Population differentiation in functional traits shapes plant–consumer interactions along an elevational gradient

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Keywords: Intraspecific variation, Functional traits, Plant-insect interactions, Plant-pathogen interactions, Elevation gradient

Abstract

1. Understanding how intraspecific variation in functional traits shape species interactions is central to predicting ecological responses to environmental change. The relative contribution of genetic differentiation and phenotypic plasticity to trait variation and their consequences for species interactions remain poorly understood.
2. Here, we conducted a reciprocal transplant experiment using *Plantago lanceolata* along an elevation gradient in the Eastern Swiss Alps to disentangle genetic differentiation and genotype-by-environment interactions underlying trait variation along a steep climatic and edaphic gradient. We measured several functional traits as well as arthropod herbivory and fungal infection prevalence.
3. We found strong evidence for trait differentiation between populations and weaker evidence for genotype-by-environment responses to transplant elevation or soil conditions. Herbivory showed little variation among transplant sites, whereas fungal disease decreased strikingly with increasing elevation and disease also varied according to population origin. Importantly, several traits showing population differentiation were linked to variation in plant consumer damage.
4. Our results suggest that variation in functional traits contribute to variation in plant-consumer interactions. More broadly, this study highlights the usefulness of identifying the sources of trait variation when predicting plant-consumer dynamics under environmental change.

1 Introduction

Functional traits govern how organisms acquire resources, grow, and defend themselves, and thus provide a mechanistic framework for understanding how organisms respond to both their biotic and abiotic environments (Funk et al., 2017; Violle et al., 2007). Intraspecific variation in traits may arise from genetic variation among individuals, phenotypic plasticity in response to local conditions (Bradshaw, 1965), genetic variation in phenotypic plasticity (i.e. genotype-by-environment interactions; Byers, 2005; Via & Lande, 1985), and ontogenetic changes during development (Rudolf & Rasmussen, 2013). Such variation in functional traits may substantially affect the ecological relationships a species engages in (Bolnick et al., 2011; Des Roches et al., 2018). Recent empirical work on competitive (Hogle et al., 2022), mutualistic (Arroyo-Correa et al., 2023) and trophic interactions (Harrison et al., 2018) all point towards a key role of intraspecific trait variation in the assembly, stability and dynamics of ecological assemblages. In plant communities, variation in functional traits mediates both attractiveness and resistance to primary consumers, such as herbivores and pathogens (Awmack & Leather, 2002; Cronin & Abrahamson, 1999; Halliday et al., 2021; Halliday, Czyżewski, et al., 2023). Therefore, disentangling the determinants of functional trait variation is essential for predicting biotic interactions under environmental change. However, empirical studies that explicitly link trait variation, and its drivers, to interactions with primary consumers remain limited.

Plant functional traits that underly resource allocation towards growth and defence are particularly important in mediating interactions with primary consumers. A major axis of plant variation is represented by the leaf economic spectrum, which describes a trade-off between resource acquisition and tissue longevity (Díaz et al., 2016; Wright et al., 2004). Functional traits that align with this axis, like specific leaf area (SLA; ratio of leaf dry mass per leaf area), have been shown to correlate with disease load (Cappelli et al., 2020) and trade-off with investment into molecular defence repertoires (Giolai & Laine, 2024). While these observations were made at the plant community and species level, respectively, there is evidence for a positive relationship between SLA and disease also within species (Gagliardi et al., 2023; Halliday, Czyżewski, et al., 2023). Further, multiple traits along the leaf economic spectrum are associated with variation in insect herbivory (Zhu et al., 2024). Beyond structural traits, leaf metabolic characteristics, such as the production of secondary metabolites, represent an additional dimension of plant functional trait space (Walker et al., 2023). Because plant secondary metabolites affect a multitude of plant-environment interactions (Kessler & Kalske, 2018), variation in these compounds may directly alter interactions with herbivores and pathogens.

