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Heritable variation in root secondary metabolites is associated with recent climate

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Handling Editor: Nicole van Dam**Abstract**

1. Plants can adapt to changing environments by adjusting the production and maintenance of diverse sets of bioactive secondary metabolites. To date, the impact of climatic conditions relative to other factors such as soil abiotic factors and herbivore pressure on the evolution of plant secondary metabolites is poorly understood, especially for plant roots.
2. We explored associations between root latex secondary metabolites in 63 *Taraxacum officinale* populations across Switzerland and climatic conditions, soil abiotic parameters, root herbivore pressure and cytotype distribution. To assess the contribution of environmental effects, root secondary metabolites were measured in F0 plants in nature and F2 plants under controlled greenhouse conditions.
3. Concentrations of root latex secondary metabolites were most strongly associated with climatic conditions, while current soil abiotic factors or root herbivore pressure did not show a clear association with root latex chemistry. Results were similar for natural and controlled conditions, suggesting heritable variation rather than environmental plasticity as underlying factor.
4. *Synthesis.* We conclude that climatic conditions likely play a major role in the evolution of root secondary metabolites. These results may hint at a novel role of root latex metabolites in tolerance of abiotic stress.

KEYWORDS

climatic conditions, dandelion, environmental gradient, herbivore defence, intraspecific variation, latex, multifunctionality, secondary metabolites

1 | INTRODUCTION

Plants produce a tremendous variety of structurally diverse organic compounds, so-called secondary or specialized metabolites. These metabolites defend plants against herbivores and pathogens (Mithöfer & Boland, 2012), increase abiotic stress tolerance (de Costa, Yendo, Fleck, Gosmann, & Fett-Neto, 2013; Hazarika & Rajam, 2011; Qi, Yang, Yuan, Huang, & Chen, 2015), facilitate mutualisms (Peters, Frost, & Long, 1986; Schäfer et al., 2009; Stevenson, Nicolson,

& Wright, 2017), promote micronutrient uptake (Hu et al., 2018; Kobayashi & Nishizawa, 2012) or act as growth and defence regulators (Francisco et al., 2016; Kim, Ciesielski, Donohoe, Chapple, & Li, 2014; Malinovsky et al., 2017). Although individual secondary metabolites can have highly specialized functions, there is growing evidence that many of them serve multiple purposes (Hu et al., 2018; Katz et al., 2015; Li, Schuman, et al., 2018; Malinovsky et al., 2017; Møller, 2010). Multifunctional secondary metabolites help the plant to minimize the effort required for biosynthesis and compound maintenance and are therefore seen as a cost-effective resource allocation strategy (reviewed in Neilson, Goodger, Woodrow, & Møller, 2013).

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Given the importance of secondary metabolites in adjusting a plant's physiology to its continuously changing environment, abiotic and biotic factors are expected to exert strong selective pressure on plant secondary metabolism (Hartmann, 2007). Hence, metabolite profiles can vary substantially even within the same species. The unique set of secondary compounds produced by a plant population likely reflects the particular demands of the plant's ecological niche and its current selective environment (Moore, Andrew, Külheim, & Foley, 2014). In *Arabidopsis thaliana* populations, for instance, geographic variation in the abundance of *A. thaliana* chemotypes is strongly associated with the geographic pattern in the relative abundance of two specialist herbivores (Züst et al., 2012). Patterns of secondary metabolite profiles across populations have also been directly or indirectly linked to geographical gradients such as latitude or elevation (Abdala-Roberts, Moreira, Rasmann, Parra-Tabla, & Mooney, 2016; Anstett, Ahern, Johnson, & Salminen, 2018; Coll Aráoz, Mercado, Grau, & Catalán, 2016; Moles et al., 2011; Woods et al., 2012). As changes in geographic locations are associated with substantial variation in both biotic and abiotic traits, integrated analyses that take different environmental parameters into account are helpful to identify the environmental factors that shape the evolution and expression of plant secondary metabolites in natural populations.

Intraspecific variation in secondary metabolites can be constitutive (Züst et al., 2012), and can be further amplified by phenotypic plasticity (Huber, Bont, et al., 2016). To partition this natural variation into constitutive, genetically fixed and inducible, plastic components, common garden experiments provide a useful tool by controlling for the contribution of the variation induced by the local environment (Anstett et al., 2018; Hahn, Agrawal, Sussman, & Maron, 2019; Stevens, Brown, Bothwell, & Bryant, 2016). In a common garden study with *Artemisia californica*, for instance, Pratt, Keefover-Ring, Liu, and Mooney (2014) showed that genetically based variation in terpene composition and monoterpene concentration are associated with latitude of the source population and the corresponding differences in precipitation. Furthermore, comparing the production of secondary metabolites under controlled environmental conditions with their production in the plant's natural habitat allows the assessment of environmental plasticity (Abdala-Roberts et al., 2016; Castillo et al., 2013). Thus, studies that measure secondary metabolites among populations in both their natural habitat and in common gardens can help determine to what extent a plant's chemical phenotype is fixed or plastic in response to its environment (Hahn et al., 2019).

Many secondary metabolites are found in both roots and shoots of a plant, yet as a result of the distinct functions of these two plant parts (van Dam, 2009) composition and regulation of metabolites often differ above- and below-ground (Hartmann, 2007; Johnson, Erb, & Hartley, 2016). Changes in abiotic factors result in different morphological and physiological responses in roots compared to shoots, with different metabolic patterns that seem to allow complementary adjustments above- and below-ground through phenotypic plasticity (Gargallo-Garriga et al., 2015; Mithöfer & Boland, 2012; Rasmann & Agrawal, 2008). Above-ground, climatic conditions of natural habitats have been shown to shape heritable intraspecific variation in secondary

metabolites by affecting both the biotic (Hahn et al., 2019) and abiotic (Pratt et al., 2014) environment, indicating that climate can select for specific chemotypes. Below-ground, climatic conditions likely influence heritable variation in secondary metabolites as well, but experimental evidence for such effects is lacking so far. Furthermore, soil physical and chemical properties such as humus content or pH may affect plant physiology by determining the amount and composition of available nutrients (Dubuis et al., 2013), which in turn can result in differences in plant chemistry (Cunningham, Summerhayes, & Westoby, 1999; Meindl, Bain, & Ashman, 2013). In addition to abiotic factors, biotic factors such as herbivores have been identified to drive intraspecific variation in defensive secondary metabolites in the leaves (Agrawal, 2011; Schuman & Baldwin, 2016; Züst et al., 2012) and recently also in the roots (Huber, Bont, et al., 2016). Climatic and resource gradients therefore shape the intraspecific variation in plant defence above- and below-ground likely through an interplay of changing abiotic and biotic factors along the gradients, including variations in nutrient availability and herbivore community composition (Hahn & Maron, 2016; Moreira, Petry, Mooney, Rasmann, & Abdala-Roberts, 2018). Although the effects of specific environmental factors on plant secondary metabolites have been studied extensively, the simultaneous and combined effects of abiotic and biotic factors including climatic conditions, soil geochemical properties and herbivores on heritable variation in plant secondary metabolites remain poorly understood, especially below-ground.

