 0.75 (Fig. 2; see also Supporting Information, Table S2). There is a highly significant ($P \leq 0.0001$) association between temperature and tree growth at the high frequency domain with $r = 0.41$ (elevational mean). Spruce also shows similar year-to-year fluctuations, although the coherence among chronologies is slightly lower ($Rbar_c = 0.68$); the influence of temperature is slightly weaker ($r = 0.35$; elevational mean). Within the elevation belt 1000–1450 m a.s.l., larch growth dynamics are still similar, although $Rbar_c$ decreases to 0.60 and growth is no longer significantly associated with temperature. Spruce still shows highly coherent growth variations ($Rbar_c = 0.67$) at these elevations, although the influence
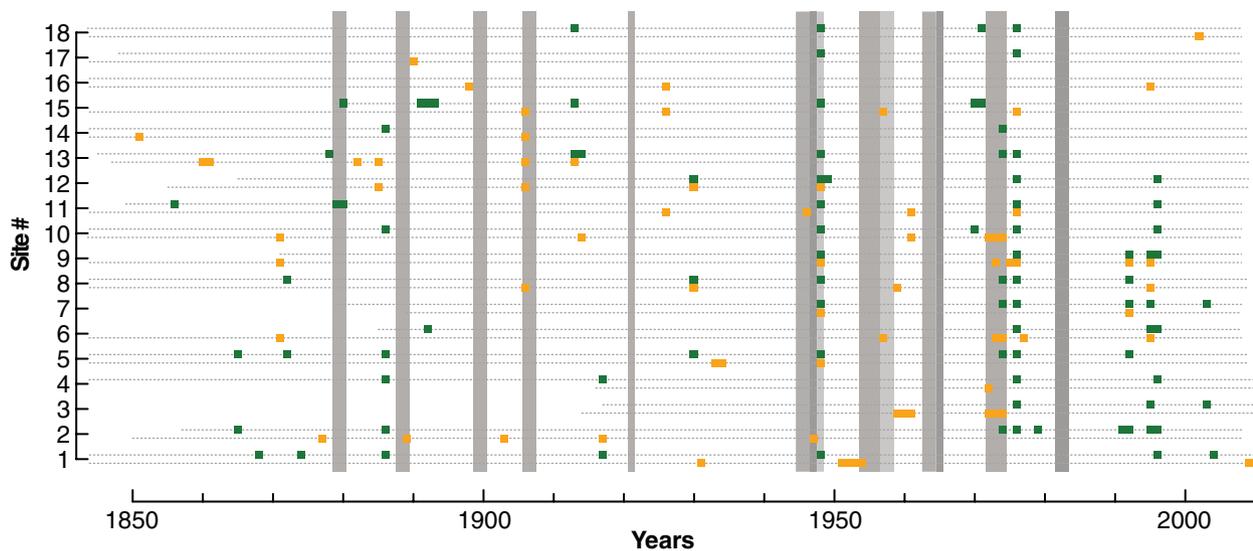
Figure 3 Comparison of reported larch budmoth (LBM) outbreaks in the Central and Eastern Alps (grey bars, based on Baltensweiler & Rubli, 1999) with growth anomalies (>2 × SD based on Fig. 2) in larch (orange) and spruce (green) 30 year spline detrended ring width indices (RWI$_{30}$)-chronologies from the Northern pre-Alps. Sites are sorted by elevation. Dotted lines represent individual chronology lengths (Table 1). Grey bars indicate LBM outbreaks in the Central Alps; these are light grey in the Eastern Alps and dark grey in both the Central and Eastern Alps. [Colour figure can be viewed at wileyonlinelibrary.com].

of temperature is inconsistent. At elevations below 1000 m a.s.l., site-specific growth variability occurs in the larch chronologies and Rbar$_c$ decreases to 0.41; temperature effects are low. The spruce growth pattern is still very coherent, which is emphasized by a high Rbar$_c$ value of 0.67. The influence of temperature on spruce growth is even significantly negative ($r = -0.18$; $P \leq 0.05$) at these elevations.