Environmental gradients provide powerful systems to disentangle the genetic and environmental components of trait variation. Specifically along elevation gradients, trait differentiation and plasticity in key plant functional traits is common (Halbritter et al., 2018; Pellissier et al., 2010; Read et al., 2014). Using reciprocal transplant experiments, where individuals originating from multiple elevations are grown in both their native and foreign sites, it is possible to measure the reaction norms of functional traits across contrasting environments (Blanquart et al., 2013; Kawecki & Ebert, 2004). Reaction norms (Schmalhausen, 1949; Wolterek, 1909) describe how trait values vary among focal populations and across environmental conditions (Oomen & Hutchings, 2020; Stearns, 1989). Shifts in traits within populations across transplant sites indicate phenotypic plasticity, consistent differences among populations across environments reflect genetic differentiation, and variation in reaction norm slopes among populations indicates genotype-by-environment interactions (Kawecki & Ebert, 2004). Taken together, determining the reaction norms of relevant functional traits across environmental gradients offers the opportunity to quantify the underlying evolutionary and ecological processes that affect plant-consumer relationships.

Here, we performed a reciprocal transplant experiment along an environmental gradient, including the reciprocal transplantation of both plants and soils, to disentangle the determinants of intraspecific functional trait variation and to test how this variation relates to plant-consumer interactions. We measured several chemical, physiological and morphological traits, as well as arthropod herbivory and fungal infection, in three populations of the perennial plant *Plantago lanceolata* originating from different altitudes in the Eastern Swiss Alps. With this design, we tested the hypotheses that: (i) functional traits differ among populations, reflecting genetic differentiation along the elevational gradient; (ii) functional traits also vary plastically across transplant environments, indicating environmental effects and genotype-by-environment interactions; (iii) consumer pressure varies across transplant environments and among populations, indicating both variation in plant susceptibility and local variation the biotic environment; and (iv) variation in functional traits is associated with differences in plant-consumer interactions, such that trait differentiation among populations predicts variation in herbivory and fungal disease.

2 Methods

2.1 Reciprocal transplant experiment

To investigate the drivers of trait variation, herbivory and fungal infection in *P. lanceolata*, we conducted a reciprocal transplant experiment along a mountain slope in the Eastern Swiss Alps (Calanda Mountain, Canton of Grisons). Along this elevation gradient, the mean temperature varies predictably and decreases by 0.57 °C per 100 m (Halliday et al., 2021). In June 2021, we installed nine common gardens, three within each of three grasslands at ~700m, ~1000m, and ~1700m. We harvested seeds in 2019 and 2020 from each grassland population and germinated the seeds in a controlled growth chamber in May 2021. To mimic the diversity found in natural grassland communities, we planted *P. lanceolata* alongside three naturally co-occurring species from the same populations: the perennial herb *Plantago media*, and two perennial grasses, *Dactylis glomerata* and *Phleum pratense*. To disentangle the effect of climatic and edaphic environmental variation on plant traits, we implemented a fully crossed design of *P. lanceolata* population of origin, soil origin and transplant elevation. We collected soil from each common garden, filled plastic pots with the soil, and reciprocally distributed these pots among the gardens so that each site contained soils originating from all three elevations. Approximately six weeks after germination started, we embedded the pots in the ground at their target site and planted one seedling per species into each pot, resulting in 27 experimental combinations (three plant origin populations, three soil origin elevations and three transplant elevations). Each pot thus contained four individuals, one of each species, originating from the same grassland, giving a total of 324 pots. This design allowed us to analyse the effect of origin population, soil origin elevation, and transplant elevation on plant traits, herbivore damage and pathogen infection.

2.2 Measurements

We measured plant functional traits, arthropod herbivory, and fungal infection prevalence three times, at 21-day intervals, between August and September 2021. To functionally characterise the plants, we measured the number of leaves, the length and width of the longest leaf, and chlorophyll content with a SPAD-502Plus chlorophyll meter (Konica Minolta [China] Investment Ltd) placed on the centre of the two youngest fully expanded leaves. For analyses, we used the leaf number, length and width from the final measurement timepoint when plants were most mature, while we averaged SPAD values across all three timepoints to produce a single measurement per plant. At the second timepoint, we removed the youngest fully expanded plant leaf and kept the leaf hydrated in a plastic bag on moist paper tissue on ice. Then, we imaged the fresh leaves with a hand scanner (IRIscan Book 500, IRIS) and measured the leaf area with ImageJ 1.53k (Schneider et al., 2012). Subsequently, we oven-dried the leaves for 48 hours at 60°C, weighed the leaves, and calculated SLA (the ratio of leaf area (in cm^2) to leaf dry mass (mg)), which is indicative of a fast or slow life-history strategy (Garnier et al., 2001). We further determined iridoid glycoside concentrations from these leaves. *Plantago lanceolata* produces monoterpene-derived iridoid glycosides, which are secondary metabolites that are known to affect insect herbivore feeding behaviour (Bowers *et al.*, 1992) and fungal pathogen growth (Biere et al., 2004). We describe the iridoid glycoside quantification in detail in '2.3 Chemical analysis'.