In this study, we investigated the role of abiotic and biotic factors in shaping variation in root secondary metabolites of the globally distributed common dandelion, *Taraxacum officinale* agg. (Asteraceae), as a model system. Dandelion is described as a species complex that consists of diploid outcrossing, triploid apomictic and, in rare cases, tetraploid individuals (Verduijn, van Dijk, & van Damme, 2004a, 2004b). Because of these different reproduction systems, the cytotype distribution within a dandelion population can affect trait heritability. Dandelion accumulates toxic secondary metabolites primarily in latex, a milky, often sticky sap that is transported and stored in pressurized laticifers, to be released upon damage by herbivores. Laticifers allow for compartmentalized storage and deployment of toxic compounds while also preventing autotoxicity by the often highly reactive substances (Hagel, Yeung, & Facchini, 2008). Latex can be found in approximately 10% of all flowering plant species and contains a rich variety of secondary metabolites (Agrawal & Konno, 2009; Castelblanque et al., 2017). Based on its physical and chemical properties, latex has been associated with defensive functions against herbivores and pathogens, and no other functions are currently known (Konno, 2011).

Our previous work revealed that latex of *T. officinale* contains three major classes of secondary metabolites: the sesquiterpene lactone taraxinic acid β -D-glucopyranosyl ester (TA-G), hydroxyphenylacetate inositol esters with either two or three side chains (di-PIEs respectively tri-PIEs) and several triterpene acetates (TritAc; Huber et al., 2015). Both TA-G and PIEs are involved in defence against herbivores and are highly variable among natural populations (Agrawal, Hastings, Fines, Bogdanowicz, & Huber, 2018; Bont et al., 2017; Huber, Bont, et al., 2016; Huber, Epping, et al., 2016), and we have found evidence that the concentration of TA-G is shaped by selection

from the major native root herbivore *Melolontha melolontha* (Huber, Bont, et al., 2016). However, both abiotic and biotic environmental factors can influence the quantity of latex exudation (Barton, 2014; Raj, Das, Pothen, & Dey, 2005; Woods et al., 2012) and the relative composition of the diverse latex secondary metabolite mixtures may be likewise affected by environmental conditions, although experimental evidence for this assumption is scarce.

Here, we investigated environmental drivers of intraspecific variation in root latex secondary metabolites of *T. officinale*. Focusing on the main secondary metabolites of *T. officinale* latex, we determined metabolite profiles of 63 populations growing in their natural habitat and of their offspring grown under controlled conditions in the greenhouse. We recorded and inferred current and historic root herbivore abundance as well as soil geochemical parameters in the natural habitats of the different populations. We determined the cytotype distribution of each population and estimated vegetative growth of the plants. We furthermore retrieved climatic conditions of the different habitats over the last 20 years and performed model selection to determine which environmental variables are most strongly associated with naturally expressed and heritable variation in root secondary metabolites. A previous version of this work has been placed on a preprint server (Bont, Züst, Huber, & Erb, 2020).

2 | MATERIALS AND METHODS

2.1 | Study species

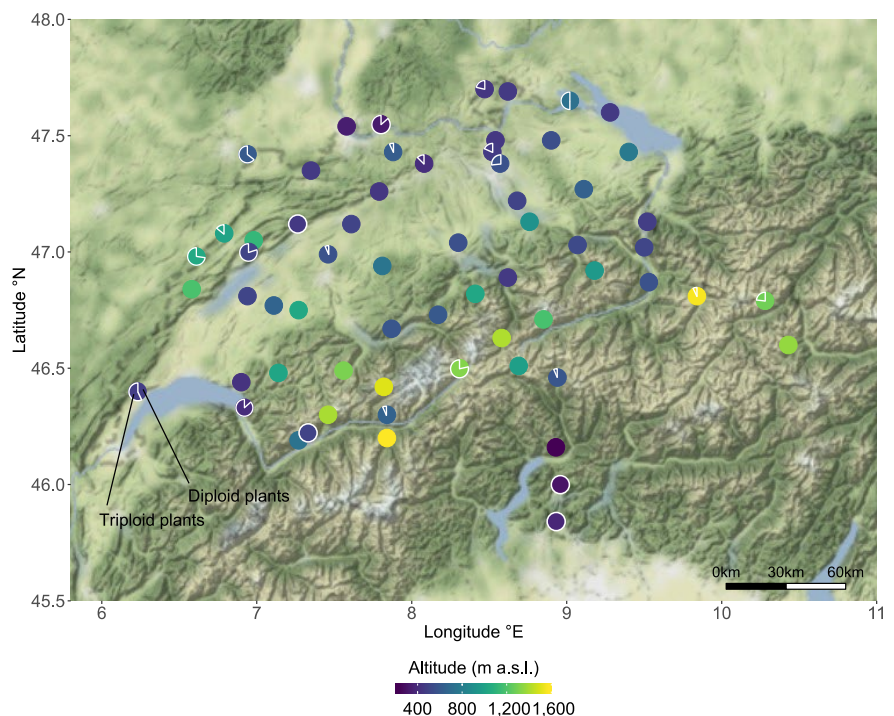
The common dandelion, *T. officinale*, is a latex-producing perennial herb native to Eurasia (Stewart-Wade, Neumann, Collins, & Boland, 2002). In Switzerland, *T. officinale* most commonly colonizes low- and

mid-elevation habitats, but can also be found at altitudes higher than 2,000 m a.s.l. (Calame & Felber, 2000). The main peak flowering time of *T. officinale* in the northern hemisphere is from April to June, with plants growing in warmer habitats at lower altitude flowering earlier than plants growing in colder habitats. Approximately 10–12 days after flowering, seed maturation is completed and each capitulum produces several hundred seeds equipped with a parachute-like structure to facilitate wind dispersal (Honek & Martinkova, 2005). Using a simulation model for wind dispersal, Tackenberg, Poschlod, and Kahmen, (2003) calculated that more than 99.5% of released dandelion seeds land within 10-m distance, whereas 0.014% had the potential to be dispersed >1 km. Pollination, in contrast, occurs mainly within a range of a few metres (Lázaro & Totland, 2010; Takakura, Matsumoto, Nishida, & Nishida, 2011). Thus, although occasional long-distance seed dispersal events occur, gene flow between distant populations is likely restricted due to limitations in dispersal distances of pollen and seeds.

2.2 | Field sites and environmental data

From April to June 2016, we identified and characterized 63 *T. officinale* populations across Switzerland in situ. Populations were selected based on proximity to meteorological monitoring stations of MeteoSwiss, the Swiss Federal Office for Meteorology and Climatology, with all field sites being located within a maximal distance of 1 km from a station. Based on this criterion we evenly distributed the sampling sites across Switzerland, with altitudes of populations ranging from 200 to 1,600 m a.s.l. (Figure 1; Table S1). Each population was visited once towards the end of its flowering period. On each field site, we marked a square of 25 m² in a representative area of the field and haphazardly selected 15 *T. officinale*

FIGURE 1 *Taraxacum officinale* sampling locations across Switzerland. Each circle displays one of the 63 sampled populations. Colour gradient of the circle fill represents the altitude of the populations. The proportion of the circle that is outlined in white colour corresponds to the percentage of triploid plants of the respective population, whereas the unmarked part of the circle corresponds to the percentage of diploids



plants within this square for latex and seed collection. As a measure for cytotype distribution within the populations, the percentage of diploid plants was calculated (see below). Where available, information on land use intensity over the last decades was obtained from landowners. To characterize long-term climatic conditions, 10 variables were selected from the MeteoSwiss database (Table 1). The chosen variables represent temperature, precipitation, light and air pressure conditions of the populations, which are important abiotic factors affecting plant physiology and production of secondary metabolites (Wallis, Huber, & Lewis, 2011; Zhou et al., 2017; Zidorn, 2010). Data were obtained for the years 1996–2015 and averaged over this period for each population. Note that for four of the 63 populations, not all of the variables were available from the monitoring stations.

