On the occurrence of cyclic larch budmoth outbreaks beyond its geographical hotspots

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Introduction

One of the most intensively investigated and probably best-documentedcyclic behaviourin ecological systemsare regularlarch budmoth (*Zeiraphera diniana* [Gn.]; LBM) mass outbreaks (Berryman 1996, Baltensweiler et al. 2008), which occur every 8-10 years in travelling wavesacross most of the European Alps (Baltensweiler 1993). Periodical mass outbreaks of this foliage-feeding insect are mainlyrestricted to itshost species, the European larch (*Larix decidua* Mill.). Suitable habitatscoverthe subalpine zoneof the central Alpine arc (Baltensweiler et al. 1977), with the optimum elevational zone of outbreak foci being estimated to 1700-2000 m asl (Baltensweiler et al. 2008, Johnson et al. 2010).Due to mass outbreaks, larch trees discolorate and might completely defoliate(Baltensweiler et al. 1977).This tree defoliation generally reduces radial growth significantly during and after an outbreak year so that LBM events leave distinct fingerprints in tree-ring width and density (Schweingruber 1979, Esper et al. 2007, Baltensweiler et al. 2008, Büntgen et al. 2009, Johnson et al. 2010). The resulting patterns allowed reconstructinga 1200-year long record of LBM mass outbreaks in Swiss subalpine valleys(Esper et al. 2007), as well as a 300-year record with a wider spatial coverage(Büntgen et al. 2009).

Otherstudies assessedthe mechanisms ofthe varying LBM density including the drivers of itscyclicity(e.g. Fischlin & Baltensweiler 1979, Anderson & May 1980, Baltensweiler 1993, Turchin et al. 2003),as well as the synchronicity of outbreak events across the Alps (e.g. Bjørnstad et al. 2002, Johnson et al. 2004, Price et al. 2006). All of these investigations focused on the well-known outbreak regions in the centre of the Alps. However, the natural distribution range of the host species European larch (Fig. 1) clearly exceeds these LBM hotspot regions and it remains unclear to which extendregular LBM cycles also occur at the edge of the host's distribution range, and through which environmental factors outbreak regions are spatially constraint. A recent study, for instance, revealed theabsence of cyclic LBM mass outbreaks in the Tatra Mountains (Konter et al. 2015a).

Here, we test for the occurrence of cyclic LBM outbreaks in severalaltitudinal belts of different larch habitatsacross the Western and Northern Alps, as well as the Tatra Mountains.

Material and Methods

Study design

Tree-ring data from three different European larch habitats were used in this study (Fig. 1, Table 1). The Western Alps belong to the main distribution range of European larch and represent a LBM hotspot.Eleven sites were sampled ranging from 985-2200 m asl. The Northern Alps constitute the edge of the larch core habitatand information about LBM mass outbreaks is missing.In this region,18 stands were sampled, encompassing different altitudes from 527-1670 m asl. In the Tatra Mountains, representing a disjunctive habitat of larch, cyclic LBM outbreaks were recently reported to beabsent (Konter et al. 2015a,b). Data from two sites in 950 and 1500 m asl were used for control.

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At each site, ten dominant larch trees were coredtwice at breast height. After TRW measurement, using TSAP-Win scientific software and a LINTAB 6 measurement device (Rinn 2003), cross-dating accuracy was verified visually and statistically using COFECHA (Holmes 1983). Descriptive statistics of raw chronologies include the mean segment length (MSL), average growth rate (AGR) and first-order autocorrelation (lag-1). Inter-series correlation (Rbar) and expressed population signal (EPS) were calculated to estimate the internal coherence of the chronologies (Table 1).

