

Tree-ring evidence for the historical absence of cyclic larch budmoth outbreaks in the Tatra Mountains

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Abstract

Key message The absence of larch budmoth outbreaks and subsequent consequences on tree rings together with a distinct climate–growth relationship enhance the dendroclimatic potential of larch ring width data from the Tatra Mountains.

Abstract Regular population oscillations are generally considered to arise from trophic interactions, though it is unclear how such cycles are affected by biotic and abiotic factors. Cyclic outbreaks of the larch budmoth (LBM; *Zeiraphera diniana*), perhaps the most prominent example

of periodic insect population dynamics, leave distinct “fingerprints” in the annual rings of host trees, and have been reconstructed over 1,200 years in the European Alps. Although LBM individuals are known to exist in other regions, it is unclear whether recurrent mass outbreaks historically occurred elsewhere. Here, we present new larch (*Larix decidua*) host and pine (*Pinus cembra*) non-host chronologies from the Slovakian Tatra that comprise 323 ring width samples dating back to 1612 AD. May–June and May–July temperatures control larch and pine growth ($r_{1951-2011} = 0.63$ and 0.57 ; $p < 0.001$), respectively. LBM outbreak-induced defoliation patterns and subsequent ring width reductions were absent over the past three centuries, during which larch (host) and pine (non-host) growth was significantly synchronized ($r_{1725-2012} = 0.48$; $p < 0.001$). Spatially limited host forests of overall low stand densities along the northwestern Carpathian arc together with a relatively warm climate envelope are most likely responsible for the absence of cyclic LBM outbreaks. Tree-ring chronologies from these ecotones, free of pulsed disruptions, therefore, represent unique paleoclimatic archives ideal for reconstructing interannual to multi-centennial variations in Eastern European summer temperature.

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Introduction

The dynamics of insect populations vary considerably among species with some exhibiting equilibrium dynamics, others having regular cycles, or chaotic patterns (Bjornstad and Grenfell 2001). Cyclic population behavior has been

reported for many species of foliage-feeding Lepidoptera (Berryman 1996), including the larch budmoth (LBM: *Zeiraphera diniana* Gn.), which exhibits particularly regular cycles of 8–10 years, with recurrent high population densities causing extensive forest defoliation in the subalpine zone of the European Alps (Baltensweiler 1993a; Baltensweiler et al. 1977). These defoliation episodes alter ring width formation of host larch trees and dendrochronological methods have been used to reconstruct the timing of historical outbreaks over the past 1,200 years (Büntgen et al. 2009; Esper et al. 2007; Rolland et al. 2001; Weber 1997). Surprisingly, the amplitude of regular LBM mass outbreaks has been greatly diminished since the early 1980s (Baltensweiler 1993b; Ims et al. 2008; Johnson et al. 2010). The fact that this abrupt cessation of outbreak intensity coincides with unprecedented warming has been noted and hypotheses for causal roles of climate change in the variation of LBM dynamics have been advanced: The temperature-induced optimal altitudinal envelope of LBM outbreak epicenters may have shifted up and down during historical periods of climatic warming and cooling, respectively. In the most recent period of climatic warming, the region favorable for LBM outbreaks appears to have shifted to elevations beyond the upper limits of larch occurrence, thus explaining their cessation (Johnson et al. 2010).

Outside the greater Alpine region, other known natural stands of *Larix decidua* Mill. (larch) are restricted to the lowlands of south Poland and the Carpathian arc including

the Slovakian Tatra Mountains (Matras and Pâques 2008). While local foresters have reported LBM populations to exist in the Tatra (Baltensweiler et al. 1977; Büntgen et al. 2009), it is unclear whether extensive outbreaks have ever occurred sporadically or regularly in larch populations over the past decades to centuries. Dendroecological information about the historical occurrence of LBM mass outbreaks outside the European Alps could potentially shed light on climatic constraints to their frequency and severity, ultimately helping us to better understand the role of climatic changes in the cessation of these well-synchronized mass outbreaks across the Alpine arc. Considering the ecological and climatic similarities between the Alps and the Tatra Mountains, the question arises, whether the pattern of recurring LBM outbreaks and associated effects on larch trees widely observed in the Alps has also occurred in the Tatra Mountains.