For soil analysis, soil samples were taken from each field site. We used a 'Swiss Sampler' (Eric Schweizer AG) to take 15 soil samples of the top 15–20 cm soil layer along one diagonal of the 25-m² square. Soil samples were then pooled and stored at 4°C after returning to the laboratory. Each pooled sample was then analysed for PEP (proof of ecological performance; performed by Labor für Boden- und Umweltanalytik, Eric Schweizer AG). From these data we selected humus content and soil pH for further analyses because both are important determinants of the amount and composition of available nutrients for plants and thus influence plant physiology (Dubuis et al., 2013).

To assess the abundance of below-ground herbivores, we used the following two approaches: first, three of the 15 selected dandelion plants were excavated in the field, and the number of below-ground herbivores in the rhizosphere and surrounding soil core (approximately 15 × 15 × 15 cm) was counted and averaged

per plant. Second, we categorized the field sites belonging to either an area with historically high density of *M. melolontha* or an area with no or only low density of *M. melolontha* over the last decades (Huber, Bont, et al., 2016). The larvae of *M. melolontha* are one of the major native root herbivores of *T. officinale* and can severely impair the plant (Haus & Schütte, 1976; Huber, Bont, et al., 2016). Due to the low mobility of larvae and habitat fidelity of adults, local populations of *M. melolontha* remain stable over long periods of time, and in a previous study we found that past *M. melolontha* abundance is a good predictor of present *M. melolontha* pressure (Huber, Bont, et al., 2016). Note that past *M. melolontha* abundance reflects solely herbivore pressure by the larvae of *M. melolontha*, while counting the number of below-ground herbivores per plant also includes root-feeding larvae of other species such as wireworms.

2.3 | Generation of F2 plants

To investigate heritable variation in latex secondary metabolites at the population level, we grew plants from field-collected seeds in a greenhouse for two generations. F2 plants were obtained by controlled hand-pollination between F1 plants of the same population. Initially, we collected one seed head from each of the 15 selected F0 mother plants per field site during the field visits. In August 2016, F1 seeds were germinated in a greenhouse (22°C day/18°C night; 16 hr light/8 hr darkness) by sowing 10–15 seeds per collected seed head into a small pot (5.5 cm diameter) filled with moist seedling substrate. After 3 weeks, three seedlings of each mother plant were transplanted together as a seed family into one bigger pot (13 × 13 × 13 cm) filled with potting soil (five parts field soil, four parts peat and one part sand). As not all seeds germinated, we obtained between 6 and 15 seed families per population, with a total of 931 pots. One week after transplantation, pots were put outside for growth and natural vernalization during fall of 2016. In November 2016, pots were transported into a semi-controlled greenhouse (temperature between 15 and 25°C, 16 hr light and 8 hr darkness), where flower production started after 1–2 months. Across all populations at least one plant per population produced flowers; however, number of flowering plants varied between populations. To avoid cross-pollination between populations, flower buds were covered with a tea bag before flower opening. Whenever flowers of two plants from different seed families within the same population were open concurrently, tea bags of those flowers were removed, flowers were carefully rubbed against each other for pollination and then covered again with tea bags until seed collection. As triploid plants reproduce clonally, pollination is only necessary for the obligate outcrossing diploids. However, at the time of pollination, ploidy level of F1 plants was unknown; thus, hand-pollination was done for all plants. After collection, seeds were stored at 4°C.

To grow F2 plants for latex analysis, we included all populations for which we could collect seeds from three to six different F1 plants per population. We excluded eight of the 63 populations for having fewer than three seed-producing F1 plants. Ploidy level analysis of

TABLE 1 Correlations of climatic variables with the first two principal components (climPCA1, climPCA2) from a principal component analysis of the climatic conditions of the sampled *Taraxacum officinale* populations

Climate variable	Description	climPCA1	climPCA2
AIR	Annual mean of air pressure	0.413	-0.113
PRE	Annual precipitation	-0.026	-0.356
PRED	Days per year with precipitation	-0.145	-0.503
RAD	Annual mean of global radiation	-0.175	0.546
SUN	Annual sunshine duration	0.114	0.500
TM	Annual mean temperature	0.435	-0.008
TMN	Annual mean of the minimal temperature per day	0.342	-0.125
TMX	Annual mean of the maximal temperature per day	0.375	0.107
T0D	Days per year with minimal temperature below 0°C	-0.401	0.112
T25D	Days per year with maximal temperature over 25°C	0.396	0.138

F1 plants (see below) revealed that populations with mixtures of diploid and triploid cytotypes were frequent (Figure 1). F1 parent plants were selected according to their ploidy level to represent the ratio of diploid and triploid plants of each population. Rarely occurring tetraploid plants were excluded. For populations with more than 75% diploid plants, all parent plants for the F2 seeds were chosen to be diploid. For populations with 50%–75% diploid plants, two third of diploid plants and one third of triploid plants were chosen as parent plants. For populations with 25%–50% diploid plants, one third of diploid plants and two third of triploid plants were chosen as parent plants. For population with <25% diploid plants, all parent plants were chosen to be triploid. Seeds were germinated in a greenhouse (22°C day/18°C night; 16 hr light/8 hr darkness) on moist seedling substrate. After 3 weeks, one seedling per parent was transplanted into a pot (9 cm × 9 cm × 9 cm) filled with garden soil (Selmaterra, Eric Schweizer AG), resulting in a total of 256 pots. Pots were kept in the greenhouse in a randomized fashion until latex collection.

In order to investigate whether environmental factors are associated with changes in vegetative growth potential, and whether vegetative growth potential is correlated with latex chemistry across populations, additional F2 plants were grown from the same parent plants as described above. Three weeks after germination, the seedlings were transplanted individually into pots (13 cm × 13 cm × 13 cm) filled with garden soil (Selmaterra, Eric Schweizer AG). After three more weeks, in mid-June, the pots were moved from the greenhouse to outdoor experimental beds due to insufficient space in the greenhouse. Three months after germination, the length of the longest leaf was measured for each plant. This parameter is a strong predictor of root and leaf dry mass across different dandelion populations (Huber, Epping, et al., 2016) and can therefore be used as a proxy for vegetative growth.

