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GLOBAL CHANGE ECOLOGY - ORIGINAL RESEARCH

Tree growth response along an elevational gradient: climate or genetics?

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Abstract Environment and genetics combine to influence tree growth and should therefore be jointly considered when evaluating forest responses in a warming climate. Here, we combine dendroclimatology and population genetic approaches with the aim of attributing climatic influences on growth of European larch (*Larix decidua*) and Norway spruce (*Picea abies*). Increment cores and genomic DNA samples were collected from populations along a ~900-m elevational transect where the air temperature gradient encompasses a ~4 °C temperature difference. We found that low genetic differentiation among populations indicates gene flow is high, suggesting that migration rate is high enough to counteract the selective pressures of local environmental variation. We observed lower growth rates towards higher elevations and a transition from negative to positive correlations with growing season temperature upward along the elevational transect. With increasing elevation there was also a clear increase in the explained variance of growth due to summer temperatures. Comparisons between climate sensitivity patterns observed along this elevational transect with those from

Larix and *Picea* sites distributed across the Alps reveal good agreement, and suggest that tree-ring width (TRW) variations are more climate-driven than genetics-driven at regional and larger scales. We conclude that elevational transects are an extremely valuable platform for understanding climatic-driven changes over time and can be especially powerful when working within an assessed genetic framework.

Keywords Dendrochronology · Climate impact · Gene flow · Forest productivity · Alps

Introduction

Recent climatic warming has been implicated as a driver in shifts of physiological and ecological processes (e.g. timing and rates of growth, species range shifts) of both plants and animals worldwide (Parmesan 2006). These changes may reflect the inherent ability of individuals to respond plastically to environmental variation, but it remains unclear if some of these observations point to genetic adaptation and possible evolutionary change within species (Hoffmann and Sgrò 2011; Donnelly et al. 2012). Further understanding of the interaction between genetics and plant response to environmental drivers is crucial to improving forecasts of species survival and provide accurate conservation planning under increasing environmental pressure.

The question of genetic versus plastic response is of particular relevance for trees because they are long-lived, stationary, and spend relatively long periods of time in juvenile (non-reproductive) states (Jump et al. 2006). Recent rapid climate change has led to uncertainty about the ability of some tree species to keep pace with their changing environmental envelopes with unknown

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consequences for future forest composition (McLachlan et al. 2005; Visser 2008). Because about 30 % of the Earth's land surface is covered by forests (FAO 2010), these ecosystem changes will have consequences for carbon and water cycles, rates of net primary production and many other ecosystem services that human societies rely upon (Courbaud et al. 2011).

Dendrochronology is a method used frequently in tree and forest growth research. Annual growth rings are used to interpret the biological response to climate and the stability of this response across inter-annual to centennial time-scales. Although tree-ring data are commonly employed to reconstruct climate variability (e.g. Frank et al. 2010; Büntgen et al. 2011), dendrochronology has also been used to evaluate how the growth of tree populations might respond under future climate scenarios. For example, Goldblum (2010) used white oak chronologies distributed across its range in North America to model the response to past climate, and in tandem with temperature projections, predicted radial growth decreases across much of the species' northern range. Similarly, Pasho et al. (2011) analysed the influence of water availability on eight Mediterranean tree species across a climatic gradient in north-eastern Spain. The latter authors found high variability in species responses across the gradients investigated, and concluded that, under more frequent and severe droughts, most trees within the study area would be adversely affected. While we do not wish to review all dendrochronological articles that have not explicitly considered the genetic composition of the populations under investigation, these two studies are representative of many previous works that implicitly assume observations were driven solely by physiological responses to climatic change with no genetic contribution.

The importance of considering the underlying genetic composition of populations is demonstrated by Ohsawa and Ide (2008), who found differences in genetic diversity with altitude in 70 % of studies they reviewed, with more than 50 % of these studies observing inter-population genetic differentiation. The presence of differentiated populations is an indication that natural selective pressures and in situ adaptive response may exist, casting doubt on the ability to assess future species response to climate variability without consideration of the genetics of populations under study. However, it should be considered that genetic differentiation among populations is a direct function of migration, i.e. gene flow, and random genetic drift. Proximity of populations and large effective population size thus likely prohibit genetic differentiation. Moreover, gene flow counteracts local adaptation, so that only strong selection may lead to adaptation under high migration rates.

Two prominently used approaches to study the genetics of populations are common gardens and molecular

markers. Common garden (provenance) tests are classic experiments that attempt to separate climatic and genetic signals by growing plants from different environments in a single location and measuring their growth response (Kawecki and Ebert 2004). Considering trees, these studies require a significant amount of time, as a second generation is required to measure the true heritability of traits. More recently, studies have turned to neutral molecular markers (e.g. microsatellites) to investigate genetic variability and differentiation within and between tree populations (Holderegger et al. 2010). A shift to molecular methods is being prompted by faster processing times, the ability to sample a far greater number of individuals within a population and lower costs (Selkoe and Toonen 2006). Clearly, these markers do not directly inform the adaptive responses of populations (or absence thereof), but are taken as indicators of demographic processes and of gene flow. Accordingly, one may interpret measures of extensive gene flow, as obtained from neutral molecular markers, as indirect evidence of reduced chances for local adaptation, because very strong selective pressures would be required to overcome the constant immigration of non-local alleles (Savolainen et al. 2007).

Here, we perform a comprehensive study of climatic influences on tree growth after considering possible genetic effects. Increment cores and tissue samples were collected from two conifer species (*Picea abies* and *Larix decidua*) along a 900-m elevational transect. We first test if populations are genetically well-mixed along the length of the elevational gradient. We then aim to quantify the climatic controls on intra-annual tree growth and assess if this transect may be used to further investigate alpine conifer response to projected climate warming. We compare our results from the elevational gradient to a dataset of sites from across the Alps to evaluate tree growth response across larger spatial scales and hypothesise what role genetics may play in these relationships.

