Contribution of climate vs. larch budmoth outbreaks in regulating biomass accumulation in high-elevation forests

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Abstract

Forest growth and biomass response to environmental change depends upon climatic, but also upon interactions with biotic drivers, such as insect outbreak activity. In this study we use tree-rings along a temperature gradient to assess the relative importance of climate versus altered larch budmoth (*Zeiraphera diniana*) outbreak cycles for forest biomass accumulation at high elevations.

We established climate-growth relationships and performed outbreak-growth response analysis for >500 individuals from host (*Larix decidua*) and non-host trees (*Picea abies*) at different elevations (from 1300 to 2200 m a.s.l.) in the Swiss Alps. We quantified outbreak-induced reductions of absolute biomass increment and modelled effects of the recent absence of outbreaks.

Our results reveal that average outbreaks reduced biomass accumulation by 1130 kg ha⁻¹ y⁻¹ during the four years after the event, having an equal or even greater impact on carbon sequestration than climate. Recent growth increases previously observed at the study sites are largely attributable to the outbreaks absence since 1981, suggesting that regular outbreaks have hampered host-trees from realising their growth potential for centuries.

The presented impact analysis quantifies the importance of non-lethal insect activity on forest biomass dynamics, revealing the relevance of including such biotic drivers and their interactions with climate in models assessing the future productivity and carbon sink capacity of forests.

Highlights

- High-elevation forest growth responds to climate and insect outbreak activity.
- Biomass reconstructed with tree-rings aids in quantifying insect outbreak impact.
- Outbreaks can reduce forest biomass accumulation by 1130 kg ha⁻¹ y⁻¹.
- Recent outbreak absence explains current growth increase better than climate alone.

1. Introduction

Forest ecosystems are essential in regulating earth-atmosphere fluxes. By capturing on average $\approx 30\%$ of anthropogenic CO₂ emissions within woody biomass, forests play a key role in dampening global warming (Friedlingstein *et al.*, 2010; Pan *et al.*, 2011). Hence, it is of great interest to know how climate change will affect the distribution, composition, and productivity of forest ecosystems and consequently their carbon storage capacity (Frank *et al.*, 2010; Kirtman *et al.*, 2013; Reitalu *et al.*, 2013).

Forest inventory data, satellite imaging, and model simulations often show non-consistent patterns of forest net primary productivity and biomass responses to climate change (Fang *et al.*, 2001; Nemani *et al.*, 2003; Etzold *et al.*, 2014; Wu *et al.*, 2014). Some of this uncertainty is caused by challenges in adequately incorporating various drivers affecting forest productivity, including: management practises, forest age and structure (Lindner *et al.*, 2010; Nabuurs *et al.*, 2013; Pretzsch *et al.*, 2014), nutrient and CO₂ fertilization (Hyvönen *et al.*, 2007), wind throws and wildfires (Seidl *et al.*, 2011; Trotsiuk *et al.*, 2016), and insect activity (Hicke *et al.*, 2012; Klapwijk *et al.*, 2013). This array of physiological, ecological, biogeographical, and environmental controls on tree growth generates uncertainty in predicting the future role of European forests as a carbon sink (Ciais *et al.*, 2008; Nabuurs *et al.*, 2013).

Tree-ring investigations in European forests at high elevations have shown an increase in tree growth in the recent decades (Rolland *et al.*, 1998; Büntgen *et al.*, 2008). As tree growth at these locations is mainly limited by temperature (Büntgen *et al.*, 2007; Babst *et al.*, 2013), growth increases have usually been attributed to more favourable growing conditions due to the recent warming. Yet, detailed observations performed on high-elevation forests indicate that growth of *Larix decidua* trees has increased more than other species such as *Picea abies* (King *et al.*, 2013a, b), questioning whether climate alone is responsible.

The larch budmoth (*Zeiraphera diniana* Guénée) outbreaks play an important role in reducing growth of the host *L. decidua* across the European Alps (Baltensweiler *et al.*, 2008; Konter *et al.*, 2015). This insect has an annual life cycle, with its larvae hatching in spring and feeding on the new flushes of needles as well as producing masses of webbing, causing severe defoliation of its host up to 3 years after an outbreak (Baltensweiler and Rubli, 1999; Baltensweiler *et al.*, 2008). The outbreaks occurred in more or less regular 9-year cycles over the past millennium, although they have not been observed after the 1980s (Esper *et al.*, 2007; Büntgen *et al.*, 2009). This change in outbreak regime has been attributed to changes in forest

structure and species composition (Battipaglia *et al.*, 2014), changes in nitrogen, water, starch and sugar content of foliage (Turchin *et al.*, 2003; Asshoff and Hättenschwiler, 2006), but also to increasing winter temperature (Kress *et al.*, 2009; Johnson *et al.*, 2010; Iyengar *et al.*, 2016). This raises the question whether changing insect activity competes with the direct physiological effects of warming as a possible explanatory factor for the recent growth increase of *L. decidua*.

To assess future productivity of high-elevation forests, we analyse; i) the relative contribution of climatic and biotic drivers on tree growth and ii) the absolute impact of larch budmoth outbreaks on aboveground biomass accumulation. To understand the interaction between climatic and biotic drivers, we take advantage of the well documented outbreak history (cf. Esper *et al.*, 2007) and the potential for reconstructing aboveground biomass dynamics with tree rings (cf. Babst *et al.*, 2014a). We sampled co-occurring populations of budmoth hosts (*L. decidua*) and non-hosts (*Picea abies*) species along a steep elevational gradient, which show different climate sensitivities (cf. Moser *et al.*, 2010; King *et al.*, 2013b). This dataset allows us to disentangle growth responses caused by insect outbreaks and climate variation. We assessed climate-growth relationships and performed outbreak-growth response analysis to model their impact and importance. The quantification of the relative contribution of climate and insect activity on biomass accumulation offers a unique opportunity to improve our understanding on the future fate of high-elevation forest productivity.