Growth anomaly comparison in host and nonhost chronologies

A total of 71 growth anomalies are detected in the N-Alps larch RWI$_{30}$-chronologies and 90 growth anomalies are present in the spruce RWI$_{30}$-chronologies (Fig. 3). For overview purposes, the most frequent extremes or overlaps of anomalies are referred to in the present study. Five larch chronologies (out of 16; note chronology lengths in Fig. 3) display growth anomalies in 1906; four chronologies show negative growth extremes in 1948, 1973 and 1995; three chronologies in 1926, 1961, 1972, 1974 and 1976 (all out of 18); and three chronologies in 1871 (out of 15). The frequency of synchronous growth anomalies in the spruce chronologies is higher: 14 chronologies show negative extremes in 1976; 12 in 1948; eight in 1996; six in 1974; five in 1992 and 1995 (all out of 18); and six in 1886 (out of 17).

Negative growth anomalies occur synchronously between host and nonhost species within the same stand in 13 cases. This is especially pronounced in 1948, although it also occurred in 1913, 1930, 1976, 1992 and 1995 (Fig. 3). The synchronous occurrence of negative growth anomalies in the host and nonhost species indicates that these growth suppressions are likely not related to LBM outbreaks.

By comparing anomalies with known LBM outbreaks for the 'Central Alps' (Fig. 3, grey bars), the years 1906 and 1972/73/74

(where a minimum of two chronologies showed extremes) can be confirmed as growth anomalies caused by LBM and, for the 'Eastern Alps' (Fig. 3, light grey bars), anomalies in 1948 and 1957 are confirmed by historical records.

Growth responses to known LBM outbreaks

Temporal alignment of growth during known LBM events using SEA reveals no clear or consistent LBM pattern in the N-Alps (Fig. 4). Six N-Alps sites show significant growth reductions during known LBM events (year 0) in the 'Central Alps', although no suppression occurs at elevations below 1310 m a.s.l. Generally, no growth response can be associated with LBM events in the 'Eastern Alps'. The comparison with the nonhost growth suggests a growth reduction coincident with LBM at five sites 2 years after 'Central Alps' events and at three sites 1 year after the 'Eastern Alps' events. By contrast, the W-Alps larch trees reflect an obvious LBM-induced growth suppression during the events and up to 3 years after LBM outbreaks. This is true for trees at high elevations (≥1400 m a.s.l.), although trees at two low elevation sites (≤1100 m a.s.l.) show no response to LBM outbreaks.