Methods

Study area

Our study location was the Lötschental, an inner-alpine valley located in the central Swiss Alps (46°23'40"N, 7°45'35"E; Fig. 1). The valley is oriented along a north-east-southwest direction and connects to the Rhône Valley (canton of Valais). Sampling sites were established on the forested slopes around the town of Ferden, consisting of primarily evergreen Norway spruce [*Picea abies* (L.) Karst.] and deciduous European larch (*Larix decidua* Mill.) extending from 1,300 to ~2,300 m a.s.l. (within the manuscript, species are addressed by genus names). The

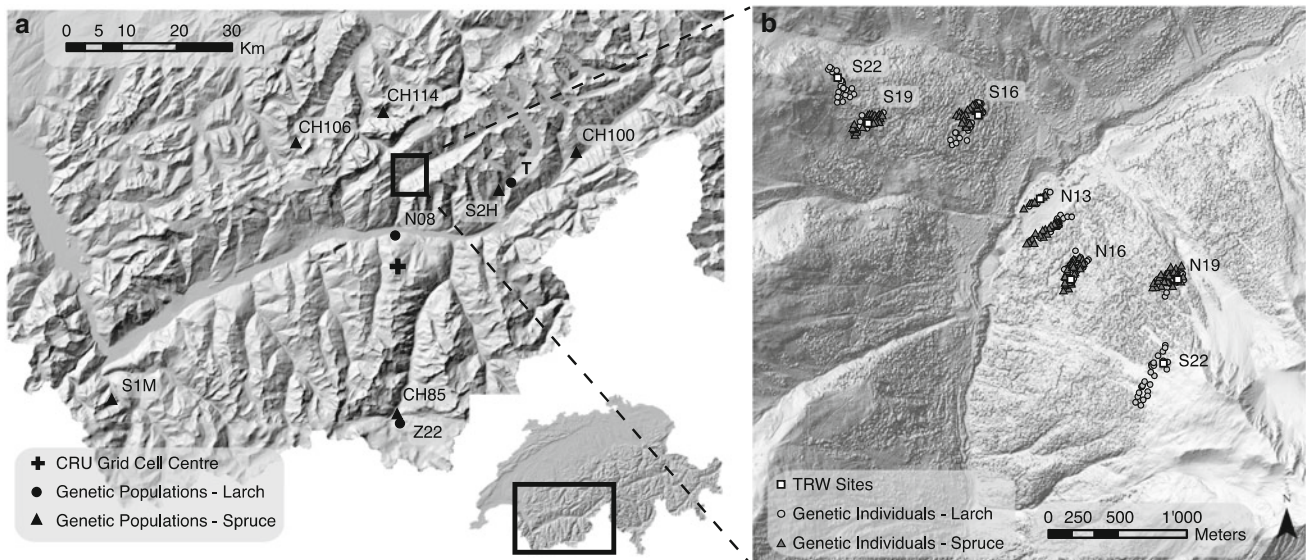


Fig. 1 **a** Regional relief map showing the location of the sampling area (*black rectangle*) and the regional genetics sampling populations in *filled black circles* (*Larix decidua*) and *filled black triangles* (*Picea abies*). The *black cross* represents the grid point center for the Climatic Research Unit (CRU) data covering the period 1901–2009.

b Hillshade digital elevation model of the Lötschental indicating the tree ring sampling locations (*white squares*) and the location of each individual for genetic analysis with *light grey circles* (*L. decidua*) and *dark grey triangles* (*P. abies*)

valley has a cool, dry climate with a mean annual temperature of 6 °C, ranging from −3 (January) to 15 °C (July) and a mean annual precipitation exceeding 800 mm (data from MeteoSwiss surface observation network). The valley soils are formed from calcareous-free substrate, including moraines and crystalline bedrock (gneiss and granite) from the Aar massif. This contributes to acidic soils characterised by coarse stone content and low amounts of clay. Several soil types were observed, ranging from Leptosol, Cambisol to Podzol, with intermediates.

Climate and meteorological data

In situ air temperatures (Onset, U23 Pro loggers) were recorded at 15-min intervals beneath the canopy at each sampling site as part of ongoing research along this elevational gradient (Moser et al. 2010; King et al. 2013). Temperature differences along the gradient were calculated with monthly averages over a 4-year period (2008–2011). Gridded ($0.5^\circ \times 0.5^\circ$) historical temperature and precipitation records (Climatic Research Unit (CRU) TS 3.10; Brohan et al. 2006) were used to correlate with the tree-ring records from the Lötschental. The CRU data were extracted from the closest grid point to our field site (grid centre: 46.25°W, 7.75°E) and covered the period 1901–2009. Anomalies were calculated on a monthly basis with respect to 1971–2000 mean conditions. Additional downscaled climate data at a spatial resolution of 1 km² was used to calculate annual temperature and precipitation

amounts for comparisons between our transect sites and sampling sites across Europe (WorldClim; Hijmans et al. 2005).

Tree-ring data and analyses

Seven sites were selected along the 900 m elevational transect; a single site at the valley bottom (~1,300 m a.s.l.) and three sites at ~300 m elevation intervals along both the north and south slope aspects to ~2,200 m a.s.l., just below the upper forest limit. Codes for aspect (N and S) and elevation (in hundreds of metres) were assigned to each site, e.g. N16 for northern aspect at 1,600 m a.s.l. At each site, with the exception of N22 and S22, which contain no *Picea*, two radii from mature trees of both species were sampled at breast height (~1.3 m). An average of 23 ± 4 trees (43 ± 7 series) were sampled per site for a total of 272 trees (518 series) sampled overall.

Standard dendrochronological techniques were used to collect and prepare samples for tree-ring width (TRW) measurement (Schweingruber 1996). Ring variations were visually cross-dated and measured using a LINTAB tree-ring measuring system (precise to 0.001 mm). Two radii per tree were measured in all but a few cases. Cross-dating accuracy was verified with the software program COFECHA (Holmes 1983). Comparisons among different detrending methods (e.g. regional curve standardisation, negative exponential, varying spline lengths) were conducted, but no significant differences in the climate

sensitivity/response among techniques were found (data not shown). Age-related trends were ultimately removed from individual raw data using a 100-year spline to preserve inter-annual to multi-decadal variability. Mean site chronologies were calculated using the robust bi-weight mean. Chronologies were well replicated over time, with the common period of all sites (minimum of five series) beginning in 1876. If the increment cores did not contain the innermost ring, pith-offset estimates were made using standard techniques based upon ring curvature, multiple cores per tree and a transparency with concentric circles. The time taken for trees to reach coring height (~ 1.3 m above the ground) makes the dendrochronological ages younger than the germination age. We use the term tree age to refer to the estimated age of the tree at breast height.

Coherence, trends and absolute rates of growth were assessed and calculated from raw TRW measurements aligned by tree age. Average growth over the first 50 years for each species at each elevation was calculated. Sample depth, expressed population signal (EPS) and running Rbar (mean inter-series correlation) statistics were calculated for each site (Online Resource 1, 2). Following detrending, pairwise correlations among all trees were calculated and plotted as function of elevation difference. Further comparisons among the standardized site chronologies revealed strong agreement between slopes and subsequent climate-growth correlations were performed with chronologies grouped by elevation for each species.

Pearson correlations between elevation chronologies for each species and gridded temperature and precipitation data were computed for all months from previous June to current December and included two seasonal averages of April–September (AMJJAS) and June, July and August (JJA). To compare spatial data patterns, *Picea* and *Larix* JJA temperature correlations from each site in the Lötschental were plotted against mean annual temperature and then compared with data from the same species (*Larix decidua*, $n = 65$; *Picea abies*, $n = 220$) from a network of published TRW chronologies from across the Greater Alpine Region [4–19°E, 43–49°N; Babst et al. 2013]. Linear models were fit to each dataset for both species.