2. Materials and methods

2.1. Study area and sampling design

Our study was conducted in the central Swiss Alps (Lötschental, 46°23'40"N 7°45'35"E; Fig. 1a), where the occurrence of budmoth outbreaks ($\approx$ 9-year cycles; as explained by Turchin *et al.*, 2003) has been documented over the past millennium until 1981 (Esper *et al.*, 2007; Büntgen *et al.*, 2009). The valley is characterised by steep slopes ($>60\%$) and covered by coniferous forests comprised of *Larix decidua* Mill. (the host species) and *Picea abies* (L.) Karst (hence referred to as *Larix* and *Picea*). The mean annual temperature in the valley bottom is approximately 5 °C and mean annual precipitation exceeds 800 mm, where the growing season temperature from 1975-2009 showed a significant positive trend of 0.6 °C per decade (data from MeteoSwiss surface observation network; cf. King *et al.*, 2013b). The mean annual temperature difference between the tree line and valley bottom is $\approx$ 2.5 °C (measured at $\approx$ 1300 and 2200 a.s.l. from 2008 until 2015).

The study uses tree-ring measurements to construct a model of growth responses to both climate and larch budmoth outbreaks, and assess the development of biomass increment over time. For growth-response modelling, trees were randomly sampled at four elevations from the valley bottom to the upper tree-line along both the north- and south-facing slopes near the town of Ferden (Fig. 1; at ≈ 1300 m, 1600 m, 1900 m, and 2200 m a.s.l.). In addition, we established three circular fixed plots (17 m radius) positioned at comparable elevations to address aboveground biomass increment (ABI), on the south- (Fig. 1; near Blatten, representative for the conditions at S22) and north-facing slope (near N19 and N13).

2.2. Tree sampling and ring-width measurements

Between 2007 and 2014, we sampled 973 wood cores from 285 *Larix* and 228 *Picea* trees (Table 1). Along the two transects, trees larger than 10 cm diameter at breast height (DBH, 1.3 m) were pseudo-randomly sampled (i.e. irrespective of size and social status). For each site, trees were selected along the same elevation and within a horizontal distance of approximately 500 m from the research sites described in King *et al.*, (2013a). For the fixed plots, all trees with a DBH greater than 5.6 cm, including dead trees and stumps, were measured in order to capture the population characteristics (Babst *et al.*, 2014a; Nehrbass-Ahles *et al.*, 2014). For 57 % of the sampled trees we measured DBH and height (using a Vertex, Haglf Sweden), while maximum bark thickness at breast height on two opposing sides of the stem was measured on 24 % of the trees.

We used increment borers (Haglf Sweden) to collect approximately two radial cores per tree stem at breast height and perpendicular to the slope to avoid reaction wood. Standard dendrochronological techniques were used to prepare, measure (cf. Schweingruber, 1996; using either TSAP Rinntech Inc. or WinDENDRO Regent Instruments) and visually and statistically cross-date tree-ring width series collected from the transects and fixed plots (cf. Fig. S1; COFECHA Holmes, 1983).

2.3. Aboveground biomass assessment

The annual ABI was calculated for the fixed plots by using species and region specific volume and mass allometric relationships, as applied by the Swiss national forest inventory (NFI data; Brassel and Lischke, 2001) and DBH-height and -bark thickness relationships established per elevation with measured data (Fig. S2). Aboveground wood volume was calculated according to allometric equations (Etzold *et al.*, 2014) that were simplified based on Kaufmann (2001) to require only DBH and height as input variables (instead of the additional diameter at 7 m height) by summing stem (V_{stem}), branches (V_{branch}) and twigs (V_{twig}) volume:

Larix

$$V_{stem} = 0.042 + 0.372 \cdot height \cdot DBH^2 - 0.027 \cdot height \cdot DBH^3 \quad (1)$$

$$V_{branch} = V_{stem} \cdot e^{(-1.934 - 0.017 \cdot DBH)} / (1 + e^{(-1.934 - 0.017 \cdot DBH)}) \quad (2)$$

$$V_{twig} = V_{stem} \cdot e^{(-4.940 + 0.062 \cdot DBH)} / (1 + e^{(-4.940 + 0.062 \cdot DBH)}) \quad (3)$$

Picea

$$V_{stem} = 0.017 + 0.417 \cdot height \cdot DBH^2 - 0.083 \cdot height \cdot DBH^3 \quad (4)$$

$$V_{twig} = V_{stem} \cdot e^{(-1.206 - 0.019 \cdot DBH)} / (1 + e^{(-1.206 - 0.019 \cdot DBH)}) \quad (5)$$

Picea does not have an equation for branch volume, as the definition requires branches to be >7 cm in diameter, otherwise they are classified as twigs. DBH was reconstructed using the cumulative radial tree-ring increment following Bakker (2005), including pith-offset estimates using the curvature of the last ring (the concentric circles method, as described in Pirie *et al.*, 2015). If the curvature was not visible, DBH excluding bark was used to estimate the missing distance. We used wood density values of 500 g/cm³ for larch and 390 g/cm³ for spruce to convert wood volume to biomass (Brändli, 2010). Plot level ABI was derived from the sum of tree-growth increment of all individuals in the fixed plot and scaled up to kg ha⁻¹. For the analysis of the stand biomass accumulation and stand density developments we only considered the last ≈50 years of the reconstructed ABI, as we confirm no human intervention during this period. To address the absolute effect of outbreak absence we compared the mean ABI for the fixed plots over the periods 1961-1980 with outbreaks and 1990-2009 without outbreaks. We chose the 1990-2009 period to reduce the effect of the last budmoth outbreak of 1981 on growth and compared it to a period of equal length.