2.4 | Ploidy level

To estimate the percentage of diploid, triploid and tetraploid plants per population, DNA ploidy level of F1 plants was determined by flow cytometry. A CyFlow Cube (Sysmex Partec GmbH) with a Partec CyStain UV precise P kit (ref. 05-5002) was used following the manufacturer's instructions. Ploidy level was determined using fresh tissue from one leaf per plant per pot. As external standard, leaf tissue of *T. officinale* plants with known ploidy level (diploid or triploid) was used. Ploidy levels of F1 plants were estimated by comparing the sample peak to the standard peak. Approximately 1,500 nuclei were measured per sample. The percentage of diploids determined in F1 plants was then used as measure for the cytotype distribution within each population.

2.5 | Latex collection and chemical analysis

Latex from F0 plants was collected in each field site from the 15 plants that were selected for seed collection. Latex from F2 plants

was collected in the greenhouse when plants were 3 months old. To obtain taproot latex, each plant was cut 0.5 cm below the tiller and 2 µl of the exuding latex was pipetted immediately into 200 µl methanol. After returning to the laboratory, latex samples were stored at -20°C until processing. For extraction of latex secondary metabolites, tubes were vortexed for 10 min, ultrasonicated for 10 min, centrifuged at 4°C and 17,000 g for 20 min and supernatants were stored at -20°C. For F0 plants, pooled samples per population were made for chemical analysis by mixing 10 µl of methanol extract from each of the 15 plants per population in an Eppendorf tube. For F2 plants, methanol extracts from individual samples were used for chemical analysis and average concentrations per population were calculated afterwards. Relative concentrations of TA-G, di-PIEs and tri-PIEs were determined as described in Bont et al. (2017). In brief, methanol extracts were injected into an Acquity UPLC-PDA-MS (Waters) with electrospray ionization in positive mode, consisting of an ultra-performance liquid chromatograph (UPLC) coupled to a photodiode array detector (PDA) and a single quadrupole mass detector (QDa). For quantification, peak areas were integrated at 245 nm for TA-G and at 275 nm for di- and tri-PIEs, while concurrently recorded characteristic mass features were used to confirm compound identities.

2.6 | Statistical analysis

To disentangle heritable variation in latex secondary metabolites and variation due to environmental plasticity, we performed linear regression analyses within each class of secondary metabolites to investigate how the chemistry of F2 plants is related to the chemistry of F0 plants. Tri-PIEs were log-transformed prior to regression analysis to improve data distribution. If, within a class of secondary metabolites, the linear regression between F2 plants and F0 plants was statistically significant, we used the slope of this regression as an approximate estimate for narrow-sense heritability at the population level (pseudo- h^2 ; Falconer, 1981). We also compared the patterns of covariation among latex metabolites by testing for correlations between the three metabolite classes within F0 plants and within F2 plants separately. The robustness of the regressions and correlations was tested by excluding one population with a very high concentration of tri-PIEs and another population with a very low TA-G content.

To explore the effect of abiotic and biotic factors on the latex profile of *T. officinale*, we characterized the environmental conditions of the 63 populations using climate, soil, herbivory and cytotype variables and tested for their impact on latex secondary metabolites in a set of linear models across all populations. For soil and herbivory measures, we included two variables each, whereas for characterizing the cytotype distribution, we used the percentage of diploid plants per population. The climatic data consisted of 10 meteorological variables, some of which were strongly correlated (Table 1). Therefore, we first applied a principal component analysis (PCA) on the 10 selected meteorological variables to reduce dimensionality. We scaled the variables and used the function 'prcomp'

in R to extract the values of the first (climPCA1) and the second (climPCA2) axes. Both axes together explained 76% of the variation in the original climate data and were then used to represent the climatic conditions of each population. climPCA1 explained 52.6% of the total variation in climatic variables, and climPCA2 explained a further 23.4% of the total variation (Figure S4a). Loading scores indicated that climPCA1 was primarily determined by variation in annual temperature (Table 1; Figure S4a), while climPCA2 was determined by sunshine intensity and was inversely correlated with precipitation (Table 1; Figure S4a). In order to analyse whether the climatic conditions are linked with the geographical location of the populations, we tested for correlations between the climatic PCA axes and altitude, latitude and longitude of the populations. The analysis revealed that climPCA1 was highly correlated with altitude (Pearson's $r = -0.95$, $p \leq 0.001$, Figure S4b), whereas climPCA2 was correlated with latitude (Pearson's $r = -0.53$, $p \leq 0.001$, Figure S4b). Neither climPCA1 nor climPCA2 was correlated with longitude (Pearson's $r = 0.01$, $p = 0.96$ respectively Pearson's $r = -0.14$, $p = 0.28$). Further, we tested for correlations among the variables that represent climatic conditions, soil geochemical properties, root herbivore abundance and cytotype distribution. No correlations were found among the climate, soil and herbivory parameters (Table S2). The percentage of diploid plants per population was negatively correlated with climPCA2 (Pearson's $r = -0.36$, $p = 0.006$, Table S2) and soil pH (Pearson's $r = -0.37$, $p \leq 0.003$, Table S2), and positively correlated with the humus content of the soil (Pearson's $r = 0.30$, $p \leq 0.018$, Table S2).

For linear model analysis, we used the function 'lm' to fit models for each *T. officinale* generation (F0 and F2) and each latex secondary metabolite class (TA-G, di-PIEs, tri-PIEs) separately. The response variable was the population mean of the respective secondary metabolite class, and climPCA1, climPCA2, humus content, soil pH, *M. melolontha* area (yes/no), number of below-ground herbivores per plant and percentage of diploid plants of each population were used as explanatory variables. Interaction terms were not included in the models, as this would have exceeded the appropriate number of model parameters compared to the number of included populations in the analysis. If necessary, response variables were log-transformed to improve distribution of variance. Models were validated using 'plotresid' from the package RVAIDEMEMOIRE (Hervé, 2018). Significances of the effects of the explanatory variables were assessed by *F*-tests using the function 'ANOVA' from the package CAR (Fox & Weisberg, 2011). The robustness of the effects of the environmental variables on the latex secondary metabolites was tested by excluding one population with a very high concentration of tri-PIEs and another population with a very low TA-G content. To facilitate the visualization of significant model effects, we additionally performed separate linear regressions between each significant explanatory variable and the corresponding response variable. Similar results were obtained with models for values of individual plants, which included population as random factor in a mixed-effects model framework using the package LME4 (Bates, Maechler, Bolker, & Walker, 2015), compared to linear models for mean values per population.

To investigate the effect of environmental factors on vegetative growth, a linear model was built with the mean maximal leaf length per population as response variable and all environmental factors including the percentage of diploid plants per population as explanatory variables. The model was validated and significance of effects was tested as described above. For significant variables, a regression analysis was performed to visualize the effects. To investigate if vegetative growth influences latex chemistry, multiple linear regression analyses were performed between maximal leaf length and each class of secondary metabolites for both *T. officinale* generations (F0 and F2).

A map of all populations was created with GGMAP (Kahle & Wickham, 2013), VIRIDIS (Garnier, 2018) and GGSN (Baquero, 2017). Results were visualized using GGLOT2 (Wickham, 2016) and FACTOEXTRA (Kassambara & Mundt, 2017). All statistical analyses were performed in R 3.4.0 (R Core Team, 2017).