Genetic sampling and molecular analyses

To assess genetic differentiation among tree populations along the elevational gradient, we collected living plant material from 30 individuals of each species at each sampling elevation and aspect. There was significant overlap between the trees sampled for genetics and increment core collection. Four cambial probes per individual were collected with a TREPHOR puncher (Rossi et al. 2006) and dried immediately on silica gel. Each individual's geographic position was collected using a handheld GPS unit.

To avoid parental influence through spatial autocorrelation in relatedness, individuals were located a minimum of 30 m from each other.

Needle samples from additional populations outside the study area were included to test if more distant populations showed higher genetic differentiation than that comprised within a single valley. We selected three population samples of *L. decidua*, one of which represented a subsample of the population described in Pluess (2011), and five locations of *P. abies* (Gugerli et al. 2001; C. Sperisen, unpublished data).

We extracted genomic DNA from isolated cambial tissues or needles with the 96-well DNeasy Plant Kit (Qiagen, Hilden, Germany), following the manufacturer's instructions. Multiplex polymerase chain reactions (PCRs) for nuclear microsatellite (nSSR) genotyping comprised PCR Multiplex Kit (Qiagen), primer premix with amounts per primer adjusted to obtain balanced amplifications (Online Resource 3), water and about 5 ng DNA. On the basis of previous studies (Tollefsrud et al. 2009; Pluess 2011), the following loci were selected: bcLK189, bcLK228, bcLK229, bcLK235, bcLK253, bcLK263, bcLK211 (Isoda and Watanabe 2006), and UAKLLy6 (Khasa et al. 2000) for *L. decidua* and EATC1B02, EATC1E03, EATC2B02, EATC1G05 (Scotti and Paglia 2002), and SpAC1F7 (Pfeiffer et al. 1997) for *P. abies*. Three loci were excluded from the final data set of *L. decidua* because of inconsistent amplification (bcLK211) and the likely presence of null alleles (significant deviation from Hardy–Weinberg equilibrium (HWE) in each population; bcLK263, UAKLLy6), which left us with five loci for data analysis in each species.

Amplified fragments were separated electrophoretically on an ABI3130 automated capillary sequencer (Applied Biosystems, Foster City, CA) with GeneScan 400HD (ROXTM) (Applied Biosystems) as an internal size standard. Allele calling and binning was performed manually using Genemapper 3.7 (Applied Biosystems).

After confirming that there were no consistent deviations from HWE, except for the two loci excluded from the *L. decidua* data set (see above), and testing for possible linkage disequilibrium (LD), we calculated expected heterozygosity (H_E) per locus, averaged over all populations, an analysis of molecular variance (AMOVA), and matrices of pairwise genetic differentiation (F_{ST}) among populations per species using Arlequin 3.5.1.3 (Excoffier and Lischer 2010). Statistical significance was assessed at the 0.05 level by generating a null distribution over 1,000 permutations. In addition, nSSR data were used to calculate pairwise relatedness among all individuals on the transect (Lynch and Ritland 1999), using GenAlEx 6.4 (Peakall and Smouse 2006). Each of these values was then multiplied by 2 to create a scale ranging from -1 to 1.

Results

Climatic change and elevational transects

Gridded, long-term, instrumental climate records (CRU TS 3.10, Fig. 2a, b) revealed warming air temperatures and no trend in precipitation sums over the past century. A linear model of climatic anomalies over the period 1901–2009 showed that growing season (AMJJAS) temperatures had a significant positive trend of 0.13 °C/decade ($F_{1,107} = 39$, $P < 0.001$), while winter temperatures (December–February) showed a similar positive trend of 0.14 °C/decade ($F_{1,106} = 20.8$, $P < 0.001$). These rates correspond to a 1.4 °C temperature increase over the 109-year record. The temperature records also revealed an accelerating warming trend during the period 1975–2009, with more frequent positive anomalies both during winter and the growing season. Over these 35 years, the decadal warming trends increased almost five-fold to 0.6 °C/decade in the growing season, and increased by about 40 % during the winter. An examination of the range of seasonal anomalies provided an assessment of the inherent climatic variability at our sites. The warmest growing season occurred in 2003 (2.4 °C departure from mean) while the warmest winter on record (2.3 °C), took place 4 years later in 2007. The lowest winter temperature anomaly of −3.9 °C was in 1963 and the coldest growing season in 1910 (−1.7 °C). Taking into account these extremes, temperatures showed an approximate range of 4.0 ± 0.8 °C during the growing season and 6.2 ± 1.1 °C for the winter.

The sampled elevational gradient showed a maximum air temperature difference of 4.2 °C between the lowest and highest elevation (Fig. 2c). This difference is slightly greater than the 4.0 °C range of temperature anomalies from 1901 to 2009. Inter-site differences were more prominent during the growing season than during winter when absolute temperatures along the transect were generally within 2.0 °C. Notably, there was greater temperature variability over elevation than between the slope aspects, although the southern aspect was slightly warmer (~ 0.3 °C) for most elevations.

Radial tree growth along the transect

To better understand the growth trends of trees along the transect, we plotted raw TRW and made comparisons between species, slope aspects and elevations. These data show that tree age increased with elevation, that trees are generally older on the north aspect and that *Larix* are older than *Picea*. *Larix* showed consistently higher series inter-correlation and mean sensitivity than *Picea*, and EPS for most sites was above the commonly applied threshold of 0.85 (Online Resource 1, 2).

Alignment of site TRW chronologies by tree age reveals that radial growth decreased broadly as elevation increased, and that radial growth was generally greater on the southern aspect (Fig. 3a). Absolute growth rates over the first 50 innermost rings (tree age 1–50) ranged from 1.09 mm/year (1,300 m) to 0.44 mm/year (2,200 m) for *Larix* and 1.14 mm/year (1,300 m) to 0.65 mm/year (1,900 m) for *Picea*.

Comparisons of standardised TRW chronologies over the common period (1876–2007) revealed differences between species and among elevations, but very high similarity between slope aspects (Fig. 3b). The most conspicuous patterns were intermittent, abrupt reductions in ring width of *Larix* occurring approximately every decade (especially prominent between 1940 and 1980). These patterns were generally synchronous among elevations above 1,300 m and contributed to the higher mean sensitivity and R_{bar} in *Larix*.

Growth and genetic coherence along the transect

To assess the common signal of the standardised TRW chronologies along the elevational gradient, we computed the pairwise correlations of inter-individual TRW records. These demonstrated a notable decrease in median correlation as elevational distance between individuals increased (Fig. 4a). Overall, *Larix* showed greater inter-tree correlation than *Picea*, but both species had their highest median correlations between trees at the same elevation. Additionally, computed correlations between *Larix* and *Picea* were all extremely low (< 0.1) and were consistent across all elevations (data not shown). The variability of the correlations decreased in both species with greater elevation difference, although there were also fewer pairwise observations.