2.4. Growth-response modelling

We constructed elevation specific chronologies combining the north- and south-facing slope to perform growth-response modelling and disentangle the importance of climatic variables and budmoth outbreaks. We applied multiple detrending methods, including; regional curve standardization (RCS), basal area correction (BAC) and conservative detrending (CD), to verify that biases related to age/size removal were not artificially altering the tree-ring indices (Briffa and Melvin, 2011; Bowman *et al.*, 2013; Peters *et al.*, 2015; Groenendijk *et al.*, 2015). Detrending was performed using the dplR package in R (Bunn, 2008; R software, version 3.2.00, R development core team 2013).

Due to prominent rapid increases in growth indices in RCS and BAC chronologies at 1300 and 1600 m, which might be caused by replication changes of fast and slow-growing trees (Fig. S3), we decided to use the more conservative tree-specific detrending with linear or negative exponential curves (CD) to account for tree age/size effects and also correct for differences in growth level. A bi-weight robust mean chronology was constructed, including the stabilization of variance to minimize artefacts from changes in sample replication (Osborn *et al.*, 1997; Frank *et al.*, 2007). To further minimize the effect of possibly retained release effects and canopy dynamics on trends in tree-growth that might affect the climate-growth relationship in the CD time-series, we isolated the high-frequency signal of these chronologies by detrending the series with a cubic smoothing spline, with a 50 % frequency cut-off at 10 years (henceforth spline-detrended; cf. Cook and Peters 1981).

We constructed tree-ring chronologies with an average of 73 individuals per elevation and species (total of 513). Sample replication ranged from 35 to 118 individual trees and was greater at higher elevations (Table 1). We found strong common signals between individuals from the same species and elevation, with a mean inter-series correlation ranging from 0.49 to 0.67. The final chronologies had at least 10 trees covering a period from 1850 till 2011 (Fig. S1).

2.4.1. Climate-growth response analysis

Climatic datasets were obtained by interpolating daily values of MeteoSwiss weather stations from 1930 to 2011 down to a resolution of 100 m and then aggregating them into monthly mean time-series (Thornton *et al.*, 1997). To extend the downscaled MeteoSwiss data back to 1850, we adjusted the mean and variance of an additional climate dataset (HISTALP; Auer *et al.*, 2007) to the elevation specific time-series. For temperature, anomalies were calculated by subtracting the long-term (1930-2008) monthly means from the entire HISTALP time-series, while relative anomalies were calculated for precipitation (1930-2003, observed precipitation divided by monthly means). These anomalies were added to (or multiplied with, in the case of precipitation) the MeteoSwiss baseline climatology.

To test the short-term inter-annual climate signal of the spline-detrended chronologies we also spline-detrended the climate time-series, to ensure similarity in their frequency domains. Pearson correlations were performed over the 1850-2011 period after confirming normality of the residuals. We included seasonal climate aggregates from 1 to 12 months (from January prior to the growth year to current October). The climate correlation analysis for *Larix* was performed by excluding the years influenced by the budmoth, i.e. the outbreak years and the two subsequent years ($\approx 1/3$ of the data, leaving ≈ 110 years for the analysis). As outbreak events, we used the years reported in Esper *et al.* (2007), who reconstructed the outbreak history for the Lötschental based on ring width, wood anatomical and density observations from tree rings. The outbreak years were visually validated on our sampled material by observing narrow ring widths and thin latewood.

Subsequently, the three-month aggregation of climate (as it supplied the strongest and most consistent correlations) was used within a stepwise multiple regression using forward/backward elimination to identify the most important climatic drivers (cf. Venables and Ripley, 2002). This selection process starts by including the predictor (i.e. the three month climate aggregate) with the highest goodness of fit and adds predictors, at each step considering whether the criterion (based on goodness of fit and model complexity) improves by removing a previously added variable or keeping both previously selected and added variables. For the multiple regression analysis, we used the spline-detrended ring-width chronologies and 10-year spline-detrended climate data. We accounted for outbreaks by including an average growth response curve after an outbreak (see next paragraph) or excluding outbreak years and the two years after outbreak. Multiple regressions were performed using the R Commander package (Rcmdr; Huthcheson, 2012). The final model variables were chosen based on Bayesian

Information Criterion (BIC), as it appeared to be more conservative in selecting independent variables (Burnham and Anderson, 2003). We addressed multicollinearity by excluding models with variance inflation factors larger than 10 (cf. Graham, 2003; Chatterjee *et al.*, 2012). With the individual seasonal climate correlations and the multiple regression analysis, we established a common set of climate variables relevant across the gradient.

2.4.2. Outbreak-growth response analysis

To model and verify the impact of the budmoth outbreaks on *Larix* tree growth, we performed an outbreak-growth response analysis. We aligned the CD individual specific tree-ring series to year since outbreak and divided the post-outbreak annual ring-width indices by the growth level of the 5 years prior to the outbreak, to reduce overlap with the effect from the previous outbreak cycle (occurring every ≈ 9 years). We calculated median outbreak-growth responses per site and years since outbreak and applied a smoothing (cubic smoothing spline with a 50 % frequency cut-off at 10 years) to reduce climatically induced inter-annual variability in the response curves. We chose the cut-off at 10 years, as this spline rigidity resulted in a good fit of the raw median curve. For the final response curves, the original first four values after outbreak were used, after which we added the smoothed values until 13 years after outbreak (with values thereafter replaced by the value of year 13, due to data scarcity and the possible confounding climate effect of the post 1980 period). Within this analysis, we included 13 events (cf. Baltensweiler and Rubli 1999; Esper *et al.*, 2007): 1856, 1864, 1880, 1888, 1908, 1915, 1923, 1937, 1945, 1954, 1963, 1972 and 1981 with an exception at 1300 m elevation, where our tree-ring data did not show signs of outbreaks prior to 1930.