Climatic control of larch growth in the different regions

The influence of temperature on larch growth shows dependencies with elevation for all habitats, although the elevation-dependent temperature sensitivity differs among regions (Fig. 5). In the N-Alps, the response to temperature is predominantly positive and correlation coefficients generally increase with elevation. At sites below 1250 m a.s.l., r is <0.2, whereas, above this elevation, the coefficients become
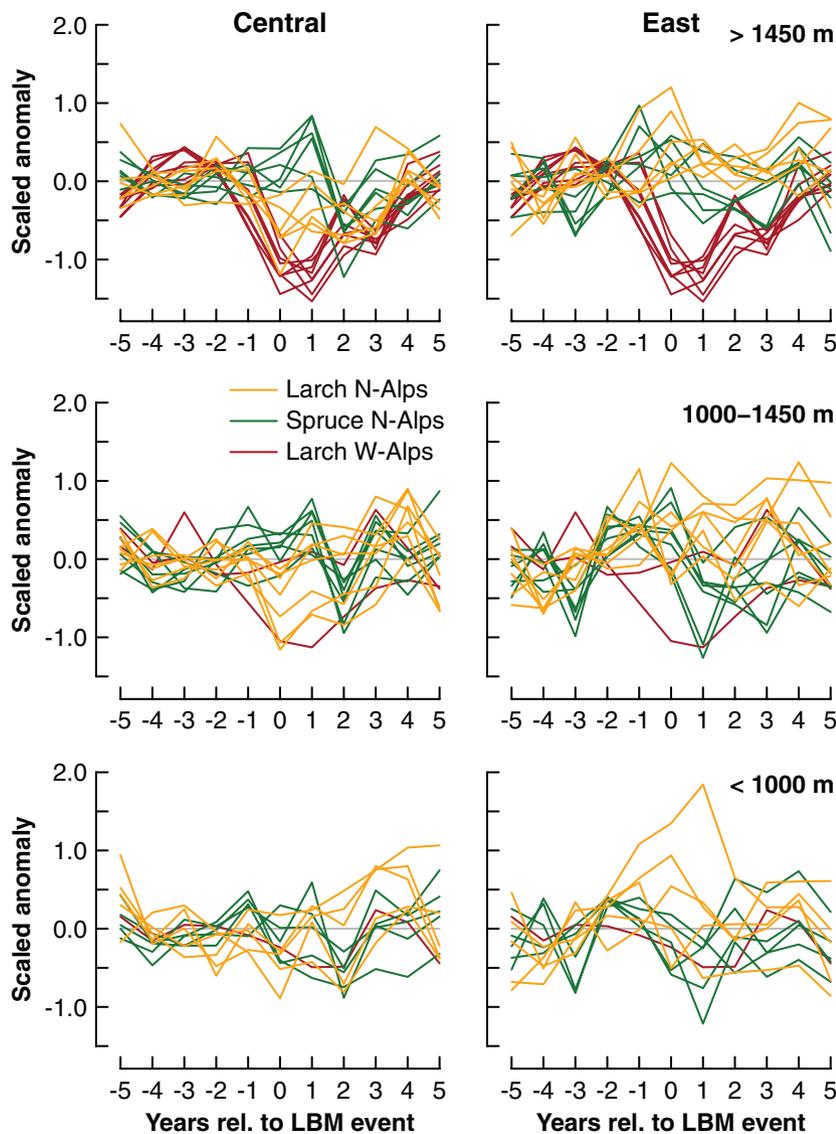
Figure 4 Superposed epoch analysis for N-Alps larch (orange) and spruce (green) 30 year spline detrended ring width indices (RWI$_{30}$)-chronologies. Records are aligned (= year 0) considering reported larch budmoth (LBM) outbreaks in the Central (1906, 1921, 1946, 1954, 1963, 1972 and 1982) and Eastern Alps (1947, 1957, 1965 and 1982). The typical LBM outbreak pattern is indicated by the W-Alps larch chronologies (red). These records were aligned (= year 0) considering outbreaks in 1900, 1908, 1915, 1923, 1929, 1937, 1945, 1954, 1963, 1972 and 1981. [Colour figure can be viewed at wileyonlinelibrary.com].

significant ($P \le 0.05$) for all seasons. The highest correlations are generally reached with JJA-temperatures and at sites ≥ 1500 m a.s.l.; correlation coefficients are mainly >0.45 with maximum $r = 0.51$ at 1620 m a.s.l. In the W-Alps, larch growth is negatively correlated with temperature up to 1400 m a.s.l. At sites ≥ 1575 m a.s.l., growth is significantly ($P \le 0.05$) positively correlated with temperature, with $r > 0.25$. Highest coefficients are mainly observed in the MJJA-season reaching a maximum $r = 0.43$ at 1900 m a.s.l. Growth shows the highest correlations with temperature in the Tatra for the MJJ-season with a slightly negative relationship at 950 m a.s.l. and a maximum $r = 0.51$ ($P \le 0.05$) at 1500 m a.s.l.

The effect of precipitation on growth not only varies among the regions, but also with elevation within a region. The correlation of larch growth with precipitation in the N-Alps is weak or absent in the lower elevations, although correlation coefficients become negative with increasing elevation. Overall, the absolute r values are highest in the MJJ-season and partly significant ($P \le 0.05$). The strongest relationship ($r = -0.26$) can be found

at 1620 m a.s.l. (site 17). In the W-Alps, precipitation influences larch growth positively at elevations up to 1400 m a.s.l., although the relationship turns negative at the high elevation sites. At lower elevations, correlation coefficients reach significance and the maximum response is $r = 0.27$ at 1100 m a.s.l. for the MJJ-season. Larch growth in the Tatra is positively correlated with precipitation at the low elevation site and significantly negatively correlated at 1500 m a.s.l., with $r = -0.20$. Again, the MJJ-season appears to be the most influential season.