An assessment of pairwise genetic relatedness for each individual across all sites (including both slopes) revealed that both species have high genetic similarity (Fig. 4b). Additional comparisons were made between each Lötschental population and other populations of both *Larix* and *Picea* collected around the canton of Valais (Fig. 1) in an attempt to provide additional evidence that gene flow at the landscape scale faces barriers. Values of pairwise F_{ST} showed that there is a lower degree of genetic differentiation within the Lötschental than between the Lötschental populations and additional populations outside of the valley (Table 1).

An analysis of molecular variance (AMOVA) showed that both *Picea* and *Larix* have greater genetic variance estimated to occur within populations (99.56 and 99.43 %, respectively) than partitioned between slope aspect groups (0 % for both species) or among populations within groups (0.46 and 0.80 %, respectively).

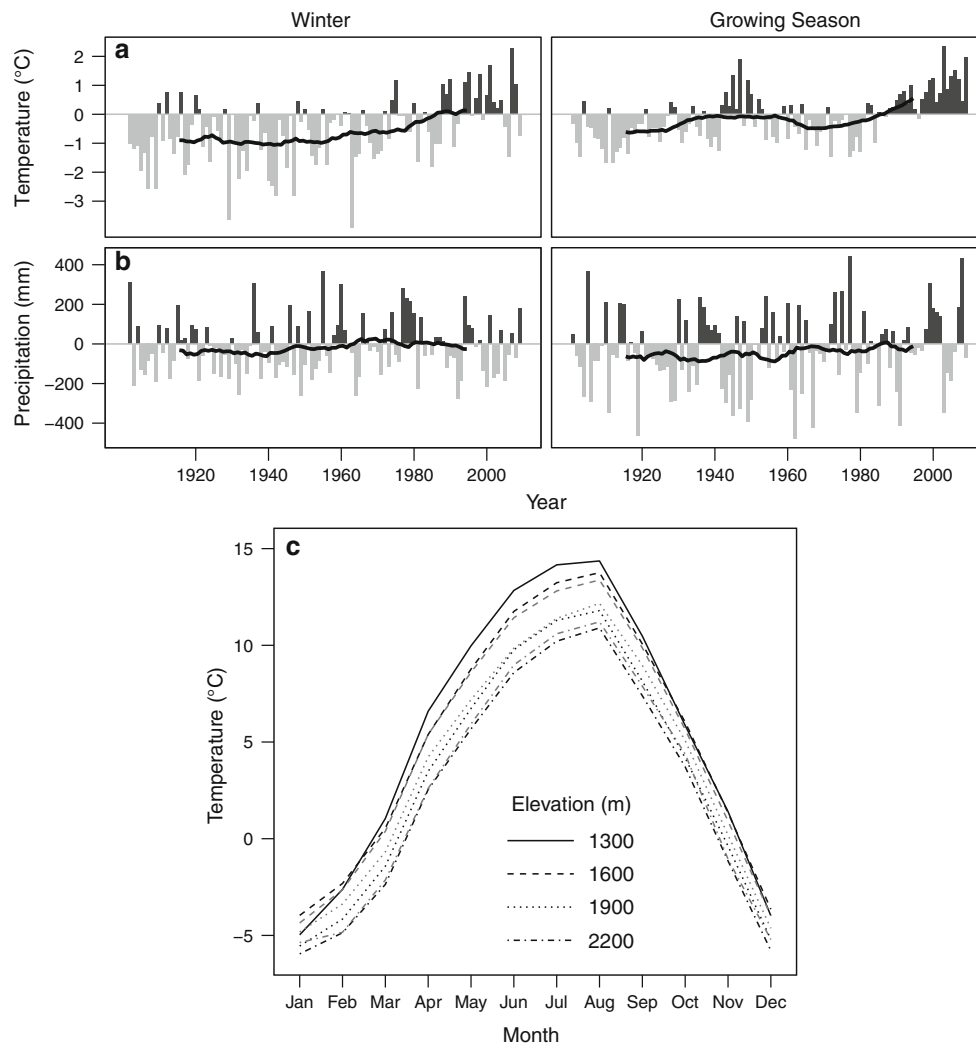


Fig. 2 **a** Temperature and **b** precipitation anomalies for the period 1901–2009 (departure from 1971–2000 average) for winter (December–February) and growing season (April–September). *Light grey* and *dark grey bars* show negative and positive anomalies, respectively.

Black lines 30-year running means. **c** Seasonal course of air site temperatures averaged over the period 2008–2011. Elevations are presented as *different line types* and slope aspects as *different colours* (*black* north aspect, *grey* south aspect)

Climate response along the transect

To better understand the climate (precipitation and temperature) response of each sampling elevation across the transect, we calculated Pearson's correlations over the 1901–2007 period (Fig. 5; Online Resource 4, 5). Several patterns emerged, including a tendency for higher correlations in both species as elevation increased. At all elevations, *Picea* responded positively to precipitation with significant correlation coefficients during both the previous and current summer. The positive precipitation response of *Picea* in the year prior to ring formation increased towards high elevations—a response contrasted with a decrease of sensitivity to current year precipitation. *Larix* tended to show negative correlations to precipitation with the exception of the lower-most elevation where significant positive correlations ($r_{105} = 0.36$,

$P < 0.05$) with precipitation in June were obtained. Conversely, *Larix* response to temperature was generally positive and significant for current summer conditions, the exception being the lowest site, where response to current June temperature was significantly negative ($r_{105} = -0.24$, $P < 0.05$). During the growth year, both single-month and aggregated summer temperature correlations (JJA and AMJJAS) reached a maximum at the highest site on the transect. Although not significant, *Picea* also revealed stronger response to current summer temperatures as elevation increased. Considering the influence of the previous growing season, *Picea* showed an increasingly negative correlation with previous July and August temperatures as elevation increased, whereas *Larix* responded similarly at the lowest site for both previous year temperature and precipitation, but revealed diverging responses with increasing elevation.