Here, we analyze growth patterns in host larch and non-host pine ring width chronologies and detect the influence of temporally variable climate parameters on the growth of both tree species. Growth depressions, indicative of potential defoliation events, are identified in larch hosts and investigated for cyclic dynamics.

Materials and methods

We sampled 37 trees (99 cores: three/two cores per tree) from living larch trees at a locally dispersed mixed stand at

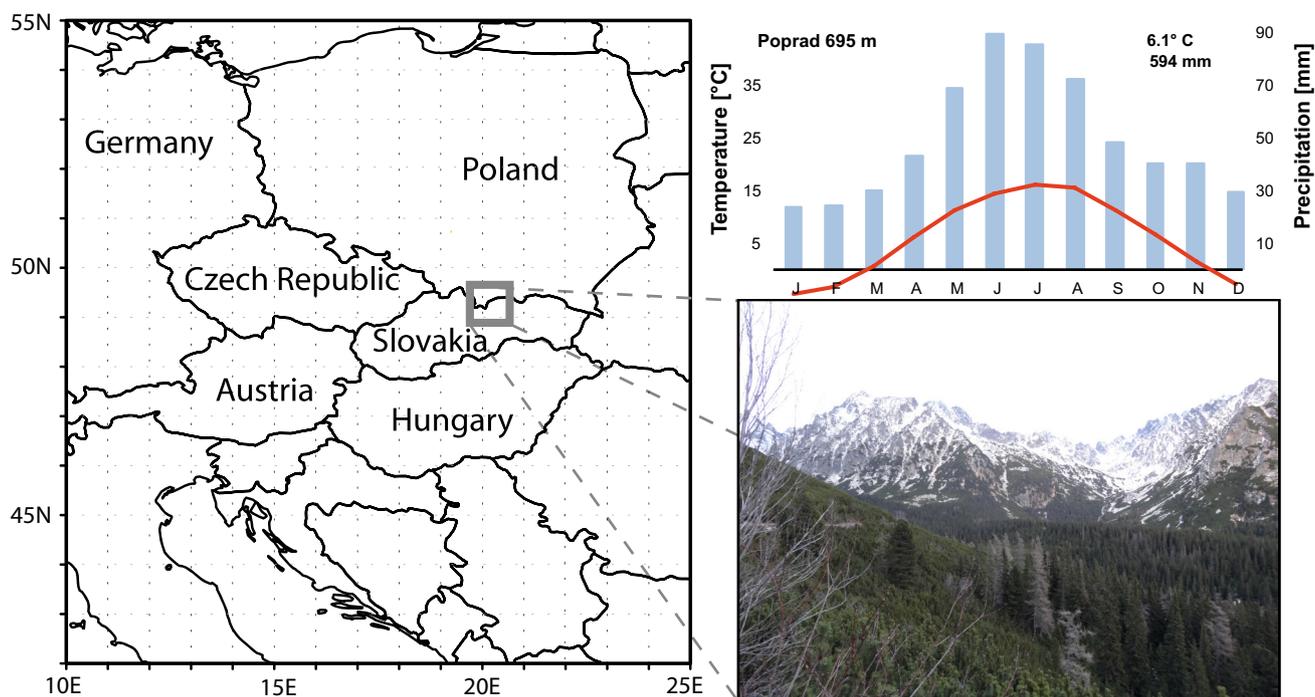


Fig. 1 Sampling site. *Left* map of Eastern Europe, *gray square* indicates sampling area, *upper right* climate data of nearby meteorological station Poprad, *lower right* image of zoomed in sampling site at 1500 m asl