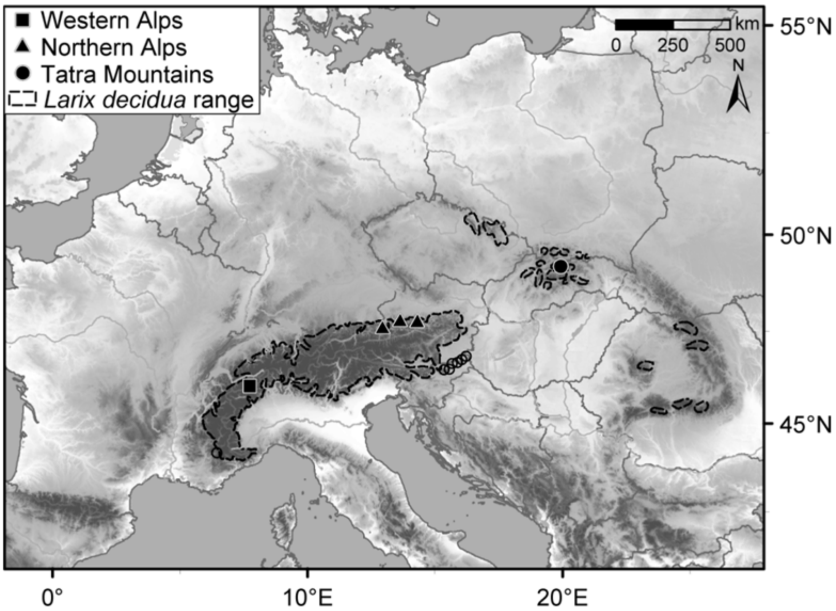

Figure 1: Map showing the location of the sampling sites in the Western Alps (square), Northern Alps (triangles), and Tatra Mountains (circle) together with the natural distribution range of Larix decidua (dashed line). Distribution data was compiled and provided by E. Welk, AG Chorology, Geobotany Department University Halle, based on map 21b in Meusel et al. (1965).

Chronology building and time series analyses

Raw ring width data weretransformed into indices to remove age and size related growth trends and potential disturbance signals (e.g., forest management). To emphasize high-frequency variability,a cubic smoothing spline with a frequency cut-off of 50% at 30 years was applied to the individual series (Cook & Peters 1981). Site chronologies were built by averaging the detrended single series usinga robust mean (Mosteller & Tukey 1977), truncated at a minimum replication of 5 series.

To explore cyclical patterns in the individual site chronologies, potentially caused by LBM outbreaks, spectral analysis was applied. The red-noise spectra were estimated, computing the spectrum of each time-series using the Lomb-Scargle Fourier transform (Schulz & Mudelsee 2002). A continuous wavelet transform of the time series was further used considering the Morlet wavelet as a base (Torrence & Compo 1998) to assess potential variations over time.

All statistical procedures were performed using R 3.1.1 (R Development Core Team 2014) and the package dplR (Bunn et al. 2012).

Results

Descriptive chronology statistics indicate comparable datasets among the larch habitats (Table 1). MSL of larch chronologies ranges from 78-216 years in the Western Alps, and 92-271 years in the Northern Alps. Trees in the Tatra are older reachingMSL of ~230 years. Larch AGR in theWestern Alps (0.67-1.56 mm) is slightly lower than in the Northern Alps (0.72-2.00 mm) and lowest in the Tatra Mountains (0.57-0.76 mm), representing the varying age structure of trees in the different regions. Lag-1 autocorrelation is high in all larch habitatsranging from 0.67-0.89. Rbar values show distinct coherency among individual TRW series inall chronologies and range from 0.60-0.74 in the Western Alps, 0.54-0.74 in the Northern Alps, and 0.71-0.77 in the Tatra Mountains, demonstrating highest internal coherence in the latter. EPS values of all larch sites exceed the widely accepted threshold of 0.85 (Wigley et al. 1984), indicating sufficient internal signal strength inall investigated sites.

Table 1: Location and characteristics of raw larch site chronologies sorted by elevation within a region.