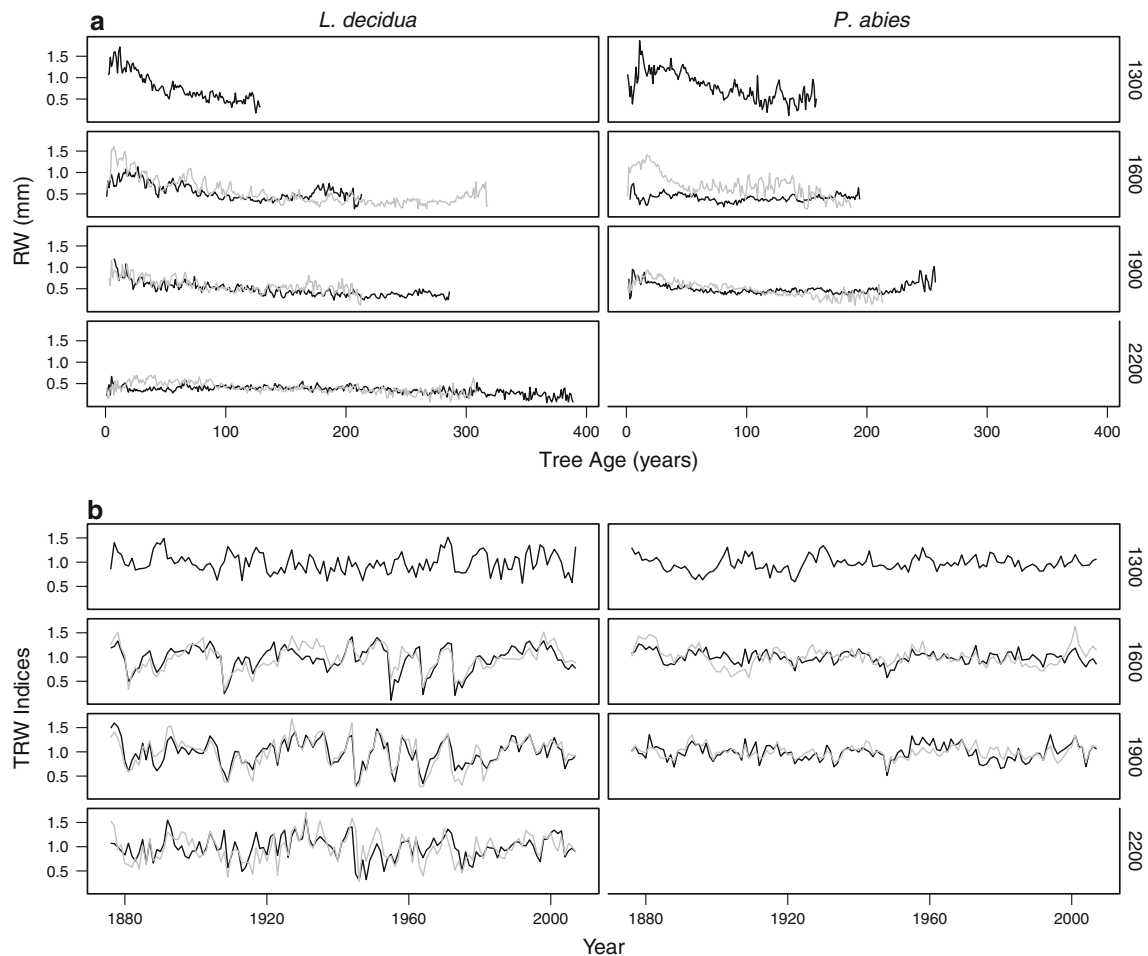


Fig. 3 **a** Site averaged raw tree-ring width (TRW) chronologies over the complete record, aligned by tree age. **b** Site averaged standardised TRW indices (using a 100-year spline) for the complete period of series overlap (1876–2007), truncated at a minimum of five series.

Chronologies are split by species (left panels *L. decidua*, right panels *P. abies*) and elevation, and by slope (black north aspect, grey south aspect)

Climate response comparison to larger site network

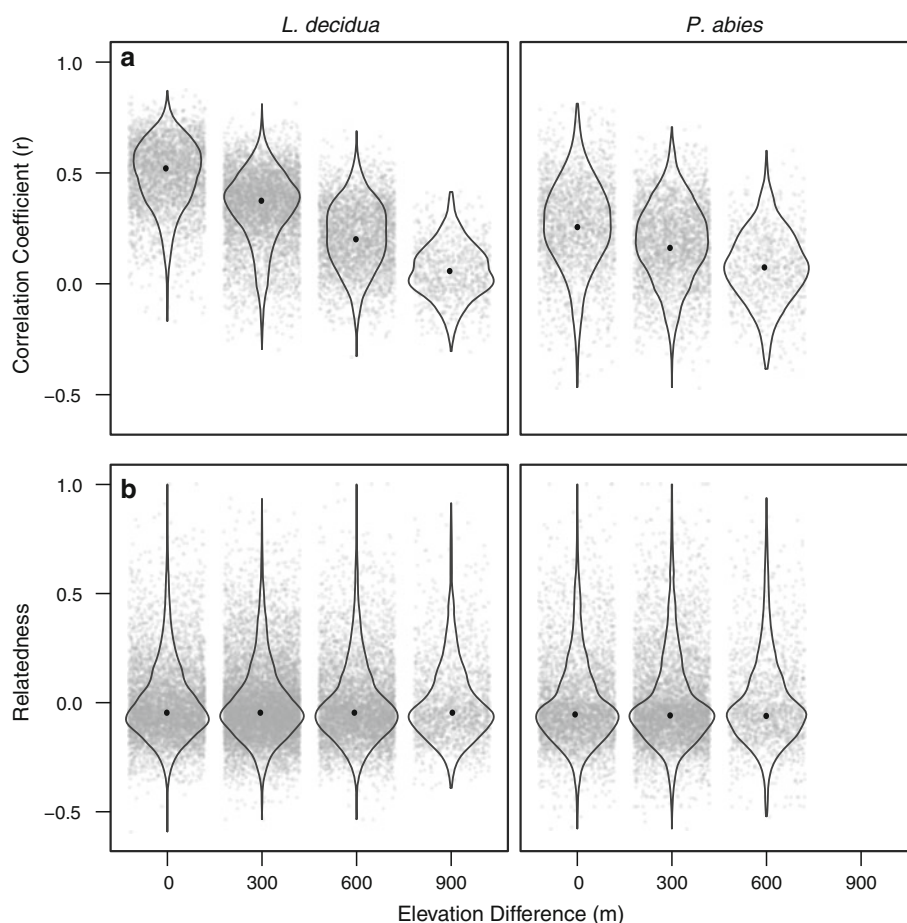
To assess signal similarity across a broader scale, *Picea* and *Larix* temperature response from the Löttschental was compared against a network of TRW chronologies from across the Alps (Fig. 6). Sites located in both the Löttschental and across the Alps revealed increasingly negative correlations with JJA temperatures as mean annual temperature increased. There was good agreement in trend between the Löttschental and Alpine datasets as revealed by similar slopes for both *Larix* (−0.11 and −0.083, respectively) and *Picea* (−0.13 and −0.085). However, comparison of intercepts between the Löttschental and Alpine datasets revealed a much closer agreement for *Larix* (0.43 and 0.44, respectively) than *Picea* (0.31 versus 0.50), demonstrative for the Löttschental *Picea* to have lower JJA temperature correlations for a given mean annual temperature than the regional counterparts.