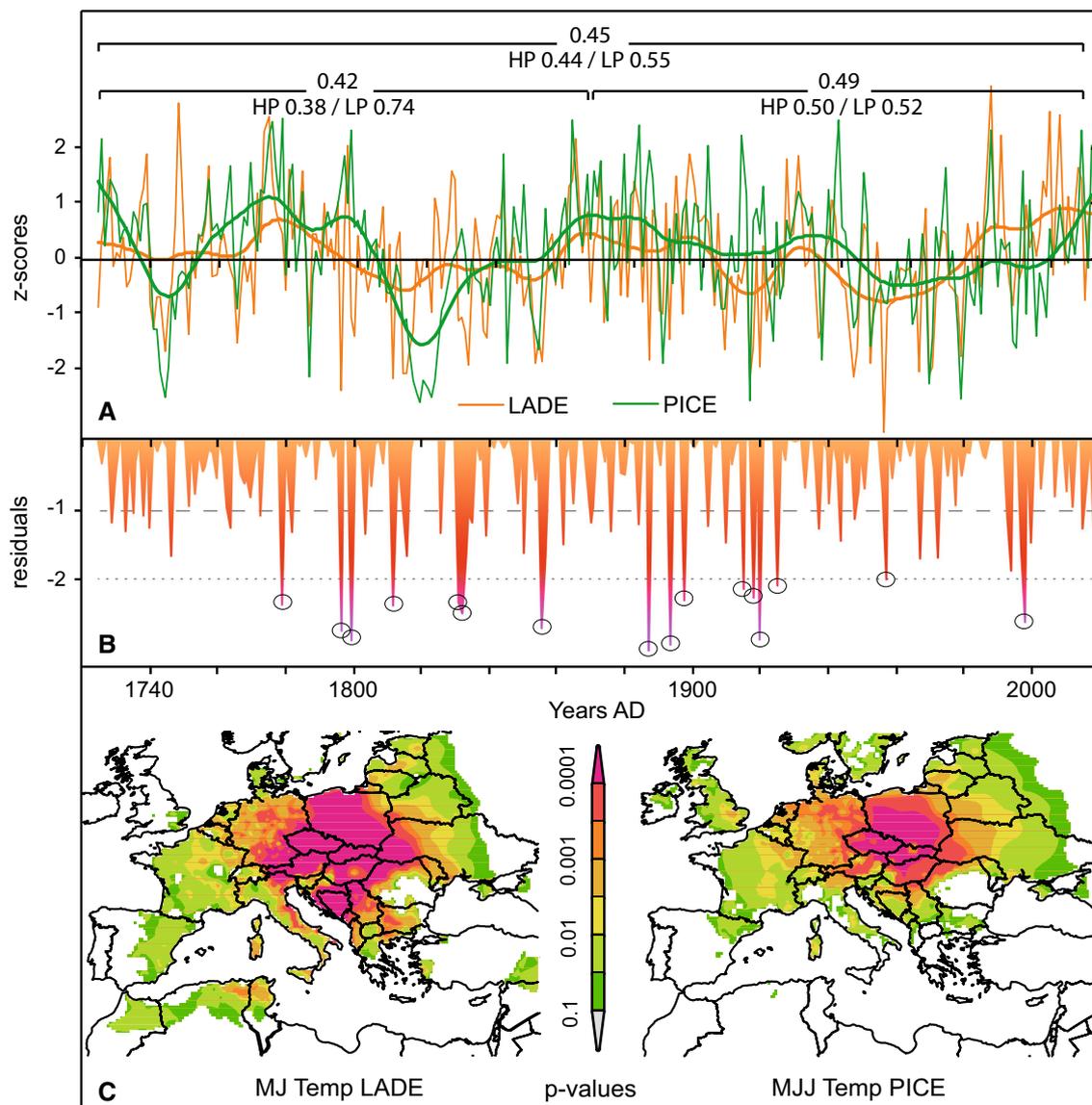


Fig. 2 Growth coherency and climate sensitivity. **a** Larch (orange) and pine (green) chronologies (bold lines indicate 31 yr smoothing splines) using a negative exponential detrending, **b** residuals between both species using 31 yr spline detrending, circles denote