Region	Lat.	Lon.	Altitude (m asl)	Period	MSL (years)	AGR (mm)	Lag-1	Rbar	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
N-Alps	47°47'	13°33'	527	1828-2010	174	1.24	0.89	0.63	0.98
	47°40'	13°01'	760	1850-2008	149	1.11	0.85	0.57	0.96
	47°50'	14°27'	894	1914-2010	93	1.91	0.87	0.57	0.98
	47°50'	14°26'	901	1916-2010	92	2.00	0.88	0.63	0.99
	47°45'	14°21'	950	1830-2009	172	1.08	0.84	0.60	0.97
	47°38'	12°51'	1040	1838-2008	163	1.21	0.84	0.60	0.95
	47°31'	12°47'	1080	1889-2008	110	1.57	0.79	0.64	0.96
	47°45'	14°26'	1150	1829-2009	173	1.05	0.84	0.59	0.97
	47°31'	12°47'	1250	1803-2008	183	1.22	0.87	0.55	0.94
	47°33'	12°48'	1310	1832-2008	164	1.16	0.81	0.60	0.96
	47°35'	12°53'	1330	1806-2008	185	1.09	0.84	0.58	0.97
	47°46'	14°25'	1350	1855-2009	144	1.37	0.85	0.54	0.97
	47°46'	14°25'	1460	1847-2009	145	1.21	0.79	0.58	0.94
	47°49'	13°35'	1500	1785-2010	193	0.89	0.71	0.73	0.95
	47°33'	12°48'	1560	1780-2008	165	1.28	0.74	0.61	0.93
	47°34'	12°49'	1600	1706-2008	271	0.72	0.74	0.74	0.97
	47°34'	12°49'	1620	1747-2008	244	0.85	0.81	0.65	0.96
	47°31'	13°01'	1670	1781-2008	193	1.18	0.82	0.66	0.97
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

Analyses of the frequency spectrum show distinct differences of cyclic reoccurrences of potential LBM outbreaks among the larch habitats (Fig. 2). The Western Alps chronologies indicate a significant periodicity between ~8 and 10 years at elevations above 1900 m asl (at two subalpine sites also between 21 and 24 years). The period length of spectral peaks increases towards lower elevations, reaching significanceat 7 to 10 years in 1400-1700 m asl, and 11 to 16 years in 1100 m asl. The low-elevation site shows no indication for LBM cyclicity. In the Northern Alps, a variety of spectral peaks occur without a clear dependence on elevation. At nine sites significant periodicity can be detected in the high-frequency domain around 2.5 to 4 years. At seven sites a 6 to 7 year cycle is present, culminatingat altitudes above 1300 m asl. Single additional, significant peaks occur between 11 and 25 years. In the Tatra Mountains, significant cycles only appear in the high frequency domain of 2 to 3 years.