2.4.3. Quantifying growth benefit of outbreak absence

Additive linear models (cf. Chambers, 1992) were constructed in R to quantify the importance of climatic variables and budmoth activity on tree-growth variance within the chronologies. These growth-response models allowed for the simulation of the impact of only climate, only outbreaks, and of both the components as determined from the previous climate and outbreak response assessments. In addition to using climatic parameters, we also simulated *Larix* growth as a function of the *Picea* growth (i.e., the non-host tree) with our budmoth response curves (cf. Table S1).

When including the outbreak components for the *Larix* data, we tested multiple response curves (Table S2) and finally used the elevation specific response curves. After fitting the model on the 1850-1981 period, a simulation was run until 2011, with and without continued outbreaks

every 9 years. This simulation was used to quantify the growth “benefit” due to the absence of outbreaks as the mean percentage differences of the values obtained for the period 1990-2011 between the continued outbreak and the original model. Similarly, the unexplained growth change was quantified as the average percentage difference between the observed chronology and the fitted model.

3. Results

3.1. Aboveground biomass increment

We assessed long-term changes in aboveground biomass increment (ABI) for the fixed plots (Table 2). The plot at 1300 m was younger than the other plots and reached an average tree age of 150 at the year 2000. Stand density at this plot, as reconstructed from the live trees per year from the ring-width measurements (Fig. 2), decreased between the early 20th century and 2011 from 550 to 420 trees ha⁻¹. However, we observed constantly increasing ABI from 1901 (decadal mean: 2716±279 kg ha⁻¹ y⁻¹) to 1980 and a levelling off afterwards (mean: 6205±820 kg ha⁻¹ y⁻¹). After the last reported outbreak in 1981, the plots at 1900 m and 2200 m showed a strong increase in mean ABI (Fig. 3a), predominantly caused by increased growth of *Larix* (Fig. 3b). Between 1950 and 1980 the ABI rates were relatively stable at high elevations, with 2291±476 kg ha⁻¹ y⁻¹ at 1900 m; and 1632±518 kg ha⁻¹ y⁻¹ at 2200 m (Fig. 2). Until 1960, stand density was stable at both sites with mean tree ages above 150 years, after which a strong *Picea* recruitment occurred at 1900 m, causing an increase in stand density (Fig. 2).

The three budmoth outbreaks in 1954, 1963, and 1972 had a dramatic impact on ABI for all three plots (Fig. 2). Taking into account the standard deviations (sd) of the five years prior to the outbreak as a measure of regular inter-annual variability, the 1972 outbreak caused a > 2 sd growth decrease in the 4 following years at 1300 m (where the stand basal area consists of 50 % spruce and 50 % larch), reducing ABI to 4347-4908 kg ha⁻¹ (compared to the pre-outbreak mean of 6491 kg ha⁻¹). In 1963, growth reduction exceeded the 2 sd threshold during the first three years after the outbreak (1100-2000 kg ha⁻¹), whereas in 1954 a strong negative impact (2.5 sd or 980 kg ha⁻¹) was restricted to the first year after the outbreak. Negative impacts on ABI could be observed at 1900 m, where in 1972 and 1963 growth was reduced by 1100 kg ha⁻¹ (mean sd = 485 kg ha⁻¹) in the 3 years following the outbreak. The budmoth outbreak of 1963 caused a 3.5 sd departure at 2200 m, reducing the ABI from 2613 kg ha⁻¹ to 1018 kg ha⁻¹. The other two outbreaks also reduced growth in the year of outbreak until at least the second

year following the outbreak by 1000-1600 kg ha⁻¹, which is equivalent to 2-3.5 sd (mean sd = 476 kg ha⁻¹).

3.2. Climate-growth response

Correlations between growth and temperature were stronger than precipitation (strongest $r = -0.582$, $p < 0.001$ for previous year July-September temperature; and 0.441 , $p < 0.001$ for previous year July-September precipitation; Fig. 4). High-elevation *Larix* growth was positively correlated with current year June-August temperature (2200 m: $r = 0.413$, $p < 0.001$; 1900 m: $r = 0.290$, $p < 0.001$). Towards the lower elevations, summer temperature correlations decreased notably and even became negative. Additionally, *Larix* showed to be responsive to previous year September-November temperature (mean $r = 0.227$, $p < 0.05$). For *Picea* we found strong negative correlations with previous year July-September temperature (average across elevations $r = -0.486$, $p < 0.001$). We also observed a strong positive relationship with previous year July-September precipitation across elevations (mean $r = 0.306$, $p < 0.01$), although this variable is negatively collinear with temperature of the same period.

Climate variables selected according to the BIC (Table 3) within the multiple regression analysis were similar to the strongest correlations described above (Fig. 4). Considering the common response across elevations, we selected for *Larix* current year June-August and previous year September-November temperature, and current year June-August precipitation. For *Picea*, previous year July-September and current year May-July temperature, and previous year October-December and current year July precipitation were selected. However, discrepancies are observed for *Picea* where previous year October-December precipitation was selected instead of previous year July-September (Fig. 4), which is likely due to co-linearity with temperature. Additionally, temperature of current year May-July was selected instead of current year June-August.

3.3. Budmoth impact analysis

Larix growth decreased on average by 19 % for eight years following a budmoth event compared to ring-width index (RWI) of the five years prior to outbreak (Fig. 5). When considering the biomass growth of a 150-year old *Larix* tree within the valley, this would result in an annual reduction of 1.6 kg ABI. We observed the strongest growth reductions in the first year after an outbreak followed by the second and third year (42 %, 29 % and 22 % in RWI, respectively). Typically, it took eight years for the RWI to return to the pre-outbreak levels.