~1,500 m asl in the Slovakian part of High Tatra Mountains (Fig. 1). These new measurements were combined with a previously developed dataset of 43 trees (64 cores: three/two cores per tree) from the same locality (Büntgen et al. 2013), resulting in a well-replicated composite for the period 1671–2012 (>10 series in each year). Moreover, 62 *Pinus cembra* L. (pine) trees were sampled at the same location (155 cores: three/two cores per tree), spanning the period 1725–2012 (replication >10 series/year). All cores were absolutely cross-dated at annual resolution and well-known juvenile growth trends were removed using commonly applied detrending techniques: Spline (30 and 200 years) and negative exponential functions (NegExp)

results > double standard deviation, **c** spatial field correlations of larch (c), pine (d) and best-fit seasonal temperatures. Maps are compiled using the KNMI Climate Explorer at <http://climexp.knmi.nl>

(Cook 1985; Cook et al. 1995; Fritts 1976) after implementation of power transformation (Cook and Peters 1997), and variance stabilization over a 31-year moving windows (Büntgen et al. 2011; Esper et al. 2012; Frank et al. 2007, 2010). The resulting chronologies were computed using a robust (biweight) mean, while the signal strength was estimated using 31-year moving intervals of interseries correlation (R_{bar}) and the Expressed Population Signal (EPS) (Wigley et al. 1984). Frequency-dependent consistency between the larch and pine chronologies was analyzed by high- (HP) and low-pass (LP) filtering the data.

Growth–climate relationships are reported as *Pearson* correlation coefficients (r) between the TRW chronologies

and instrumental temperature measurements from a nearby (~ 25 km) meteorological station (Poprad; 1951–2012), whereas gridded temperature indices (EOBS; 0.25°) were considered for spatial correlation trials (1950–2012). Species-specific chronology residuals were calculated to detect outbreak-induced growth depressions: Extreme years with negative residual values exceeding double standard deviation (stdv) display years of high interspecies deviations. Among these extreme years only those indicative of growth depressions caused by defoliation were considered, if corresponding TRW values of the host chronology displayed negative deviations stronger than single stdv. Autocorrelation functions with varying time lags, wavelet analyses and power spectra were further applied to assess a possible cyclic behavior of these events.

Results

Species-specific coherency among all individual larch (host) and pine (non-host) TRW measurements series is distinct ($R_{\text{larch}} = 0.76$ and $R_{\text{pine}} = 0.71$), and also temporally robust as expressed by running correlations and EPS values (Fig. 2 and A1). The abiotic driver of the larch growth pattern can be attributed to early summer temperatures (Fig. A3). Positive correlation coefficients between $\text{TRW}_{\text{larch}}$ and May (M)/June (J) temperatures reveal a strong relationship, with the highest value detected for seasonal mean temperatures of MJ ($r = 0.65$, $p < 0.001$) for the 1951–2012 period. Coherently, the pine growth pattern is mainly linked to temperatures in the summer period, covering a longer seasonality, including May, June and July (J). The highest correlation value is found between TRW_{pine} and MJJ temperatures ($r = 0.50$, $p < 0.001$). Mapping correlations of seasonal temperatures with larch and pine data indicate a widespread association, covering large parts of Eastern Europe (Fig. 2).

Since both TRW datasets incorporate distinct temperature signals, a species comparison of both reveals pronounced agreement in growth trends for the common period 1725–2012 ($r = 0.45$), not only in the low- but also in the high-frequency domain ($r = 0.55$ and 0.44) (Fig. 2). Following separation of the chronologies into two

equivalent time periods of 144 consecutive years indicates temporal consistency of this association ($r_{1725-1868} = 0.42$; $r_{1869-2012} = 0.49$) again covering both, low and high frequency.