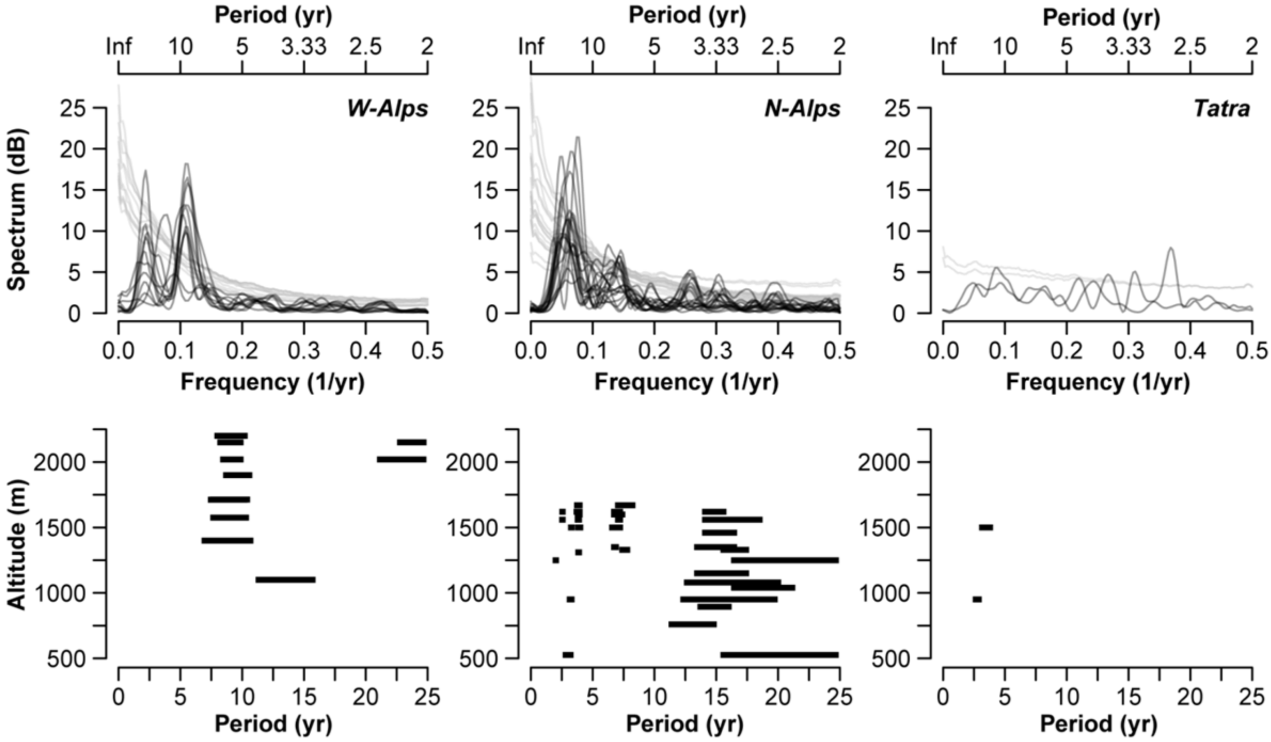

Figure 2: Red-noise spectra of Western Alps (left), Northern Alps (centre) and Tatra Mountain (right) larch chronologies (upper panels) calculated over 1860-2008. Light colours indicate the 95th percentile red noise spectra. Bottom panels show the periods with significance ordered by elevation.

The wavelet analysis again reveals distinct dissimilarities of potential LBM periodicity in the differing larch habitats (Fig. 3). In the Western Alps, significant power at ~8 years is almost continuously present for all chronologies above 1400 m asl with a short interruption between ~1910-1930. Significant cyclicity with wavelengths of 16-32 years exists almost over the entire period. In the 1000-1400 m belt, the 1400 m asl site shows a ~8 year cycleonly. The sites below this threshold provide no clear indication for a persistent and regular LBM cycle. In the Northern Alps the picture is quite diffuse. There is no clear sign for periodic LBM oscillations. In the high altitudinal belt, a significant 8 year cycle existsover a relatively short period from around 1910-1950. Some single sites in the 1000-1400 m belt show this pattern as well and even in the lowest altitudes the ~1950 events appear. The larch trees in the Tatra Mountains again reveal no evidence for a typical LBM cycle.

Discussion

Cycles of the LBM mass infestation are intensively investigated in the core habitat of its host species European larch (cf. Baltensweiler 1993, Baltensweiler & Rubli 1999, Bjørnstad et al. 2002, Johnson et al. 2004, Price et al. 2006, Esper et al. 2007, Baltensweiler et al. 2008, Büntgen et al. 2009, Johnson et al. 2010, Battipaglia et al. 2014). However, all these studies focus on the main LBM outbreak region, although the distribution range of larch exceeds these well-known hotspot areas. The drivers for cyclic LBM events are still not fully understood (Johnson et al. 2010), and their regular occurrence remains particularly debatable towards the margin or even beyond the host's main distribution (Konter et al. 2015a). We here assessed indications for a cyclic pattern of

LBM at the edge of the core habitat of larch and compared it to a LBM hotspot area (the Western Alps), and a region wherecyclic LBM mass outbreaks are likely absent (the Tatra Mountains).