Site-specific impacts of budmoth outbreaks revealed strongest growth reductions at 1900 m (57 % relative growth change in the first year following the outbreak), followed by trees at 1600 m. Outbreak events in 1854 and 1964 caused *Larix* trees at 1900 to experience the biggest decrease in growth. Outbreaks at 2200 m usually reduced growth less than at other sites, although often causing significant impacts at year 0 (23 %; Fig. 5). At 1300 m, growth recovery in the second year after outbreak was highly dampened compared to other sites, with similar growth levels as for the year following the outbreak.

3.4. Modelling growth responses

When considering only climatic variables, the best model fits were found for *Picea* at 1900 m and *Larix* at 2200 m ($R^2 = 0.21$ and 0.25 , respectively; see Table 4 for slopes and residual standard errors). The explained variance in the models strongly decreased towards lower elevations ($R^2 = 0.03$ obtained for *Larix* at 1300 m; Table 4). In the most recent years (>1990), the model underestimated *Picea* growth at 1600 and 1900 m on average by 7 %, when comparing the difference between the model including only climatic parameters and tree-ring chronologies (Fig. 6). At 1900 m, the underestimation of *Larix* growth was even larger and reached 24 % (Table 4).

Accounting for outbreaks greatly increased the explained variance of the model fit for *Larix* (Table 4). Average R^2 improved from 0.17 to 0.44 when comparing the climate and outbreaks scenarios versus climate alone. The smallest model improvement was observed at 1300 m (Table 4), while at 1900 m the best fit was found for the scenario that included outbreaks and climate ($R^2 = 0.67$).

Including budmoth outbreaks in the models also increased the ability to explain the growth increase in the most recent decades (1990 to 2011; cf. Table 4 and Fig. 3b). When simulating continued budmoth outbreaks across elevations, 23 % of the recent growth increase could be explained (Fig. 6). We observed the strongest growth benefit from the absence of outbreak at 1900 m, where the continued outbreaks are modelled to reduce growth by 29 % (Table 4). For 2200 m, unexplained growth was reduced from 9.2 % to 0.4 % when including estimates for the recent outbreak absence, although this model started to overestimate growth at lowest elevations (overestimation of growth increase by 14 %; Table 4).

4. Discussion

4.1. Importance of climate vs. outbreaks and its variation along elevation

In this study we analysed the relative importance of climate and non-lethal insect outbreaks on tree growth and their impact on forest biomass accumulation. To the best of our knowledge, no other study has provided empirical data on the above-ground biomass reduction caused by budmoth outbreaks during the past century, the relative importance of climatic versus biotic drivers, and the possible beneficial effects due to the absence of outbreaks in recent decades.

Our tree-growth model, which includes climate and outbreak responses, was able to explain up to 67 % of the observed inter-annual growth patterns of high elevation *Larix decidua*. The model performed best at 1900 m elevation, while showing weak performance at the lowest elevation (1300 m; Table 4). Climatic drivers in the growth model alone at best explained 21 % and 25 % of growth variability for *Picea abies* at 1900 m and *Larix* at 2200 m respectively. The strong positive responses to summer temperature at higher elevations match previous observations for these species (Frank and Esper, 2005; King *et al.*, 2013b; Hartl-Meier *et al.*, 2014), and agree with findings showing the sensitivity of high-elevation trees growing at mesic sites to increasing temperatures (Jacoby *et al.*, 1996; Körner and Paulsen 2004; Bunn *et al.*, 2005; Salzer *et al.*, 2009, Babst *et al.*, 2013). At the same time, negative correlations with summer temperature at 1300 m (Fig. 4) support findings of greater drought sensitivity for forests at sites with higher mean annual temperatures (Barber *et al.*, 2000; Gómez-Guerrero, *et al.* 2013; Galván *et al.*, 2015; Qi *et al.*, 2015), although the magnitude will depend upon species-specific responses (Babst *et al.*, 2013).

Growth response to the reported budmoth outbreak years (cf. Esper *et al.*, 2007) explained 39 % of the observed *Larix* growth variability across elevations (Table 4), which is twice the variance explained by climate. *Larix* at 1300 m did not show evidence of outbreaks prior to 1930 and displayed a delayed response to outbreaks (Fig. 5). This absence could be explained by the more intense land-use at lower elevations during this period, which reduced host abundance, connectivity between forest stands, and subsequently the outbreak intensity (Johnson *et al.*, 2004; Battipaglia *et al.*, 2014 ; Hartl-Meier *et al.*, 2017). We hypothesize that the delay in response may be a result from the fact that a large part of the ring had already been formed before the outbreak, or that the insect activity and outbreak intensity can be different at lower elevations. *Larix* at 2200 m appeared to be least impacted by the outbreaks and recovered

relatively quickly (Fig. 5), while trees at 1900 m suffered most from the impact. Our observations for strongest outbreak effects at 1900 m and the decreasing impact towards both upper and lower elevations confirm previous reports indicating that the optimal outbreak conditions are present at an elevation of 1700-2000 m (Baltensweiler and Rubli, 1999).

4.2. Consequences due to the absence of outbreaks

Both *Larix* and *Picea* showed increased growth rates at higher elevations (>1600 m) in recent times. Yet, recent growth increase of *Larix* since 1981 cannot be explained solely by climatic variables (Table 4), but rather, can be largely attributed to the absence of budmoth outbreaks (Fig. 6). Additionally, our outbreak-growth response analysis showed that periods of outbreak absence longer than eight years result in higher growth compared to the years prior to outbreak (Fig. 5). Thus, model simulations suggest that the growth of *Larix* might even overproportionally benefit from the recent absence of insect outbreaks, as past absence periods could not explain the recent increase. When simulating continued outbreaks after 1980 we found strongest benefits from budmoth absence especially at 1900 m (Table 4).