Bioclimatic envelope of the larch growing regions

Elevation-specific summer temperatures are quite similar between the N-Alps and Tatra, although the W-Alps are slightly warmer compared with the same elevations in the two other areas (Fig. 6). The same pattern is true regarding the winter temperatures (see Supporting Information, Fig. S2). The larch proportion differs substantially among the regions. In
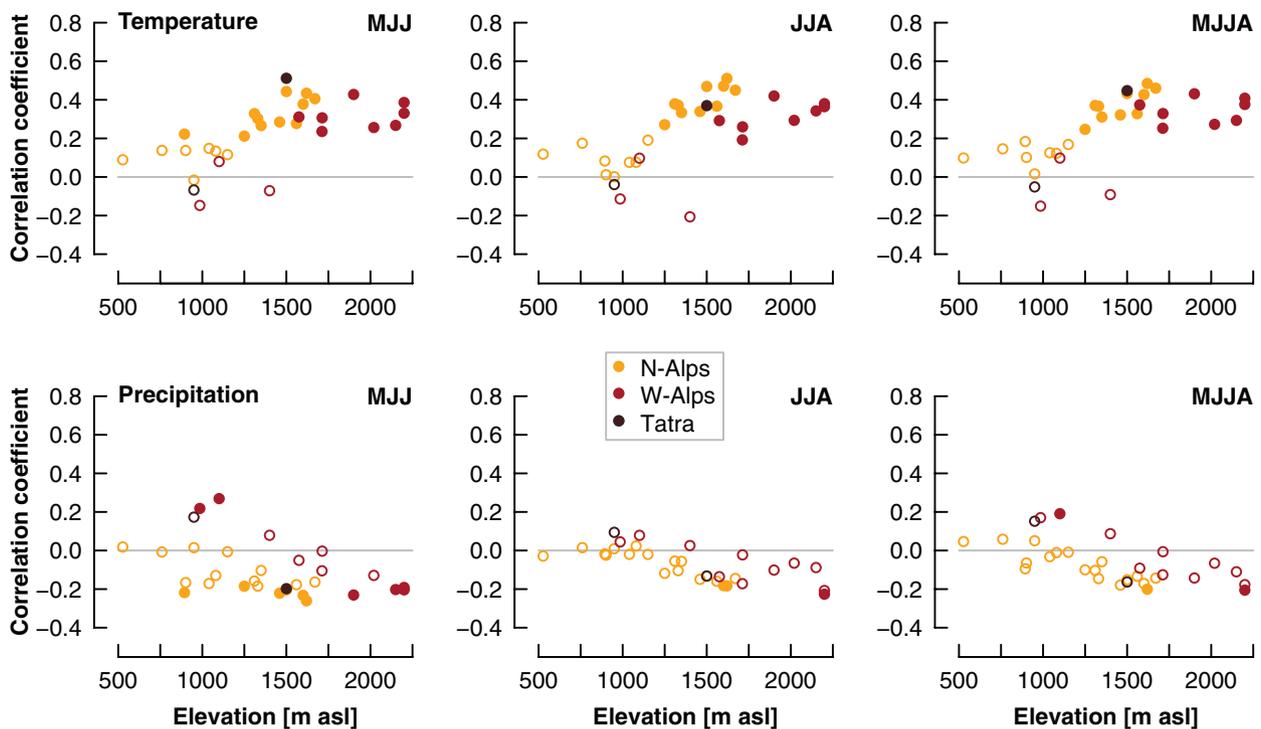
Figure 5 Seasonal growth/climate responses in different larch growing regions (orange = N-Alps, red = W-Alps, brown = Tatra) as a function of elevation. Top: results for temperatures; bottom results for precipitation. Correlations calculated using 200 year spline detrended ring width indices (RWI$_{200}$)-chronologies. Filled dots indicate significant correlations ($P \leq 0.05$). [Colour figure can be viewed at wileyonlinelibrary.com].

the N-Alps, a maximum larch proportion of 14% is reached at approximately 1300 m. Larch is most abundant in the W-Alps at 1900 m a.s.l., where it almost makes up 50% of the forested area. In the Tatra, larch constitutes no more than approximately 4% of the forests.