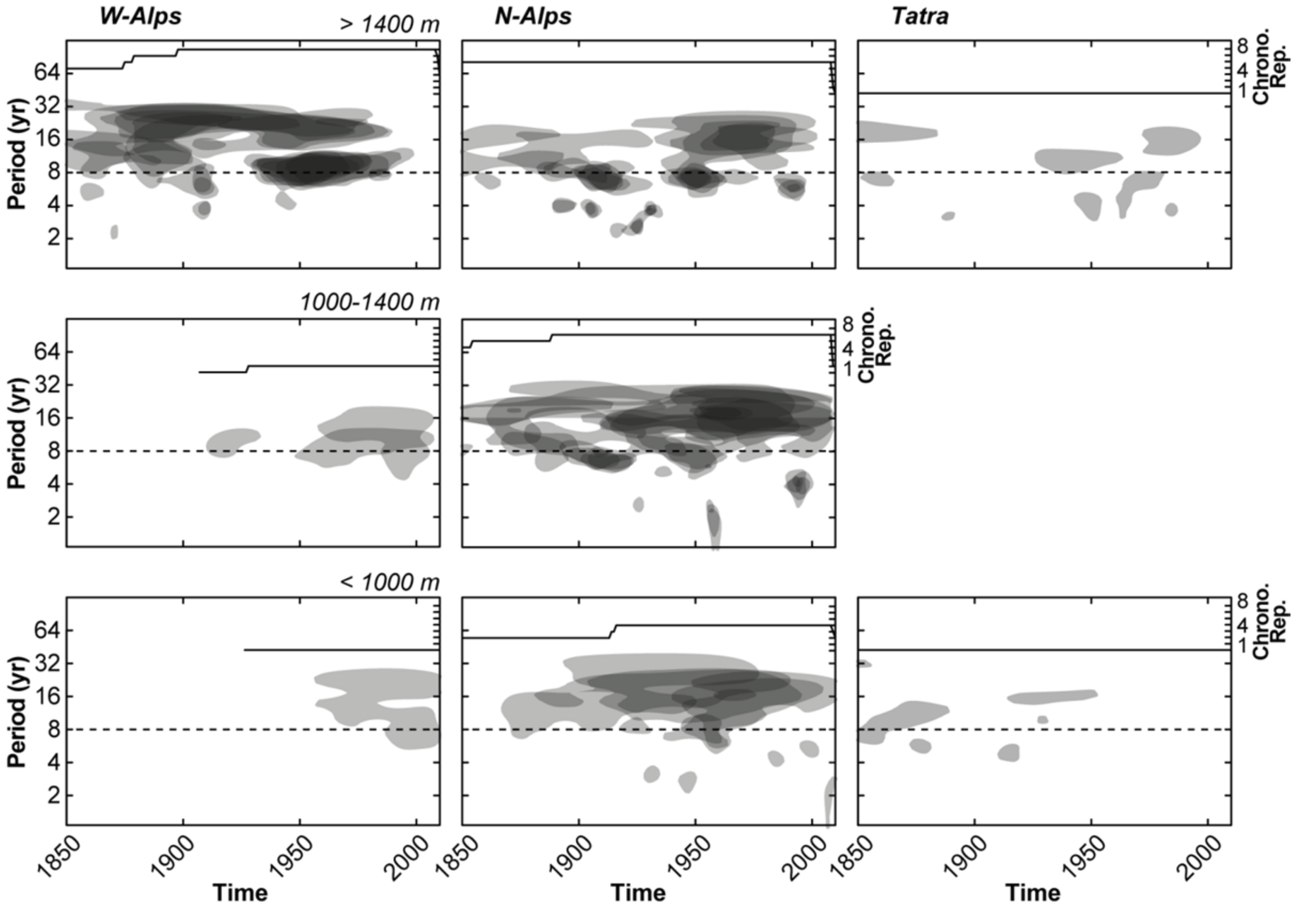

Figure 3: Superimposed wavelet power spectra of the Western Alps (left), Northern Alps (centre) and Tatra Mountain (right) larch chronologies subdivided for different altitudinal belts (> 1400 m: upper panel, 1000-1400 m: central panel and < 1000 m: lower panel). Only significant (95%) wavelet power is plotted and with high opacity factor, i.e. dark colours indicate overlapping significant wavelet power of different chronologies (note chronology replication [= Chrono. Rep.] at the upper part of each box).

Our results confirm that altitudes above 1700 m asl seem to be the optimal elevational zone for regular outbreaks (Johnson et al. 2010) where we found a distinct 8-10 year cyclicity in the Western Alps. However, regular LBM outbreaks also occurred down to 1400 m asl, but the temporal pattern is less persistent and distinct. For the Northern Alps, at the edge of the hosts' distribution range, we found some evidence for LBM outbreaks in ~1910s and ~1950s, but the pattern is not persistent over time. Surprisingly, there are outbreak indications even at lower altitudes. This might be explained by the climatic conditions in the differing habitatsanalysed here. Temperatures in the Northern Alps are lower compared to the Western Alps, as indicated by differing treeline elevations ranging from ~1800 m asl in the north (Ewald 2012) to 2200 m asl in the west (Brändli 1998). This might mean that the climatic envelope should allow the occurrence of regular LBM mass outbreaks in the Northern Alps, even at lower altitudes.
We here tested the cyclicity of LBM events in differing larch habitats but the drivers for the presence or absence of periodic mass outbreaksstill remain unclear. Further research is needed investigating the climate and ecological envelope in the different larch habitats in more detail.

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