When comparing tree-ring width indices from 1990-2011 to the modelled indices including outbreaks, it becomes evident that at intermediate elevations simulations underestimated the growth release that occurred in absence of budmoth outbreaks (Table 4). This is most prominent for *Larix* at 1900 m, where the model underestimates growth on average by 23.67 % per year, compared to only 6.4 % annual offset for *Picea*. We obtained similar underestimations when modelling *Larix* growth based on a non-host species (*Picea*) and outbreaks (Table S1 and S2), which does not require the selection of climatic variables (possibly prone to uncertainties and overfitting). However, considering the amount of the models' unexplained deviations throughout the past ≈ 150 years, the observed underestimation of recent increased *Larix* growth is not exceptional (Fig. 6).

We cannot exclude that other drivers might be responsible for the unexplained deviances, such as management activities, successional processes (e.g. natural thinning and mortality events) or non-linear climate responses. Yet, at 1900 m and 2200 m there was little evidence for management in the recent decades, which could have positively influenced remaining trees. Furthermore, the outermost years of dead trees could be dated back to the 1930s, which would speak against missed successional processes at these two sites. However, effects from increasing nitrogen deposition or higher CO₂ concentrations cannot be easily excluded (Paulsen *et al.*, 2000; Huang *et al.*, 2007; Camarero *et al.*, 2015) or invoked to explain

the growth increase (Girardin *et al.*, 2008). Alternatively, our outbreak response curve might still not capture the true magnitude of increase growth responses. The fact that the response curves were established with site-specific chronologies renders this variable not fully independent (Table 4). Furthermore, the absence of outbreak events in three decades represents an unprecedented state for the past millennium (Esper *et al.*, 2007), which is not included in our empirical outbreak response estimates.

A defoliation experiment performed on *Larix* in the Central Alps showed the impact of defoliation on non-structural carbon storage and its carbon limitation (Handa *et al.*, 2005), pointing to the mechanistic explanation that carbon available for radial growth was limited. Although more attention should be given to this mechanistic explanation, our results clearly show that the regular 9-year outbreak cycle prevented *Larix* from fully realizing its growth potential.

4.3. Implications for forest biomass accumulation

Our quantifications of the aboveground biomass increment (ABI) show that either the presence or absence of budmoth outbreaks has large consequences for forest biomass accumulation and carbon storage potential (Fig. 3). On average, budmoth outbreaks reduce tree individual ABI in the year subsequent to the outbreak by 58 % in comparison to the 5-year average growth prior to outbreak. Most severe growth reductions could be as high as 80 %, found for outbreaks at 1600 m in 1908 and 1954.

In terms of aboveground biomass, the three outbreak events occurring between 1950 and 1980 induced an average reduction in ABI of ≈ 770 and ≈ 1130 kg ha⁻¹ y⁻¹ in year 0-4 after the outbreak at 1900 and 2200 m and ≈ 300 kg ha⁻¹ y⁻¹ at 1300 m. Of the strong post-1980 increase at 1900 m, we can attribute a maximum of 770 kg ha⁻¹ y⁻¹ to the absence of outbreaks (from a total increase of 1800 kg ha⁻¹ y⁻¹; Fig. 2a). Here we assume that the absence of outbreaks explains roughly 60 % of the observed increase of *Larix* growth (Table 4). Similarly, we observed a twofold ABI increase at 2200 m (from 1500 to 3210 kg ha⁻¹ y⁻¹; Fig. 3a) that is largely caused by *Larix* and the absence of outbreaks (1420 of 1710 kg; Fig. 3b).

It is remarkable that despite large differences in age structure, stand density and recruitment, we observed nearly identical long-term trends in ABI over the last century at 1900 and 2200 m. However, one should be cautious when attributing the increase in plot level ABI to climate drivers or budmoth outbreak dynamics, as we are aware that stand development and management cause a constant loss of signal back in time (i.e. the “fading-record” problem; cf.

Swetnam *et al.*, 1999; Foster *et al.*, 2014). We want to stress that within the context of forest biomass increment, changes in forest structure, stand dynamics, distribution, and tree growth should not be overlooked when analysing long-term biomass changes (Etzold *et al.*, 2014; Pretzsch *et al.*, 2014; Hansen *et al.*, 2015). Therefore, especially for forests at 1300 m, we refrain from attributing the long-term increase in plot level ABI to climate drivers or budmoth outbreak dynamics.

Interestingly, plot level ABI at 1300 m shows a quick recovery following the outbreaks to pre-outbreak level, which could either be due to high carbohydrate reserves or due to a larger fraction of spruce ($\approx 50\%$ of the standing biomass in 2011; cf. Table 2) and favourable growing conditions in the years after the outbreaks. In the light of weak negative tree growth-summer temperature relationships, recent warmer temperatures might have partially counteracted the growth benefits expected due to lack of recent budmoth outbreaks. However, it becomes obvious from Figure 3b that *Larix* growth still increased in the 1990-2009 period, thus counterbalancing the slower growth of *Picea*.

In this study we analysed the impact of a reduced outbreak frequency, however globally many phytophagous insects show increased activity associated with shifts in distribution range (Battisti, 2008; Axelson *et al.*, 2015), improved breeding and growing conditions (Battisti *et al.*, 2000; Pasztor *et al.*, 2014), and increased frequencies and magnitude of outbreaks (Creeden *et al.*, 2014). Although there is a lack of similar tree-ring data or biomass quantification to directly compare our values, multiple studies support the relevance of insect outbreaks for tree growth and forest productivity (Kurz *et al.*, 2008; Medvigy *et al.*, 2012; Moore *et al.*, 2013). Aerial images for North-America provide evidence for large areas being affected by major forest insect species (Hicke *et al.*, 2012). Also, eddy covariance flux tower on multiple forest sites in New Jersey (USA) revealed strong reductions in net annual CO₂ exchange changes due to Gypsy moth (*Lymantria dispar* L.) defoliation, although wood increment only decreased slightly (Clark *et al.*, 2010). Although our study focusses on the Lötschental, *Larix* is an abundant species in high-elevation forests across the European Alps (EUFORGEN), indicating that these forests might increase their carbon sink relevance with persistent absence of budmoth outbreaks.