Comparison of interannual differences between host and non-host TRW data in the high-frequency domain reveals conspicuous deviations in several years. Examination of residuals of the two chronologies indicates that data from 16 years deviate stronger than twice the standard deviation (stdv) (Fig. 2) and are listed in Table 1. However, only 10 out of these 16 extreme deviations could possibly be caused by LBM outbreaks (Fig. A2), and none of these 10 years coincide with reported LBM mass outbreaks in the greater Alpine Region (Esper et al. 2007).

The wavelet power spectrum exhibits no evidence of regular cyclic events (Fig. 3). Significant cyclicity with wavelengths of 16–32 years occurs only between 1800 and 1870, a period too short for robust interpretation. A similar result is detected when analyzing TRW_{pine} , which is as a non-host unaffected by LBM outbreaks. The autocorrelation function for $\text{TRW}_{\text{larch}}$ over the 1725–2012 period reveals no significant autocorrelation in the 8–10 lag year range as expected should recurrent LBM outbreaks exist (Fig. A4). Lag 9 displays large incoherencies, varying between $r_{1725-1800} = 0.20$ and $r_{1801-1900} = -0.34$, whereas lag 8 shows negative connections, although evidence from the Alpine Region suggests the opposite (Esper et al. 2007). In addition, autocorrelation functions of the non-host show similar patterns, thereby, supporting the absence of LBM-induced cyclic growth depressions within the host data (Fig. A4).

Discussion

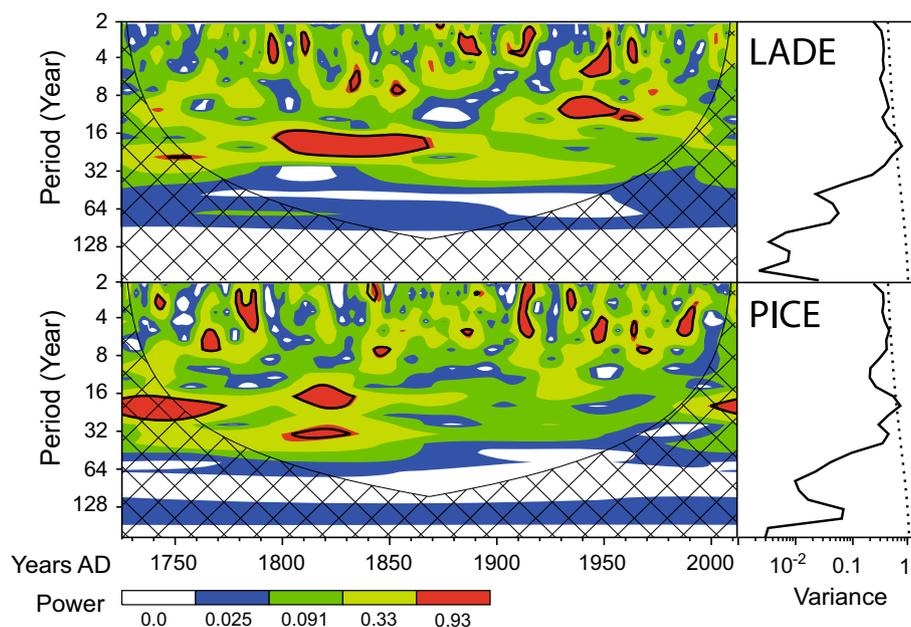
Both larch (host) and pine (non-host) TRW datasets exceed commonly accepted criteria in terms of temporal robustness and interseries homogeneity. The growth of host and non-host trees is to a great extent controlled by MJ/MJJ temperatures, though TRW deviations exist in specific years. These deviations most likely arise from species-specific dissimilarities in physiological processes rather than from LBM outbreaks. The absence of regular growth

Table 1 Potential defoliation events

	1778	1795	1798	1810	1829	1830	1853	1884	1890	1894	1911	1914	1916	1921	1952	1992
Residuals	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
TRW (host)		x	x	x	x		x	x	x	x			x		x	

Residuals: x denotes negative deviations between non-host and host TRW chronologies exceeding double standard deviation; TRW host: x denotes negative deviations of the host chronology exceeding single standard deviation

Fig. 3 Wavelet power spectra of the host and non-host (larch and pine: upper and lower panels) chronologies. Black contour indicates 10 % significance level, using a white-noise background spectrum and flexible spline detrended data. Corresponding global wavelet power spectra (black line) and significance levels (dashed line) are shown for both species on the right side



depressions in host TRW indicates that if LBM populations in this region are cyclic, the amplitude of such cycles is not high enough to reach defoliating levels that affect tree growth.