Discussion

Long-term change in the context of elevation

Annual temperature increases for the study region indicate climate warming consistent with data from the Greater Alpine Region (Auer et al. 2007) and double the global land-surface temperature warming over the past century (IPCC 2007). Based on the extent of growing season temperature differences along the elevational transect in the Löttschental, this long-term climate trend can be translated into an approximate 300 m elevation increase. The temperature gradient is also equivalent to the inter-annual variability of growing season temperature anomalies experienced over the past century. Both of these observations suggest populations in this ecosystem appear capable of tolerating a range of environmental conditions. However, with the increased speed of warming over the

Fig. 4 **a** Pearson correlation of pairwise individual tree standardized TRW series and **b** pairwise genetic relatedness of individual trees across both slopes. Both are plotted as function of difference in elevation across a transect of *L. decidua* and *P. abies*. In all panels, points (jittered with random noise and plotted with a transparency of 20 %) represent single comparisons, *black dots* show the median of the data for each elevation grouping, and *black violin plots* represent the probability density of observations as calculated from a kernel density estimator



past 35 years it is unknown if these populations can continue to keep pace and might instead result in distributional or evolutionary changes (Jump and Peñuelas 2005). Additionally, the temperature differences across the elevational transect (~ 4 °C) also approach the projected temperature increases (~ 5 °C) over the next century for Switzerland (CH2011 2011). The projected 5 °C warming would equate to a more than 900 m elevation increase and demonstrates a link between different elevations and changing climates.

Elevational transects provide a powerful observational study as tree growth can be analysed within the context of experienced long-term variability (Swetnam et al. 1999). In fact, recent results indicate that observational studies provide the best measure of response to climate change as warming experiments appear to underestimate plant response to global climate change (Wolkovich et al. 2012). A proposed explanation is that experiments attempt to isolate temperature effects where observational studies tend to integrate the complex effects of multiple climatic drivers. With the well-described link between altitude and temperature, an elevational transect offers the possibility to separate interrelated climate effects while still making observations on a natural environment (Körner 2007a, b).

Considering the ability to encompass both the historical and predicted future climate, given sufficient gene flow, this transect is a valuable platform for understanding temperature-driven changes over time.

Gene flow across elevational gradients

To fully endorse an elevational gradient as a space-for-time analogue of future climate conditions, it is essential to consider gene flow across the landscape, as significantly different biological responses (e.g. tree growth) may actually only represent the noise of local adaptation based on site conditions. F_{ST} estimates, which represent the historical genetic divergence between populations of a species (Wright 1950), support our hypothesis that tree populations along the transect show no significant genetic differentiation. Additionally, relatedness data reveals high genetic similarity among the sampled trees regardless of the among-population distance (in elevation) between individuals. This evidence suggests that historical gene flow is high, presuming that migration rate is high enough to counteract the selective pressures of local environmental variation (Savolainen et al. 2007). A review of literature considering trees' genetic variation with altitude found a

Table 1 *Larix* and *Picea* populations sampled for analysis in the study

Species	Location	Code	Elevation (m)	Latitude (°N)	Longitude (°E)	N	Mean $H_E \pm SD$	Overall F_{ST}	Proportion F_{ST} ($P < 0.05$)*	
									Lötschental	Outside
<i>Larix decidua</i>	Lötschental ^a	N13	1,300	46.39	7.76	30	0.669 ± 0.199	0.016	0.00	<1.00
		N16	1,600						0.00	<0.67
		N19	1,900						0.00	<0.67
		N22	2,200						0.00	<0.33
		S16	1,600						0.17	<0.33
		S19	1,900						0.00	<0.67
		S22	2,200						0.17	<0.67
	Gampel ^a	N08	800	46.30	7.74	30	0.713 ± 0.088		0.71	
	Aletsch ^b	T	1,900	46.38	8.01	30	0.736 ± 0.071		0.14	
	Zermatt ^c	Z22	2,170	46.00	7.75	30	0.732 ± 0.142		1.00	
<i>Picea abies</i>	Lötschental ^a	N13	1,300	46.39	7.76	30	0.559 ± 0.203	0.013	0.25	<0.50
		N16	1,600						0.00	<0.67
		N19	1,900						0.00	=0.00
		S16	1,600						0.00	<0.50
		S19	1,900						0.00	<0.17
	Schlettere ^d	CH100	1,625	46.43	8.17	16	0.574 ± 0.197		0.10	
	Sillere ^d	CH106	1,900	46.45	7.51	14	0.633 ± 0.229		0.00	
	Findelbach ^d	CH85	1,800	46.01	7.75	16	0.604 ± 0.197		0.10	
	Oeschinensee ^d	CH114	1,580	46.50	7.72	15	0.629 ± 0.154		0.60	
	Val d'Arpette ^e	S1M	1,960	46.03	7.08	30	0.596 ± 0.156		0.40	
	Aletsch ^e	S2H	1,630	46.37	7.99	30	0.557 ± 0.199		0.50	

* Number of occurrences for which population shows significant ($P < 0.05$) genetic differentiation from the other population, related to number of respective comparisons

^a Sample provided by G. King/Swiss Federal Institute for Forest, Snow and Landscape Research (WSL)

^b Sample provided by A. Plüss/Swiss Federal Institute of Technology Zurich (ETHZ)

^c Sample provided by S. Brodbeck/WSL

^d Sample provided by C. Sperisen/WSL

^e Sample provided by F. Gugerli/WSL

lack of genetic differentiation at only about half of the studies considered (Ohsawa and Ide 2008). These conflicting results within the literature indicate the importance of taking gene flow into consideration in any study comparing populations within a landscape.

Possible reasons that both *Larix* and *Picea* populations did not exhibit any significant genetic differentiation in the neutral markers across the elevational gradient in the Lötschental could include their predominant out-crossing breeding system, wind pollination, air-borne seed dispersal, and a long lifespan. Conifers, including both *Larix* and *Picea*, have both male and female reproductive structures on a single tree and attempt to avoid self-pollination by relying on differential maturity of reproductive structures and wind pollination (Williams 2009). The spread of pollen is the major mechanism of gene flow, and studies have

indicated that along steep elevational gradients pollen dispersal can exceed 1,000 m aided by upslope thermal winds and even greater distances downslope due to convection cell circulation (Ebell and Schmidt 1964).