Tree rings have a huge potential in both reconstructing ABI (Babst *et al.*, 2014b, Klesse *et al.*, 2016) as well as assessing the absolute impact of insect outbreaks on ABI. As non-lethal disturbances, such as the larch budmoth outbreaks, are rather under-represented in current ecological models (Seidl *et al.*, 2011), our study provides valuable input for modelling budmoth

induced growth reductions. Further tree-ring investigations, from other sites and species that contain necessary structural data (stand density, tree size and height), will contribute to better understanding the importance of insect outbreaks and their absence on the carbon source or sink function of forests in the future (e.g. Bale *et al.*, 2002; McMahon *et al.*, 2010; Medvigi *et al.*, 2012).

5. Conclusion

Our study provides data on the relative importance of insect outbreaks compared to climate variation on *Larix* growth. Both *Picea* and *Larix* at high elevations show positive growth responses to increasing temperature. However, our simulations show that the recent absence of budmoth outbreaks is crucial to explain the strong growth increase for *Larix* at higher elevations, far beyond what can be explained by climate alone. Additionally, the different magnitude of growth responses to insect outbreaks as a function of elevation suggests that budmoth activity and its impact are likely temperature dependent. From the biomass reconstructions it is clear that *Larix* productivity was severely dampened by regular outbreaks at higher elevations, preventing these trees from fully realizing their growth potential.

6. Author contributions

R.L.P. and S.K. conceived and designed the research, collected and analysed the data; R.L.P. and S.K. wrote the manuscript, with contribution from D.C.F. and P.F. in discussion and writing.

7. Conflict of interest

The authors declare that they have no conflict of interest.

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Figure legends

Figure 1. a) Map indicating the centre of the Lötschental sampling area and the distribution range of the studied species (source: EUFORGEN). The north- and south-facing slope are presented with an N and S, while the elevation is specified with the numbers (e.g. 22 indicated the site at ≈ 2200 m in elevation). Fixed plots are indicated with black dots, where the direction to the Blatten plot on the south-facing slope at 2200 m is provided. b) Examples of the wood structure for both species.

Figure 2. Stand level aboveground biomass increment for (a) the two high elevation plots at N19 (full lines) and Blatten (dashed lines) and (b) the low elevation plot N13. The panels below represent reconstructed stand density (mid panel) and stand age (lower panel). Stand age is defined as the mean age of all trees at a given year. Note the different y-axes in (a) and (b). The vertical dashed lines denote the reported budmoth outbreaks from the literature.

Figure 3. a) Mean aboveground biomass increments (ABI) for the fixed plots over the periods 1961-1980 with outbreak and 1990-2009 without outbreaks for both species together and b) separated.

Figure 4. Pearson correlation coefficients (r) of chronologies along different elevations of *Picea* (P) and *Larix* (L) with temperature and precipitation. A three-month moving window was used, with monthly labels indicating the last month of the window. Lowercase month abbreviations represent previous year correlations with climate, while uppercase represents the current year. Black boxes indicate the windows selected as common climatic drivers along the elevational gradient, according to the multiple regression analysis.

Figure 5. Mean impact of budmoth outbreaks occurring between 1850 and 1980 on annual growth of *Larix* and *Picea* derived from ring-width indices. Relative growth increment is defined as the current growth divided by the mean growth of 5 years prior to the outbreak. To provide an indication on the reduction magnitude, the relative growth changed was multiplied with the mean biomass increment of a 150 year old *Larix* tree from the fixed plots (as *Picea* does not show a response).

Figure 6. Modelled ring width index compared to the chronologies from *Picea* and *Larix* along the elevational gradient. For *Picea* only climatic drivers are included, while for *Larix* the outbreaks are added and simulated to continue after 1981 (cf. Table 4 for more model fitting statistics).

Tables

Table 1. Main characteristics of the species and elevation specific tree-ring chronologies.

*Mean inter-series correlation and mean sensitivity as produced by the program COFECHA (Holmes, 1983). **Expressed population signal calculated for the CD standardized individual series by the R package dplR (Bunn *et al.*, 2008).

Elevation	2200		1900		1600		1300	
Species	<i>Larix decidua</i>	<i>Picea abies</i>	<i>Larix decidua</i>	<i>Picea abies</i>	<i>Larix decidua</i>	<i>Picea abies</i>	<i>Larix decidua</i>	
Individuals (radii)	101 (204)	118 (224)	72 (133)	67 (121)	77 (144)	43 (82)	35 (65)	
Time span	1515 – 2014	1683 – 2014	1693 - 2014	1657 - 2014	1629 - 2014	1825 - 2013	1795 - 2012	
Mean series length	225	127	185	137	128	123	130	
(min/max)	(25/497)	(19/331)	(23/322)	(25/358)	(19/379)	(22/187)	(55/213)	
Mean DBH	43.34	37.68	50.72	42.25	45.81	47.24	48.81	
(min/max)	(13.4/76.7)	(5.8/74.0)	(8.4/80.4)	(16.4/79.5)	(11.5/85.4)	(14.0/92.0)	(17.6/76.6)	
Mean age	257	144	213	168	149	140	142	
(min/max)	(26/551)	(20/331)	(24/326)	(31/461)	(24/379)	(22/187)	(68/213)	
Mean inter-series correlation*	0.60	0.59	0.66	0.49	0.61	0.54	0.54	
Mean sensitivity*	0.35	0.18	0.30	0.17	0.25	0.19	0.27	
Mean EPS (1850-2011)**	0.98	0.96	0.99	0.92	0.98	0.90	0.91	

Table 2. Characteristics of the fixed plots.