Outbreaks of *Zeiraphera* sp. in the Tatra Mountains are known to have historically occurred on *Picea abies*, and have been reported for the periods 1924–1934, 1956–1959, 1965–1969 and 1977–1982 (Baltensweiler et al. 1977; Modrzyński 2003). These outbreaks generally do not correspond with growth depressions detected here in larch TRW (see Table 1) and thus there is no evidence that these outbreak populations on spruce transgressed onto larch. Furthermore *Zeiraphera* spp. has also been observed on *Pinus cembra* in the Alps where these populations occasionally reach high levels though never as wide spread as outbreaks on larch (Dormont et al. 2006). Populations of *Zeiraphera* spp. feeding on different conifer genera appear to represent distinct gene pools that occasionally hybridize (Emelianov et al. 2003).

Infrequent growth depressions were observed on larch trees in our data (see Table 1) and it is possible that they coincided with localized LBM outbreaks. However, there are other insects known from this area that are also capable of defoliating larch (e.g., *Lymantria monacha*) and thus definitive conclusions about the specific causes of growth declines in observed larch cannot be drawn. In any case, it is certain that the pattern of recurrent LBM outbreaks, common in the Alps, has not historically occurred in our study region of the Tatras.

In the Alps, the majority of the LBM outbreak area is limited between 1500 and 2000 m asl, even though the range of larch extends from 500 to 2,200 m asl

(Baltensweiler and Rubli 1999). By contrast in the Tatra, larch has a much more restricted distribution between 850 and 1,500 m asl. The fact that hosts occur at lower elevations and thus warmer conditions than the dominant LBM outbreak zone in the Alps might explain the absence of recurrent LBM outbreaks in the Tatra.

In addition, spatially continuous larch forests with high densities typical of the LBM outbreak zone in the Alpine Arc rarely occur in the Tatra Mountains. Connectivity of large continuous areas of larch appears to play a role in the formation of LBM outbreaks in the Alps (Johnson et al. 2004). The lack of these large, continuous, pure larch forests in the Tatra may thus inhibit recurrent LBM population cycles prior to reaching mass outbreak levels.

Larch as light-demanding species requires higher direct insolation in the vegetation period. The sampling site at 1,500 m asl can be classified as subalpine where trees grow under treeline conditions. Highest monthly precipitation amounts in the Tatra coincide with the period of strongest growth–climate relationship of both species, but associated cloud cover hinders tree growth of larch to a greater extent than pine (Ellenberg 2009; Hartl-Meier et al. 2014).

Our results refute the occurrence of regular LBM outbreaks and subsequent growth depressions in larch TRW series from the Slovakian Tatra Mountains. The robust chronology coherency and distinct MJ temperature signal are indicative of the potential utility of these high-elevation forest stands for the reconstruction of annually resolved and absolutely dated summer temperature variability over the previous centuries, in the absence of biological disruptions that may weaken similar approaches from the European Alps. The widespread representativeness

covering almost all regions of Eastern Europe is particularly important considering the scarcity of historical data and reconstructions for this region.

Author contribution statement This study was realized in collaboration between all authors: UB, TK and OK carried out field and laboratory work. UB and OK designed the study, computed and analyzed the data. Interpretation, discussion of and conclusions from results were a joint work of all authors. The text was written by OK and UB and revised by JE, AL, LS, and ED.

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Conflict of interest All authors declare no conflict of interest.

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