Discussion

The cyclic nature of LBM outbreaks is well known in the core habitat of its host species, European larch (Baltensweiler, 1993; Baltensweiler & Rubli, 1999; Bjørnstad *et al.*, 2002; Johnson *et al.*, 2004, 2010; Price *et al.*, 2006; Esper *et al.*, 2007; Baltensweiler *et al.*, 2008; Büntgen *et al.*, 2009; Battipaglia *et al.*, 2014). All of these studies focus on the main LBM outbreak region, even though the range of larch extends well beyond these well-known outbreak areas (Fig. 1). Knowledge of LBM dynamics near host range edges may provide insight into the causes of varying population behaviour (Holt & Keitt, 2005; Bahn *et al.*, 2006; Sexton *et al.*, 2009). The drivers for cyclic LBM events are still not fully understood (Johnson *et al.*, 2010) and, in the Tatra, beyond the host's main distribution range, periodic LBM outbreaks are absent (Konter *et al.*, 2015), although information for the N-Alps is lacking. In the present study, we investigated the existence of LBM outbreaks at the edge of the core habitat of larch, in the N-Alps. By comparing this with a known LBM hotspot area, the W-Alps, and an area where LBM outbreaks do not occur, the Tatra, the ecological habitat characteristics associated with periodic LBM outbreaks can be assessed.

The LBM at the edge of the host species distribution range

The results of the present study suggest an absence of periodic LBM oscillations in the N-Alps. The fact that the year-to-year variability is very similar among the larch chronologies, as well as similar to the spruce chronologies, is indicative of a common factor influencing yearly variability in growth of both species within this region (Fig. 2). In the higher elevations, growth variability is primarily controlled by summer temperature variations, with larch showing a higher dependence than spruce. At lower elevations, the coherency of larch chronologies decreases, whereas it is still high in the spruce chronologies. We conclude that site-specific differences have a stronger impact on larch than on spruce growth. Because spruce growth is negatively correlated with temperature, soil water availability may be a key factor for this shallow rooting species, whereas larch has greater abilities to exploit a site as a result of its deeper rooting system (Hartl-Meier *et al.*, 2014a, 2015). The higher drought sensitivity of spruce is also reflected in the higher frequency of negative growth anomalies compared with larch (Fig. 3).

The juxtaposition of extremes in growth of host and non-host species within a stand reveals 13 synchronously-occurring growth anomalies (Fig. 3). This coincidence indicates that negative growth extremes in larch chronologies are not necessarily associated with LBM outbreaks but, instead, with other local suboptimal environmental conditions. The events in 1976 and 1992 can be related to the well-known and most severe drought events for this region, and the suppressed growth in 1948 is connected to lag effects as a result of the drought in 1947 (Zang
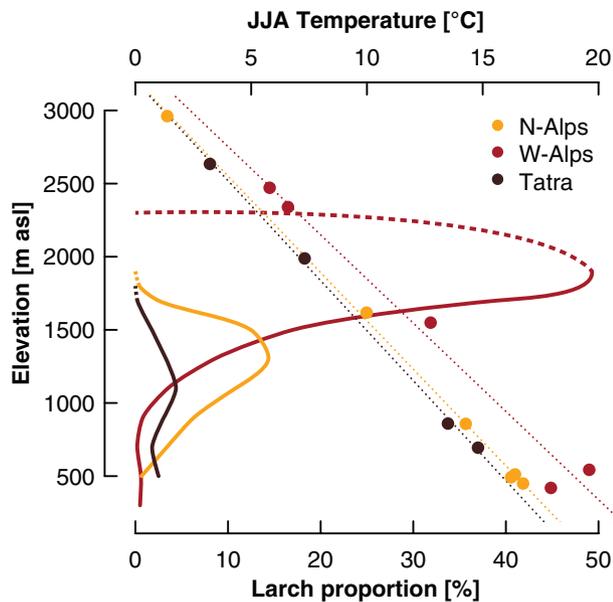
Figure 6 Proportion of European larch in the N-Alps, W-Alps and Tatra, as well as corresponding regional summer temperature conditions. JJA temperatures are derived from station data (dots, 1961–1990) and linear regressions (straight lines). Dashed curves are distribution estimates for high elevation locations up to the regional treelines. [Colour figure can be viewed at wileyonlinelibrary.com].