To assess variation in plant-consumer interactions, we exposed plants to the naturally occurring herbivores and pathogens in these grasslands over the experimental period. For each plant, we recorded arthropod herbivory and fungal infection levels for every leaf using the seven damage categories of Kozlov *et al.* (2015): 0%, 0–1%, 1–5%, 5–25%, 25–50%, 50–75%, and >76%. For herbivory, we used midpoints of each category to calculate the mean defoliation per plant across the three time points to account for seasonal variation in the arthropod herbivore community (Fernandez-Conradi et al., 2020, 2021). For fungal infection, we focused on powdery mildews (*Podosphaera plantaginis* and *Golovinomyces sordidus*), which are specialist wind dispersed pathogens of *Plantago* species and occur in the focal grassland populations (Rechsteiner, Giolai *et al.*, unpublished). We scored infections by the presence or absence of visible powdery mildew symptoms at time point 3, which overlaps with the seasonal epidemic peak.

During the experimental period, two plants disappeared, possibly due to grazing by local fauna. Further, between time points 2 and 3, a disturbance occurred at the mid-elevation when cattle gained access to one common garden, damaging an additional 21 plants. Ultimately, 301 plants were available for analysis; SLA was measured for 296, and iridoid glycosides for 283, due to sample loss or degradation.

2.3 Chemical analyses

We quantified iridoid glycosides from the oven-dried leaves by first grinding them to powder using stainless steel beads with a tissue lyser (Retsch MM 200 Mixer Grinding Mill for 3 min at 30Hzt). Next, we added 10 mg powder aliquots to 1.5 ml methanol in a 2 ml DNA LoBind tube (no. 0030108078) along with 5 glass beads. The tubes were shaken at 30 Hz for 4 minutes before centrifugation at 13’800 g for 3 minutes to pellet the plant material. We diluted the supernatant ten times by adding 900 µl of MilliQ water:methanol (80:20, v/v) to 100 µl of concentrated extract. Samples were further vortexed for 10 s and centrifuged at 13’800 g for 3 min to pellet any remaining plant particles. We collected an aliquot of 150 ul and placed it into a HPLC vial fitted with a conical insert. We used the method of Bakhtiari *et al.*, 2019 to identify and quantify iridoid glycosides using aucubin and catalpol as reference calibration curves.

2.4 Statistical analyses

To understand how consumer pressure and traits vary along the elevation gradient, and the drivers of this variation, we analysed the level of herbivory and fungal infection as well as each trait (number of leaves, leaf width, leaf length, iridoid glycoside concentration, SLA, chlorophyll content), by fitting a separate linear mixed model (LMM) or generalized linear mixed model (GLMM) with the transplant elevation, plant origin population and soil origin as well as all possible interactions between these treatments as fixed effects. Additionally, we fitted the common garden as a random effect. We normalized transplant elevation using the *scale* function part of base R, such that model coefficients represent the effect of elevation per unit of standard deviation. In addition, we log-transformed herbivory to approach a normal distribution. We analysed the length of the longest leaf, the width of the longest leaf, specific leaf area, chlorophyll content (SPAD), iridoid glycoside concentration and log-transformed herbivory with an LMM. Baudraz et al. (2025) advise against transforming the number of leaves into a continuous variable. The appropriate analysis for such discrete counts is a Poisson regression, yet its assumption of equal mean and variance was violated. Therefore, we used a GLMM with a negative binomial distribution to model the number of leaves. To analyse the presence or absence of powdery mildew symptoms, we used a GLMM with a binomial distribution. In all models, signs of genotype-by-environment interactions are indicated by significant plant origin population x transplant elevation and plant origin population x soil origin interactions. In the logistic mixed effects model of fungal infection prevalence, the full model led to convergence issues. Therefore, we excluded the transplant elevation x soil origin interaction and the three-way interaction between treatments to reduce model complexity and achieve model convergence.