3 | RESULTS

3.1 | Latex metabolite production varies greatly across populations

Both in natural habitats (F0 plants) and under greenhouse conditions (F2 plants), the production of latex secondary metabolites varied greatly across *T. officinale* populations (Figures S1–S3). In the field, TA-G differed almost 19-fold (Figure S1a), di-PIEs more than sevenfold (Figure S2a) and tri-PIEs more than 200-fold (Figure S2c) among populations. Under greenhouse conditions, mean concentrations of latex secondary metabolites were increased but varied less among populations. Nonetheless, average concentrations of TA-G still differed almost threefold (Figure S1b; average calculated without one population that produced almost no TA-G), di-PIEs more than threefold (Figure S2b) and tri-PIEs more than 150-fold (Figure S3b) among populations. The mean production of latex metabolites by F2 plants was partially predicted by mean concentrations in F0 plants for TA-G ($R^2 = 0.12$, $F_{1,52} = 6.07$, $p = 0.01$, Figure 2a) and tri-PIEs ($R^2 = 0.45$, $F_{1,52} = 41.78$, $p < 0.001$, Figure 2c). After excluding the population with very low TA-G concentration (Figure 2a), the relationship for TA-G was still marginally significant ($R^2 = 0.06$, $F_{1,51} = 3.27$, $p = 0.08$). This suggests that heritable genetic variation contributed to the variation in these secondary metabolites, with estimated narrow-sense heritabilities (slope \pm SE) at the population level of 0.39 ± 0.15 for TA-G and 0.77 ± 0.12 for tri-PIEs. For di-PIEs, no statistically significant influence of the production of plants growing in natural habitats (F0) on the production of plants growing under greenhouse conditions (F2) was found (Figure 2b).

3.2 | Environmental plasticity contributes to variation in latex secondary metabolites

In order to examine covariation of latex metabolite concentrations and to assess the additional component of environmental plasticity

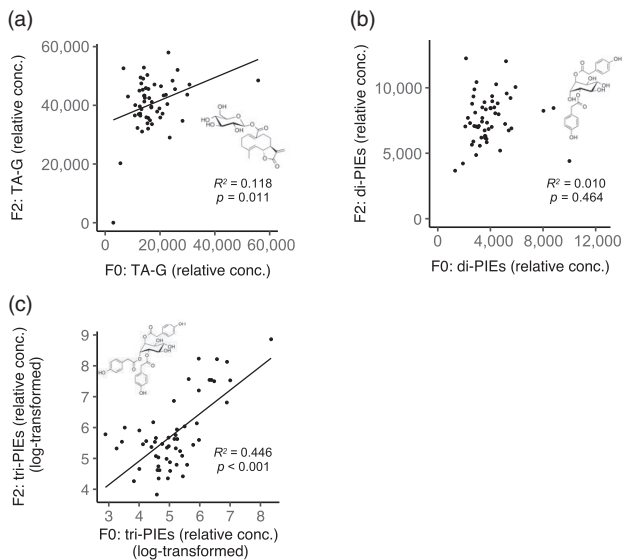


FIGURE 2 Relationship between the latex chemistry of the plants growing in natural habitat (F0) and the plants growing in greenhouse conditions (F2). Regression analyses were performed separately for TA-G (a), di-PIEs (b) and tri-PIEs (c). Each dot represents one *Taraxacum officinale* population ($N = 54$). R^2 - and p -values are displayed and, for statistically significant regressions ($p < 0.05$), linear regression lines are shown. TA-G, taraxinic acid β -D-glucopyranosyl ester; di-PIEs, di-4-hydroxyphenylacetate inositol esters; tri-PIEs, tri-4-hydroxyphenylacetate inositol esters

besides heritable variation in the latex profiles, we tested for pairwise correlations among the three classes of secondary metabolites for plants growing in natural habitat (F0) and plants growing in the greenhouse (F2). The analysis revealed that for F0 plants, TA-G, di-PIEs and tri-PIEs were significantly positively correlated with each other (TA-G and di-PIEs: Pearson's $r = 0.76$, $p < 0.001$; TA-G and tri-PIEs: Pearson's $r = 0.54$, $p < 0.001$; di-PIEs and tri-PIEs: Pearson's $r = 0.36$, $p = 0.004$; Figure 3a). Both between TA-G and di-PIEs and between TA-G and tri-PIEs, the correlations were robust to the removal of the one population with very high concentrations of TA-G and tri-PIEs (Pearson's $r = 0.66$, $p < 0.001$ respectively Pearson's $r = 0.39$, $p = 0.002$), while the correlation between di-PIEs and tri-PIEs was no longer significant (Pearson's $r = 0.19$, $p = 0.130$). In contrast, only TA-G and di-PIEs were positively correlated for F2 plants (Pearson's $r = 0.38$, $p = 0.004$, Figure 3b), while TA-G and tri-PIEs were not significantly correlated (Pearson's $r = 0.03$, $p = 0.845$, Figure 3b) and di-PIEs and tri-PIEs were negatively correlated (Pearson's $r = -0.30$, $p = 0.030$, Figure 3b). The correlation between TA-G and di-PIEs was robust to the removal of the one population with very low TA-G content (Pearson's $r = 0.41$, $p = 0.003$), and there was no change in the relationships between TA-G and tri-PIEs (Pearson's $r = 0.10$, $p = 0.456$) and di-PIEs and tri-PIEs (Pearson's $r = -0.28$, $p = 0.040$). This finding indicates that the regulation of latex secondary metabolites is plastic in response to the environment and not solely determined by genetic, heritable variation.

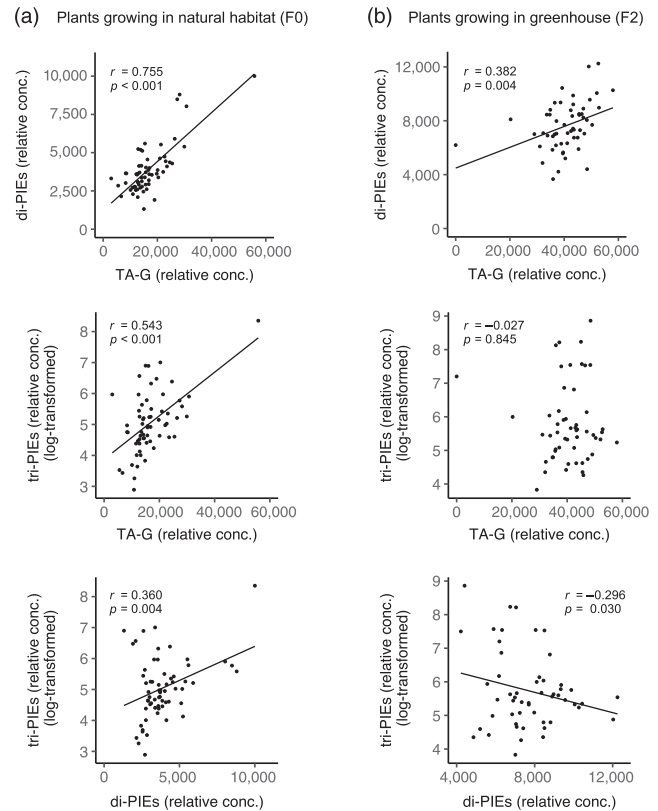


FIGURE 3 Covariation of the three analysed classes of latex secondary metabolites for plants growing in natural habitat (a) and plants growing in greenhouse (b). Each dot represents one *Taraxacum officinale* population ($N = 63$ for F0 and $N = 54$ for F2). Pearson's r and corresponding p -values are displayed. For statistically significant correlations ($p < 0.05$), estimated linear relationships are visualized with solid lines. TA-G: taraxinic acid β -D-glucopyranosyl ester; di-PIEs: di-4-hydroxyphenylacetate inositol esters; tri-PIEs: tri-4-hydroxyphenylacetate inositol esters