et al., 2014; Hartl-Meier *et al.*, 2014b, 2015). A comparison with known LBM events from nearby outbreak regions (obtained from Baltensweiler & Rubli, 1999) confirms that the growth anomalies in 1906, 1957 and 1972/73/74 were probably caused by LBM outbreaks. The SEA indicated that outbreaks in the N-Alps are coincident with those in the 'Central Alps' and less coincident with those in the 'Eastern Alps' outbreak region (Fig. 4). This agrees with the general space-time pattern of outbreaks across the Alps from West to East (Bjørnstad *et al.*, 2002; Johnson *et al.*, 2004; Price *et al.*, 2006). Nonetheless, the results derived from the SEA also illustrate how radial growth responds to LBM outbreaks: the W-Alps chronologies respond with a clear growth decline during the year of outbreak and the growth suppression persists for up to 3 years after the event (Baltensweiler *et al.*, 2008; Battipaglia *et al.*, 2014). The N-Alps chronologies do not show such a consistent pattern, suggesting that LBM outbreaks occur sporadically (and with less impact) or are completely absent. This finding is also supported by spectral analyses, which revealed no persistent or periodic pattern of a LBM cycle in the N-Alps (Hartl-Meier *et al.*, 2016).

Drivers of periodic LBM outbreaks: the bioclimatic envelope

The optimal elevational zone for LBM outbreaks has previously been identified as 1700–2000 m a.s.l. (Baltensweiler *et al.*, 2008; Johnson *et al.*, 2010). In the present study, all W-Alps sites from 1400 to 2200 m a.s.l. showed distinct growth responses during known LBM outbreaks (Fig. 4), thus slightly extending this elevational belt of optimal conditions, which is a finding also reported by Hartl-Meier *et al.* (2016). The lower elevational limit of growth suppression can be used to quantify the extreme

climatic conditions supporting LBM outbreaks. Thus, LBM outbreaks are limited to regions with summer temperatures <12.5 °C (Fig. 6) (or winter temperatures <−2.5 °C; see Supporting Information, Fig. S2). At a given elevation, summer and winter temperatures in the larch sites in the Tatra and N-Alps are generally cooler compared with the W-Alps, and these regions also vary in treeline elevations ranging from approximately 1500 m a.s.l. in the Tatra (Konter *et al.*, 2015), approximately 1800 m a.s.l. in the N-Alps (Ewald, 2012) to 2200 m a.s.l. in the W-Alps (Brändli, 1998). This suggests that the climatic envelope could allow the occurrence of periodic LBM outbreaks in the N-Alps and Tatra, even at montane elevations. This might partly explain the occurrence of sporadic LBM events at lower elevations in the N-Alps.

The climatic differences are further reflected in the growth/climate response (Fig. 5), which shows a shift of the elevations with significant correlation among the regions. In the N-Alps, significant positive correlations of growth with temperature are reached at 1250 m a.s.l. and, at sites higher than 1500 m a.s.l., correlations are mainly $r \geq 0.45$. In the Tatra, the site at 1500 m even reaches $r = 0.51$. Distinct temperature signals in tree rings from high elevations are 'common knowledge' (Babst *et al.*, 2013; Hartl-Meier *et al.*, 2014b), although the W-Alps chronologies do not reach such high correlations. This may partly be a result of the noise created by LBM outbreaks in series from the W-Alps; this noise is not present or of secondary importance in the Tatra and N-Alps. The precipitation signal is more ambiguous. Growth of larch in the W-Alps is slightly sensitive to early season summer precipitation, whereas no relationship can be detected in the N-Alps. Generally, the N-Alps are one of Europe's wettest regions (Weischet & Endlicher, 2000) and so precipitation may not be a limiting factor even at lower elevations (Hartl-Meier *et al.*, 2014a, 2015).