In addition, to test whether the number of leaves, leaf width, leaf length, iridoid glycoside concentration, SLA, and chlorophyll content was associated with herbivory and powdery mildew infection, and whether these associations vary among treatments, we fitted a second series of linear models. In these models, we included the plant population, soil origin and transplant elevation as main fixed effects, a focal trait effect, and interaction terms between the focal trait and each main effect and defined the common garden as a random effect.

We fitted LMMs using the *lme4* package (Bates et al., 2015), and GLMMs using *glmmTMB* (Brooks et al., 2017) and assessed model assumptions using DHARMa (Hartig, 2025). We tested the significance of fixed effects using Type II ANOVA Wald χ^2 as implemented in the *car* package (Fox & Weisberg, 2019). Within each of the three model series - (1) drivers of trait variation, herbivory and fungal infection, (2) trait effects on herbivory and (3) trait effects on fungal infection – we adjusted the Wald χ^2 p-values for false discovery rate using the Benjamini-Hochberg alpha correction method part of the *stats* package part of base R (R Core Team, 2021). For significant categorical effects of population of origin and soil origin in all models, we estimated marginal means and conducted post hoc pairwise comparisons using *emmeans* (Lenth et al., 2024). Finally, we calculated confidence intervals and continuous predictor estimates using the *report* package (Makowski et al., 2025). We performed all statistical analyses with R version 4.2.3 (R core team, 2023).

3 Results

3.1 Drivers of intraspecific trait variation, herbivory and fungal infection

We found that populations varied in the expression of most traits except in the case of iridoid glycoside concentrations (Fig.1, Table 1). However, we did not find significant interactions between the origin of plants and their transplant site or soil for any of the traits (Table 1). Plants originating for the highest elevation showed a higher number of leaves, a wider and shorter longest leaf, and a higher SLA compared to plants originating from the low- and mid-elevation population across all transplant elevations (for Plant $\text{origin}_{\text{low}}$ – Plant $\text{origin}_{\text{high}}$ and Plant $\text{origin}_{\text{mid}}$ – Plant $\text{origin}_{\text{high}}$ contrasts, all relevant Tukey-adjusted p-values are < 0.05, Supp. Table 1). Chlorophyll content was lower in plants originating from the lowest elevation compared to mid- and high-elevation origin plants (Plant $\text{origin}_{\text{low}}$ – Plant $\text{origin}_{\text{high}}$: -2.71, SE = 0.61, p = 0.00004; Plant $\text{origin}_{\text{low}}$ – Plant $\text{origin}_{\text{mid}}$: -1.74, SE = 0.61, p = 0.01, Supp. Table 1). Soils varied in their effect on iridoid glycoside concentrations and chlorophyll content

(Supp. Table 1). Plants growing in mid-elevation soils produced higher concentrations of iridoid glycosides compared to plants growing in high-elevation soils ($\text{Soil}_{\text{mid}} - \text{Soil}_{\text{high}}$: 6.84, SE = 2.36, p = 0.01, Supp. Table 1). Further, plants showed reduced chlorophyll content when growing in low- and mid-elevation soils compared to high-elevation soils ($\text{Soil}_{\text{low}} - \text{Soil}_{\text{high}}$: -2.82, SE = 0.61, p = 0.00002; $\text{Soil}_{\text{mid}} - \text{Soil}_{\text{high}}$: -2.74, SE = 0.61, p = 0.00003, Supp. Table 1). Finally, increasing elevation reduced both the width (slope = -0.371, 95% CI [-0.651, -0.092]; Type II Wald χ^2 = 8.209, adjusted p = 0.00002; Fig. 1, Table 1, Supp. Table 2) and the length (slope = -2.622, 95% CI [-5.317, 0.073]; Type II Wald χ^2 = 5.006, adjusted p = 0.0674, Fig. 1, Table 1, Supp. Table 2) of the longest leaf of plants.

In our analysis of plant-consumer damage, herbivory did not vary between plant populations, transplant environments and soils (Table 1). However, plant populations varied in their powdery mildew infection probability. Plants originating from the mid-elevation population had a lower probability of infection compared to high-elevation plants ($\text{Plant origin}_{\text{mid}} - \text{Plant origin}_{\text{high}}$: -2.4, SE = 1.02, p = 0.049, Supp. Table 1, Fig. 2). In addition, with increasing transplant elevation the infection probability diminished significantly (slope = -2.267, 95% CI [-3.926, -0.609]; Type II Wald χ^2 = 10.043, adjusted p = 0.012, Fig. 2, Table 1, Supp. Table 2).