Significant genetic differentiation between pairs of tree populations within and outside of the valley was found; indicating low genetic differentiation is not a regional population characteristic (Table 1). The genetic differentiation we observed is probably the result of both the distance between populations and the presence of physical barriers (e.g. mountain ridges, hanging valleys) that separate the Lötschental from other sampled populations. Our results lead us to conclude that the presence of high amounts of gene flow across the elevational transect are likely to counteract local adaptation and allow us to consider that signals detected in tree growth are more likely a

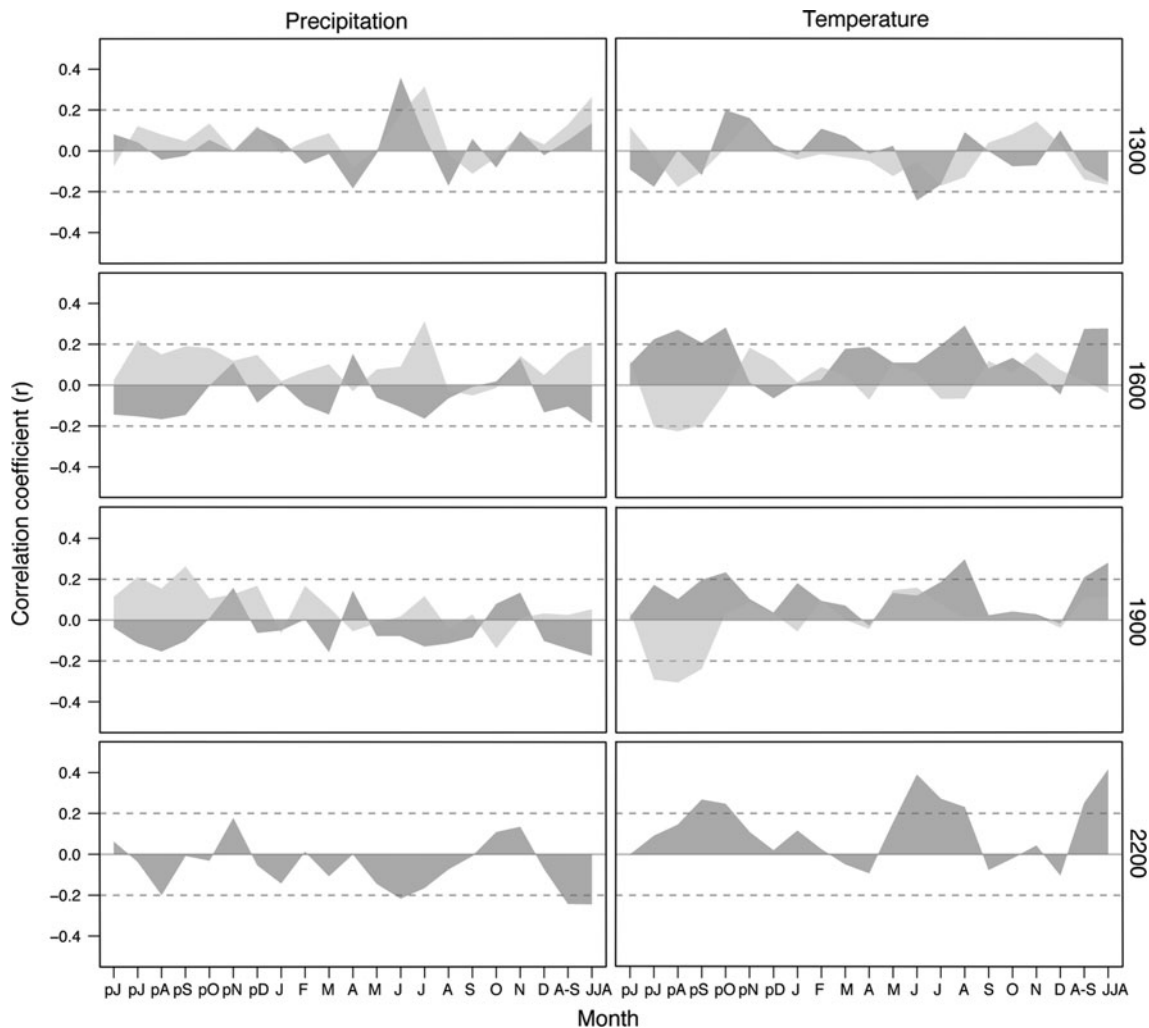


Fig. 5 Pearson correlation between standardized TRW indices averaged by elevation and species (dark grey *L. decidua*, light grey *P. abies*) and gridded climate data for the period 1901–2007. Correlations are for a series of months, from previous June to current

December as well as two seasonal averages [April–September (A–S), and June–August (JJA)]. Dashed lines 95 % confidence limits ($t = 0.02$, $P = 0.05$)

response to climate. However, this is not to say that local adaptation can be completely ruled out. As emphasised by Kawecki and Ebert (2004), only reciprocal transplant experiments covering two generations may substantiate if local adaptation occurs along such an elevation-related climatic gradient at short distance.

Tree growth patterns across elevational gradients

Standardized TRW series from both species revealed synchronous growth between trees growing at the same elevation, regardless of aspect (Fig. 3b). This is juxtaposed with previous dendroclimatology work that has suggested aspect, and in turn the radiation budget, is a primary driver of growth response (Villalba et al. 1994). However, given that air temperatures along the transect show greater similarity between aspect than among elevations (Fig. 2), our

observation of growth similarity is consistent and allows us to combine sites into elevation bands.

Growth differences are greater along the length of the transect, as productivity (TRW) decreases with elevation (Fig. 3a). In the absence of genetic differentiation and the established link between altitude and air temperature, we can interpret greater growth as primarily a temperature-driven response. Results from a previous study of conifer productivity across a longer, but lower elevational transect (700–1,500 m) agree with our observations, finding that trees at $\sim 1,300$ m show the highest growth rates with decreasing values towards the tree-line due to temperature limitations and below 1,000 m because of moisture limitations (Neuwirth et al. 2004; Frank and Esper 2005; Affolter et al. 2010). Additionally, Paulsen et al. (2000) found that *Picea* tree-ring widths from transects within treeline ecotones in the Alps decreased with elevation until

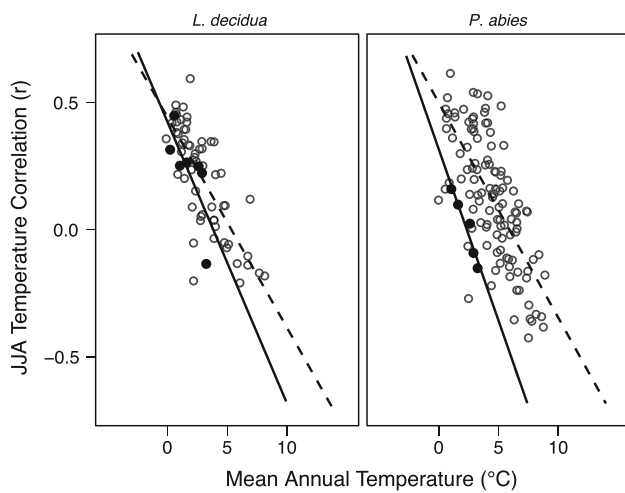


Fig. 6 Pearson correlations for June–August (JJA) temperatures plotted as a function of mean annual temperature for sites across Europe (open circles) and within the Löttschental (filled circles) for both *Larix decidua* and *Picea abies*. Trend lines are a linear model fit to European and Löttschental data (dashed and solid, respectively)

1940, but were similar for the last 60 years. They agree that the primary driver of radial stem growth is temperature, but suggest that inter-annual climate variability and threshold temperatures play an important role.