Site code	Coordinates °N	Coordinates °E	Plot radius (m)	Plot size (m ²)	Basal area (m ² ha ⁻¹)	Stem density (trees ha ⁻¹)	Dominant species # 1 (%)	Dominant species # 2 (%)
N13	46.39022	7.76325	17.0	907.92	76.70	420	<i>Larix decidua</i> (52)	<i>Picea abies</i> (48)
N19	46.38631	7.77371	17.0	907.92	47.27	540	<i>Larix decidua</i> (66)	<i>Picea abies</i> (34)
BLA	46.428609	7.823441	16.5	855.30	56.74	420	<i>Larix decidua</i> (87)	<i>Picea abies</i> (13)

Table 3. Selected climatic variables based on the forward/backward multiple regression analysis. Three-month average climate data was correlated with the elevation-specific chronologies of *Picea* and *Larix*. Outbreaks were included into the analysis by either removing the outbreak year and subsequent two years after outbreak or using an average negative growth response curve after an outbreak. For the three-month average, the last month is presented. Commonly occurring climatic variables were selected. *Selected climate variables and #highly overlapping with selected month in the final model.

Species	Outbreak	Elev. (m)	Selected variable (slope)							
<i>Picea abies</i>	None	1300	Int. (0.92)	Tsep (-0.04)*	Pdec (0.05)*	PJUL (0.09)*	Tmar (-0.01)	TJAN (0.02)	POCT (-0.05)	
		1600	Int. (0.88)	Tsep (-0.04)*	Pdec (0.05)*	TJAN (0.01)	TJUL (0.02)*	PJUL (0.08)*	POCT (-0.04)	PAPR (0.04)
		1900	Int. (0.81)	Tsep (-0.05)*	TJUL (0.04)*	Tdec (0.02)	PMAY (0.04)	Poct (0.06)	PJUL (0.06)*	PFEB (0.03)
<i>Larix decidua</i>	Removing up to two years after outbreak	1300	Int. (0.91)	Tnov (0.03)*	PJUL (0.11)#					
		1600	Int. (1.12)	Tnov (0.03)*	TSEP (0.04)	Psep (-0.09)				
		1900	Int. (1.05)	TAUG (0.07)*	Tnov (0.04)*	TAPR (-0.02)				
		2200	Int. (0.95)	TAUG (0.10)*	Tnov (0.04)*	TAPR (-0.03)	PMAR (0.078)	TNOV (-0.03)		
	Including negative outbreak response curves	1300	Int. (0.71)	Outbreak (0.24)	PAUG (0.13)*	Toct (0.03) #				
		1600	Int. (0.43)	Outbreak (0.63)	Toct (0.04) #					
		1900	Int. (0.28)	Outbreak (0.79)	Tnov (0.05)*	Tmar (0.03)				
		2200	Int. (0.54)	TAUG (0.13)*	Tnov (0.05)*	Outbreak (0.43)	TAPR (-0.03)	TSEP (-0.05)	PFEB (0.07)	

Table 4. Model fits for *Picea* and *Larix* chronologies along different elevations. Three month average climate variables for precipitation (P) and temperature (T) from previous and current year (capital letters) are presented (last month is shown). Three different types of scenarios are included; climatic variables alone, climate in combination with outbreak response curves and outbreak response curves alone. Budmoth absence growth change describes the average annual percentage of modelled ring width index gained compared to the model where outbreaks would have continued with a 9-year frequency from 1990 onwards. Unexplained growth change is the average annual percentage growth increase of observed ring width indices over the modelled *Larix* series without outbreaks. For *Picea* this value reflects the average annual percentage difference between observation and climate model. Significance codes: $p > 0.001 = **$, $0.001 < p > 0.05 = *$, $0.05 < p > 0.1 = .$

Species	Scenario	Elevation (m)	Variables (slope)					Residual standard error	Adjusted R ²	Budmoth absence growth change (%)	Unexplained growth change (%)
			Intercept	Tsep	Pdec	TJUL	PJUL				
<i>Picea abies</i>	Climate	1300	1.30**	-0.0344*	0.0002	-0.0060	0.0005*	0.134	0.11**	-	-2.45
		1600	0.89**	-0.0378**	0.0002*	0.0299*	0.0005**	0.115	0.18**	-	7.63
		1900	1.07**	-0.0515**	-2.48e-06	0.0441**	0.0002	0.101	0.21**	-	6.40
<i>Larix decidua</i>	Climate		Intercept	TAUG	Tnov	PAUG	Outbreak				
		1300	0.59*	0.0099	0.0196	0.0005*	-	0.158	0.03	-	0.27
		1600	-0.48	0.1122**	0.0278	0.0003	-	0.247	0.14**	-	15.16
		1900	-0.88*	0.1664**	0.0501*	0.0004	-	0.283	0.24**	-	23.67
	Climate +	2200	-0.22	0.1311**	0.0364*	0.0002	-	0.221	0.25**	-	9.16
		1300	0.42	-0.0041	0.0187	0.0005*	0.3761**	0.151	0.11**	19.32	-14.29
		1600	-0.51*	0.0512*	0.0168	0.0002	0.8534**	0.190	0.49**	23.44	6.60
		1900	-0.81**	0.0841**	0.0314*	0.0003	0.9087**	0.187	0.67**	28.91	19.49
	Outbreak	2200	-0.56*	0.0835**	0.0246	0.0002	0.8191**	0.180	0.50**	18.83	0.43
		1300	0.62**	-	-	-	0.3623**	0.154	0.08**	18.17	-9.76
		1600	0.14	-	-	-	0.9349**	0.194	0.47**	25.13	11.40
		1900	0.08	-	-	-	1.0248**	0.202	0.61**	31.19	25.43
		2200	0.06	-	-	-	0.9921**	0.195	0.41**	22.49	10.44

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