3.3 | Heritable variation of latex profile is associated with climate and cytotype distribution

Using a set of linear models, we tested for shaping effects of climatic, soil, herbivory and cytotype parameters of the different populations on the concentrations of latex secondary metabolites across all populations in both plants growing in natural habitat (F0) and plants growing in the greenhouse (F2). We found similar patterns for both generations of plants, which confirms a high degree of heritable variation in latex profiles (Table 2; Figure 4). The linear model analyses further revealed distinct effects of the environmental variables depending on the class of secondary metabolite (Table 2). The concentration of TA-G was negatively associated with climPCA2 alone (LM, $F_{1,49} = 7.63$, $p = 0.008$, Figure 4a for F0 and $F_{1,40} = 8.27$, $p = 0.006$, Figure 4b for F2, Table 2). As climPCA2 was positively correlated with annual sun intensity and negatively correlated with latitude (Table 1; Figure S4b), this suggests that populations from the North of Switzerland produced more TA-G than populations from the sun-intense regions in the South of Switzerland (Figure 4). Interestingly, di-PIEs were not affected by climPCA2, but negatively associated with climPCA1 (LM, $F_{1,49} = 4.46$,

TABLE 2 Summary of results from multiple linear model analyses that relate latex secondary metabolite concentrations to variables representing the environmental conditions of the investigated *Taraxacum officinale* populations. Models have been established separately for population means of each class of secondary metabolite as response variable and separately for each *T. officinale* generation. All environmental parameters (climPCA1, climPCA2, humus, pH, *Melolontha melolontha* area, below-ground herbivores, % diploids) were included as explanatory variables without interaction terms. Significances of the effects of the explanatory variables were assessed by *F*-tests. *F*-values are displayed as numbers, whereas plus and minus signs refer to the effect direction of each variable. Statistically significant effects with $p < 0.05$ (** $p < 0.001$; * $p < 0.01$; $p < 0.05$) are displayed with bold numbers and highlighted with colour patterns

Explanatory variable	F-value _{NumDF, DenDF}			T. officinale generation			
	TA-G	di-PIEs	tri-PIEs				
Climate							
climPCA1	0.18 _{1,49}	(+)	4.46_{1,49}^{*,a}	(-)	1.80 _{1,49} ^a	(+)	F0
	1.60 _{1,40}	(-)	8.13_{1,40}^{**}	(-)	1.51 _{1,40} ^a	(+)	F2
climPCA2	7.63_{1,49}^{**}	(-)	0.02 _{1,49} ^a	(-)	0.01 _{1,49} ^a	(+)	F0
	8.27_{1,40}^{**}	(-)	0.00 _{1,40}	(-)	0.31 _{1,40} ^a	(+)	F2
Soil							
Humus	0.44 _{1,49}	(-)	2.47 _{1,49} ^a	(-)	1.51 _{1,49} ^a	(-)	F0
	0.01 _{1,40}	(-)	0.08 _{1,40}	(+)	0.06 _{1,40} ^a	(-)	F2
pH	0.02 _{1,49}	(-)	0.09 _{1,49} ^a	(-)	0.62 _{1,49} ^a	(-)	F0
	0.36 _{1,40}	(+)	0.95 _{1,40}	(+)	0.06 _{1,40} ^a	(-)	F2
Herbivores							
<i>M. melolontha</i> area	0.33 _{1,49}	(-)	0.11 _{1,49} ^a	(+)	0.03 _{1,49} ^a	(-)	F0
	0.07 _{1,40}	(+)	1.07 _{1,40}	(-)	0.35 _{1,40} ^a	(-)	F2
Below-ground herbivores	1.41 _{1,49}	(-)	1.54 _{1,49} ^a	(-)	3.52 _{1,49} ^a	(-)	F0
	0.03 _{1,40}	(+)	0.25 _{1,40}	(-)	0.03 _{1,40} ^a	(+)	F2
Cytotype							
% Diploids	0.01 _{1,49}	(-)	1.46 _{1,49}	(+)	17.82_{1,49}^{***,a}	(-)	F0
	0.00 _{1,40}	(-)	2.17 _{1,40} ^a	(+)	23.79_{1,40}^{***,a}	(-)	F2

Abbreviations: TA-G, taraxinic acid β -D-glucopyranosyl ester; di-PIEs, di-4-hydroxyphenylacetate inositol esters; tri-PIEs, tri-4-hydroxyphenylacetate inositol esters.

^aLog-transformation of response variable.

$p = 0.040$, Figure 4a for F0 and $F_{1,40} = 8.13$, $p = 0.007$, Figure 4b for F2, Table 2). climPCA1 was positively correlated with annual temperature and negatively correlated with altitude (Table 1; Figure 4b), thus, plants from populations growing at high altitude in colder areas produced more di-PIEs than plants from populations growing in warmer regions at lower altitude (Figure 4). Linear model analysis further revealed that neither soil parameters nor below-ground herbivore abundance or cytotype distribution were significantly linked to TA-G or di-PIE production. Tri-PIEs were not affected by climatic, soil or herbivory parameters, but were negatively associated with the percentage of diploid plants per population (LM, $F_{1,49} = 17.82$, $p < 0.001$, Figure 4c for F0 and $F_{1,40} = 23.80$, $p < 0.001$, Figure 4c for F2, Table 2).

3.4 | Latex profiles vary independently of vegetative growth

By analysing the influence of environmental factors on maximal leaf length—a proxy for vegetative growth—and by testing the

effect of maximal leaf length on latex secondary metabolites, we investigated the contribution of this potentially underlying factor to the heritable variation of latex profiles. Linear model analysis revealed that maximal leaf length was negatively associated with climPCA2 (LM, $F_{1,40} = 5.65$, $p = 0.022$, Table S3, Figure 5) and positively associated with the abundance of below-ground herbivores (LM, $F_{1,40} = 9.27$, $p = 0.004$, Table S3, Figure 5). However, the effect of below-ground herbivores on leaf length was mainly due to one population with a high number of below-ground herbivores per plant, and the effect was no longer significant after the removal of this population (LM, $F_{1,39} = 0.65$, $p = 0.426$). Maximal leaf length of F2 plants was not correlated with the concentration of TA-G, di-PIEs or tri-PIEs, neither in plants growing in the natural habitat (F0) nor in plants growing in the greenhouse (F2; Table S4). This finding indicates that the variation in the vegetative performance of the plants, although influenced by the environment, does not explain the relationships between the environmental factors and the latex profiles.