The tree-ring data reveals a general age increase with elevation that could be linked to human management (Büntgen et al. 2006a), or may provide support for research that has found a link between tree age and initial growth rate (Bigler and Veblen 2009). The data also show periodic, abrupt growth decreases in *Larix* that are not observed in *Picea*, a disturbance signal likely the result of the larch bud moth (*Zeiraphera diniana* Gn.)—a defoliating insect that has shown continuous cyclic outbreaks (approximately every 9 years) over the past 1,200 years (Esper et al. 2007). The presence of cyclic local disturbances within *Larix* populations contributes to a greater mean sensitivity and higher inter-series correlations than *Picea*. However, similar climate responses were observed in high elevation *Picea abies*, *Larix decidua*, and *Pinus cembra* (Frank and Esper 2005) and removal of this biotic signal in maximum latewood density measurements did not significantly increase the climate sensitivity (Büntgen et al. 2006b).

Growth trends and disturbance signals fit within the linear aggregate model of TRW, a conceptual model developed by Cook (1985) to attribute the influence of different processes on ring width at a given time (t):

$$R_t = A_t + C_t + \delta D1_t + \delta D2_t + E_t \quad (1)$$

where R_t is the observed ring width series; A_t is the age-related trend; C_t is the climatic/environmental signal; $\delta D1_t$ and $\delta D2_t$ represent disturbances on a local or stand-wide scale, respectively; and E_t represents any unattributed

variability (an error term). We can hypothesize that expression of the four growth terms is controlled in part by the genotype frequencies of a population. The genotype interacts with the environment to produce an observed TRW and allows us to propose a conceptual modification of the linear aggregate model as:

$$R_t = g_1 A_t + g_2 C_t + g_3 \delta D1_t + g_4 \delta D2_t + E_t \quad (2)$$

where the terms g_1 – g_4 represent the genetic influence on radial growth processes. Model comparisons among populations with high rates of gene flow, which likely counteract local adaptation, suggest that g -terms would be approximately constant. Understanding the g_2 term would be of particular relevance for elucidating the genetic regulation on tree growth response to climatic variability.

Larix and *Picea* show stronger responses to climatic variables with increasing elevation (Fig. 5). In detail, *Larix* TRW reveals a positive response to temperature during both current and previous growing seasons at elevations above 1,300 m a.s.l., although the response is stronger earlier in the current growing season (May–August) and later in the previous growing season (September–October). Comparatively, *Picea* shows a stronger response to current growing season temperatures (June–July) and a more negative response to previous growing season temperatures, although this is likely linked with a positive signal of precipitation in the previous season. These results agree with work published on high-elevation *Larix* and sub-alpine *Picea* chronologies across the Alps (Frank and Esper 2005; Büntgen et al. 2005; Carrer and Urbinati 2006). Significant correlations with climate conditions from the previous growing season are found in both species. The persistence of climatic signals into subsequent years is linked with the accumulation of reserves for the subsequent growing season. *Larix* is a deciduous conifer with a deep root system favouring water uptake, and research has shown that the storage of carbohydrate reserves from one summer is important for wood production in the following year (Kagawa et al. 2006). Conversely, *Picea* has a shallower rooting system but retains needles necessary for photosynthesis for several years, suggesting a greater emphasis on water availability for early-season growth. Support for this conclusion is provided by King et al. (2013), who show that *Picea* appear to be much more sensitive to short-term water stress than *Larix*.

The climatic response of *Larix* at the lowest study site is generally the inverse of the observed response at higher elevations. This response is interpreted as evidence of moisture limitations as a consequence of thermal stress from the higher temperature at the lower elevations. Although *Larix* can be found within the alpine arc at elevations below 1,300 m, indications are that these populations are under intensive drought stress and are not

well-adapted to warmer lower slopes, which may exceed species climatic thresholds (Eilmann and Rigling 2012). As temperatures are projected to continue warming, this may lead to an increase in tree mortality at lower range limits (Allen et al. 2010). These observations support the hypothesis that, although populations are currently established at these sites and have tolerated environmental fluctuations, projected rapid warming may have a distinct influence on future species distribution and, accordingly, community composition.

Lötschental versus Alpine-wide climate responses

To determine if the differences in climatic response observed within the genetically well-mixed Lötschental populations are representative of larger-scale patterns, communities and ecosystems, we compared climate sensitivities in a broader spatial context. Against a *Picea abies* and *Larix decidua* dataset from across the Alps consisting of June, July and August (JJA) temperature response, the data from the Lötschental shows good agreement with climate response as a function of mean annual absolute temperature. *Picea* chronologies from the Lötschental show lower JJA temperature correlation for a given mean annual temperature, but the reasons for this relationship are unclear. Given its East–West orientation and position as an interior valley with climate systems moving from the south-west, it has been recognized that the Lötschental sits in a rain-shadow position. In combination with higher JJA precipitation correlations from the sites in the Lötschental compared to those across the Alps (not shown), lower correlations suggest that the Lötschental trees tend to be more drought stressed than those in the surrounding regions. A greater frequency of significant correlations between *Picea* and precipitation than *Picea* and temperature also support this possibility. The overall response similarity shown by the elevational transect data with high amounts of gene flow and the Alps dataset with greater genetic diversity suggest that the genetic influence on climate response (g_2 term in the conceptual model) is small and that ambient climate conditions are the most important factor in determining TRW variations across the Alps.

Conclusions and opportunities

Our study highlights the value of using elevational gradients to quantify the response of forests under natural conditions. We emphasize the importance of considering genetic differences between study sites and we were able to demonstrate high gene flow and thus presumably low local adaptation within the Lötschental. Similarities in the relationships between climate response and mean climatology

from the genetically well-mixed data in this study with those from the surrounding European Alps implies that the genetic component of the inter-annual growth response is likely small in comparison to climatic influences at the regional scale and possibly beyond. Future investigations of high-resolution wood formation across an elevational transect combined with our comprehension of gene flow and climatic influences on tree growth will enhance our understanding of forest response to continued climatic change. Additional studies linking the range of observed TRW under various environmental conditions and a known genetic framework could provide improved understanding of tree plasticity under projected climatic changes and if thresholds or limits exist for future adaptation.

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Conflict of interest The authors declare that they have no conflict of interest.

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