Given that all three of our study regions may be climatically suitable for LBM outbreak cycles, other factors must play a role in limiting most outbreaks to core regions. A key environmental factor affecting population dynamics that should be considered is host species distribution (Turner *et al.*, 2001; Samalens & Rossi, 2011). Battipaglia *et al.* (2014) related the late 20th Century decline of LBM cycles to land-use changes in the French Alps. The present study suggests that forest composition (i.e. the fraction of forested area composed of larch) may be a key factor explaining the differential occurrence of periodic LBM outbreaks among regions (Fig. 6). The delimitation of forest insect outbreak regions has often been related to the relative density of their food supply (Furniss & Carolin, 1977; Liebhold *et al.*, 1997). The very low density of larch (approximately 4%) in the Tatra may explain the probable absence of periodic LBM outbreaks there. In the W-Alps, the forested area is composed of up to 50% larch in the subalpine elevations and thereby offers a much greater resource for LBM. Density of larch in the N-Alps is much lower and thus represents a lesser resource for the sustainment of regular LBM cycles.

A lower density of host species is naturally accompanied by a higher density of nonhost species. Plant neighbourhoods and resource dilution can influence plant–herbivore systems and the presence of less favoured food types can lower the attack on host species (Root, 1973; Hjältén *et al.*, 1993; Hambäck & Beckerman, 2003; Hambäck *et al.*, 2014). In the N-Alps, for

example, Norway spruce is the most abundant tree species, comprising 50–60% of the mountain forest area (Binder, 2007; Niese, 2011). In general, a more diverse or a higher complexity of communities can reduce outbreaks of insect herbivories (Tahvanainen & Root, 1972; Jactel & Brockerhoff, 2007).

Insect herbivories must be adapted to both their host plants and their climatic environment to complete development (Bale *et al.*, 2002). Johnson *et al.* (2004) found that the core areas where regional outbreaks are initiated correspond to areas of highest connectivity of suitable LBM habitat. Johnson *et al.* (2010) found a shift of LBM epicentres to higher elevations as a result of recent warming; the lack of feeding source at these elevations might be the reason for the dampening of population cycles. Forests are more fragmented close to treeline, which also can influence insect populations (Didham *et al.*, 1996).

Understanding associations of climate with forest insect outbreaks and predicting the consequences of climate change on outbreak ranges is an urgent topic (Williams & Liebhold, 1995; Ayres & Lombardero, 2000; Bale *et al.*, 2002; Logan *et al.*, 2003; Battisti, 2008; Ims *et al.*, 2008; Kurz *et al.*, 2008; Johnson *et al.*, 2010). The results of the present study suggest that, in addition to climatic conditions, other biotic determinants of an insects' range should be considered when assessing the future geographical distributions of insect species and their outbreaks.

Acknowledgements

Supporting information

Additional Supporting information may be found in the online version of this article under the DOI reference: 10.1111/afe.12216

Table S1. Station data used for assessing the climate envelope in different larch growing regions (Fig. 6).

Table S2. Tree-ring inter-site correlations and climate signals. Correlations of the larch (orange) and spruce (green) 30 year spline detrended ring width indices (RWI_{30})-chronologies with June/July/August (JJA) temperatures (30 years-spline filtered) and intra-site larch-to-spruce correlations (grey) over the period 1850–2000.

Fig. S1. Delimitation of outbreak regions in accordance with Baltensweiler and Rubli (1999).

Fig. S2. Regional December/January/February temperatures (dots and dashed lines, 1961–1990; mean) within the different larch growing regions along elevation.

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