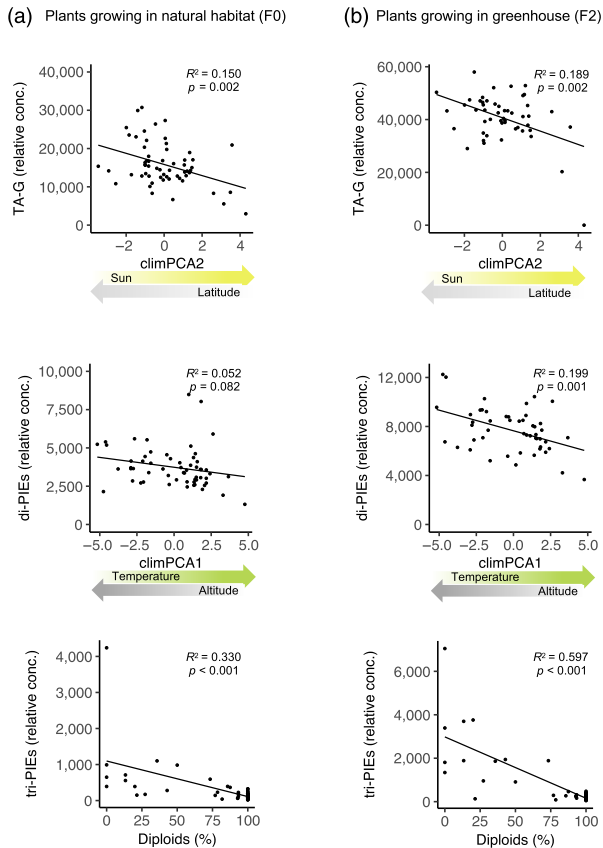


FIGURE 4 Visualization of relationships between the significant effects of the linear model analyses and the corresponding class of latex secondary metabolites for plants growing in natural habitat (a) and plants growing in greenhouse (b). Each dot represents one *Taraxacum officinale* population ($N = 59\text{--}63$ for F0 and $N = 50\text{--}54$ for F2). Linear regression lines and R^2 - and p -values of the regressions are shown. Coloured arrows illustrate intensity gradients of the corresponding environmental factors. Note that these linear regressions are different from the linear model analyses. The regressions in this figure simplify the relationships between latex metabolites and environmental factors for illustrative purposes, while the linear models in Table 2 examine the associations in a more powerful modelling framework. TA-G, taraxinic acid β -D-glucopyranosyl ester; di-PIEs, di-4-hydroxyphenylacetate inositol esters; tri-PIEs, tri-4-hydroxyphenylacetate inositol esters

4 | DISCUSSION

Plant secondary metabolites can vary considerably between populations, but the contribution of the environment in shaping secondary metabolite profiles of plants by driving selection or environmental plasticity is poorly understood. Our work shows that heritable variation in latex secondary metabolites of 63 *T. officinale* populations across Switzerland is strongly linked to climatic conditions and cytochrome distribution, but not to soil properties or below-ground herbivore abundance. Here, we discuss the implications of these findings from ecological and physiological points of view.

The *T. officinale* populations included in this study were evenly distributed across Switzerland and spanned an elevation gradient

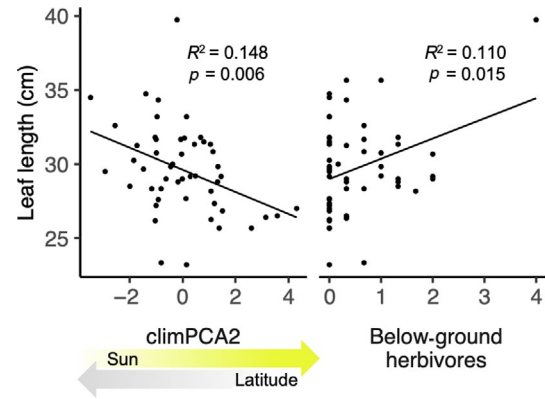


FIGURE 5 Visualization of the relationships between maximal leaf length (a proxy for leaf and root biomass) and environmental factors identified by linear model analysis (Table S3). Maximal leaf length was measured on plants growing in equal conditions. Each dot represents one *Taraxacum officinale* population ($N = 50$ for the left panel and $N = 54$ for the right panel). Coloured arrows illustrate corresponding intensity gradients of climPCA2. Linear regression lines and R^2 - and p -values of the regressions are shown. Note that these linear regressions are different from the linear model analysis and that the regressions in this figure simplify the relationships between leaf length and environmental factors for illustrative purposes

from 200 to 1,600 m a.s.l. For Switzerland, the occurrence of both sexual diploid and asexual triploid dandelions has been reported, with diploids being found at elevations higher than 700 m a.s.l. and triploids being found in lower areas (Calame & Felber, 2000). However, our ploidy analysis could not confirm such an elevation threshold, as we found diploids and triploids at all elevations and frequently observed populations with mixed cytotypes. Calame and Felber (2000) analysed the distribution of *T. officinale* cytotypes along two elevation gradients of different regions (Jura and Alps), whereas in our study we did not sample directly along elevation gradients, but analysed a broader spectrum of populations from all over Switzerland. The differences in the reported cytochrome distributions may thus be due to the different sampling ranges. Interestingly, we found that the cytochrome distribution was associated with latitude, resulting in more diploids per population in areas with less sun and more rain in the North of Switzerland. Across Europe, a latitudinal effect on cytochrome distribution in *T. officinale* has been reported, with diploids being present mainly in Central Europe, while triploids occur from Central Europe up to Northern Scandinavia (Verduijn et al., 2004a, 2004b). Furthermore, our results indicate an influence of soil geochemistry on cytochrome distribution, since the percentage of diploids per population increased in natural habitats with higher humus content and lower soil pH. Thus, soil geochemical properties could be part of the different microecological niches of asexual and sexual *T. officinale* and affect the distribution of the plants, either directly by influencing nutrient availability (Dubuis et al., 2013) or indirectly by shaping soil microbial communities (Verhoeven & Biere, 2013).

As a chemical interface between plants and their environment, some plant secondary metabolites vary highly in concentration

and composition with changing abiotic conditions (Holopainen et al., 2018; Jakobsen & Olsen, 1994; Selmar & Kleinwächter, 2013). Fluctuating patterns of sesquiterpene lactones and phenolics produced by *Tithonia diversifolia*, for instance, correlate with seasonal changes in temperature and rainfall (Sampaio, Edrada-Ebel, & Da Costa, 2016). Our results show that the concentrations of both TA-G and di-PIEs in the latex of *T. officinale* are strongly associated with the climatic conditions of the population origins, and thus emphasize the central role of abiotic conditions for shaping latex composition. Interestingly, despite the structural similarity of di-PIEs and tri-PIEs, we found no effect of climate on tri-PIEs, which points towards distinct functions and regulations of the two groups of secondary metabolites. This is also supported by the finding that diploids seem to produce more tri-PIEs than triploids, while the production of di-PIEs and TA-G is independent of the cytotype. Further, although vegetative growth of the plants varied between populations, we found no evidence that the production of latex metabolites is affected by the different growth rates of the plants. This is in line with the results of Huber, Epping, et al. (2016), who found no clear correlation between latex metabolites and vegetative growth of *T. officinale* across 17 genotypes. We therefore conclude that the association of latex metabolites with climatic conditions of the natural habitats of the populations is likely independent of vegetative growth. Climatic effects on latex profiles were consistent for plants growing in natural habitat and for plants growing under greenhouse conditions two generations later, although altered correlations among compounds in field- or greenhouse-grown plants suggest some degree of environmental plasticity in latex secondary metabolites. Nonetheless, this indicates that variation in latex profiles is at least in part heritable and suggests that climatic conditions exert direct or indirect selection pressure on latex secondary metabolites in *T. officinale*. Heritability of latex secondary metabolites was approximated by comparing the mean population levels of plants growing in their natural habitat with the mean population levels of their offspring growing in a controlled environment. Therefore, our findings allow conclusions about eco-evolutionary processes only at the population level, since constraints posed by the genetic architecture within a population were not considered. More traditional assessments of within-population heritability, such as breeding designs with siblings (Visscher, Hill, & Wray, 2008), would complement our study and help to shed light on evolutionary processes at different biological scales (Agrawal, 2020; Hahn & Maron, 2016).

Variation in plant defences between and within species is often hypothesized to follow geographical gradients, which in turn are speculated to be linked to herbivore pressure (Anstett et al., 2018; Moles et al., 2011; Pratt et al., 2014). Both TA-G and di-PIEs have been shown to be involved in herbivore defence (Agrawal et al., 2018; Bont et al., 2017; Huber, Bont, et al., 2016; Huber, Epping, et al., 2016). Our results confirm a link of both metabolites with geographical gradients, as the climatic variables, which influence TA-G and di-PIEs, are strongly linked to altitude and latitude. We found more di-PIEs in plants from high altitudes with lower temperatures, and more TA-G in plants from areas with less sun in the

North of Switzerland. However, as herbivore pressure varied independently of climatic variables, we found no evidence for a major role of below-ground herbivores in the observed genetically based variation in latex secondary metabolites, contrary to our expectations. Nevertheless, we cannot rule out the potential hidden effects of herbivores on latex metabolites. The climatic variables used in our study include 20 years of weather data at very high resolution, whereas our herbivore variables either captured a single snapshot in time, or relied on rough, potentially inaccurate historic estimates. Thus, the two herbivore variables may have failed to accurately represent the actual herbivore abundances of the past (Huber, Bont, et al., 2016). Furthermore, herbivore effects could manifest themselves through interactions with climate conditions or other variables. Plant responses to abiotic and biotic stresses are controlled by the same interactive hormonal network, hence combined stresses may lead to complex hormonal interactions (Nguyen, Rieu, Mariani, & van Dam, 2016). In maize, for example, root herbivory induces hydraulic changes in the leaves and triggers abscisic acid (ABA) accumulation (Erb et al., 2011). ABA again is essentially involved in regulating responses to abiotic stresses and stimulates for instance stomata closure, which is crucial for limiting desiccation (Daszkowska-Golec & Szarejko, 2013). Thus, by influencing the water balance of the plant, root herbivores may indirectly affect the plant's response to abiotic conditions. However, we could not test for interactive effects of the environmental variables included in our study, as the full set of required tests would have exceeded the appropriate number of model parameters compared to the number of included populations in our analysis. Thus, to shed light on this topic, further experiments are needed, which test specifically the interacting effect of climatic conditions and herbivore pressure on secondary metabolites at large-scale environmental variation. However, given the different and specific associations between PIEs, TA-G and climatic conditions and the inverse relationship between climate parameters, expected herbivore attack rates and secondary metabolite concentrations, we consider it unlikely that the climate effects observed here are the indirect result of climate-mediated herbivory alone.

There is growing evidence that many secondary metabolites are highly multifunctional and serve defensive, ecological and physiological functions at the same time, which minimizes the plant's fitness costs for biosynthesis and maintenance of metabolites (Bednarek & Osbourn, 2009; Neilson et al., 2013). Maize plants, for instance, use the same benzoxazinoid secondary metabolites for iron uptake, protection against generalist herbivores and defence signalling (Hu et al., 2018; Li, Förster, et al., 2018; Maag et al., 2016). For another important class of defensive secondary metabolites, glucosinolates, it has been shown that the metabolite 3-hydroxypropylglucosinolate has signalling capacity and inhibits root growth and development by the evolutionary old TOR (Target of Rapamycin) pathway (Malinovsky et al., 2017). In addition, recent work shows that aliphatic glucosinolates have an important role in drought conditions by regulating stomatal aperture, thus providing evidence that glucosinolates are also involved in abiotic stress tolerance (Salehin et al., 2019). Our finding that TA-G and di-PIEs are

strongly associated with climatic conditions suggests potential alternative functions of those latex secondary metabolites, and latex itself, in addition to the previous reported roles in herbivore defence (Agrawal et al., 2018; Huber, Bont, et al., 2016). Both TA-G and di-PIE concentrations were correlated with each other, but each compound class was affected by distinct climate variables: TA-G was mainly associated with sun and rain intensity (climPCA2), whereas di-PIEs were mainly associated with temperature (climPCA1). Hence, TA-G may be involved in moisture regulation or linked to physiological processes that are associated with light availability, whereas di-PIEs may play a role in temperature-sensitive processes. Of course, these are highly speculative arguments based on correlational data, and manipulative experiments are needed to further explore the role of latex secondary metabolites in climate-mediated plant physiology.

Studies of inter- and intraspecific plant trait variation across environmental gradients, such as those related to latitude and elevation, have been receiving increasing attention (Anstett et al., 2018; Hahn et al., 2019; Pellissier, Roger, Bilat, & Rasmann, 2014; Woods et al., 2012). Although such studies are beyond doubt important and useful to test classic theories predicting herbivore defence (Anstett et al., 2015; Moles et al., 2011) and resource allocation patterns (Helsen et al., 2017; Kooyers, Greenlee, Colicchio, Oh, & Blackman, 2015), they also have to cope with the difficulty of potentially hidden dynamics along gradients. Changes in abiotic and biotic factors may be correlated and interconnected to changes in geographical location, which complicates the disentangling of environmental impacts on plant traits (Hahn et al., 2019; Johnson & Rasmann, 2011). Our results emphasize the importance of considering multiple environmental factors when studying biogeographical patterns of plant traits, and of sampling a large set of natural genotypes across a wide range of environments. We propose to include the possibility of multifunctionality of secondary metabolites into the framework of studies that explore trait variation in plant defences, as patterns of defence variation may be explained by alternative additional functions of plant secondary metabolites.

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AUTHORS' CONTRIBUTIONS

Z.B., T.Z., M.H. and M.E. designed the study; Z.B. and C.C.M.A. collected the data; Z.B., T.Z. and M.E. analysed and interpreted the data. Z.B. and M.E. wrote the first draft of the manuscript. All the authors contributed to the final version of the manuscript.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.bnzs7h47p> (Bont, Züst, Arce, Huber, & Erb, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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