3.2 Trait-herbivory and trait-fungal infection relationships

Several traits showed a relationship with herbivory and powdery mildew infection. Higher herbivory was observed on plants with higher SLA values (slope = 0.017, 95% CI [-0.006, 0.041]; Type II Wald χ^2 = 13.370, adjusted p = 0.0008, Table 2, Supp. Table 3), and less herbivory was observed on plants with a higher number of leaves (slope = -0.016, 95% CI [-0.036, 0.005]; Type II Wald χ^2 = 14.375, adjusted p = 0.0008, Table 2, Supp. Table 3). Further, plants with wider (slope = 1.014, 95% CI [0.429, 1.599]; Type II Wald χ^2 = 9.388, adjusted p = 0.013, Table 2, Supp. Table 4) and longer (slope = 0.101, 95% CI [-0.040, 0.241]; Type II Wald

$\chi^2 = 5.263$, adjusted p = 0.065, Supp. Table 4) leaves showed increased infection probability. The trait effects did not vary between transplant elevations, plant populations and soils shown by the absence of significant interaction effects (Table 2).

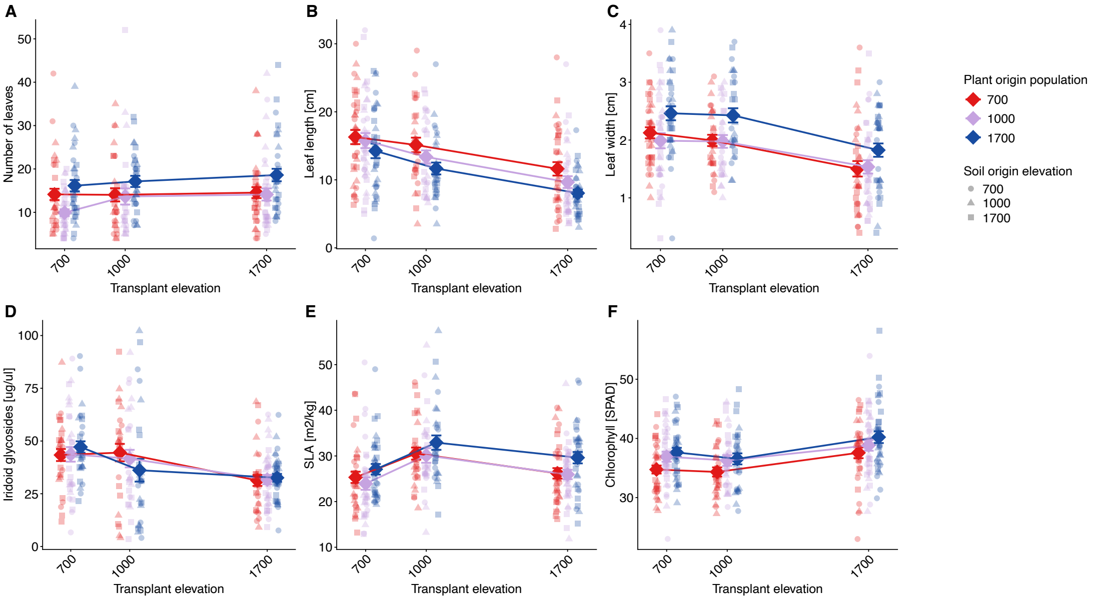

Figure 1. Reaction norms of functional traits across transplant elevations in a reciprocal transplant experiment. Trait values of *Plantago lanceolata* populations originating from three elevations (700, 1000, and 1700 m) grown across the transplant elevations. Panels show (**A**) number of leaves, (**B**) leaf length (cm), (**C**) leaf width (cm), (**D**) iridoid glycosides (µg g^{-1}), (**E**) specific leaf area (SLA; m^2 kg^{-1}), and (**F**) chlorophyll content (SPAD). Colours indicate the plant population of origin (red = 700 m, light purple = 1000 m, blue = 1700 m). Symbol shapes indicate the elevation of soil origin (circle = 700 m, triangle = 1000 m, square = 1700 m). Transparent symbols represent individual plants, whereas opaque symbols and connecting lines show mean trait values of each origin population across transplant elevations. Error bars indicate ± SE of the mean.

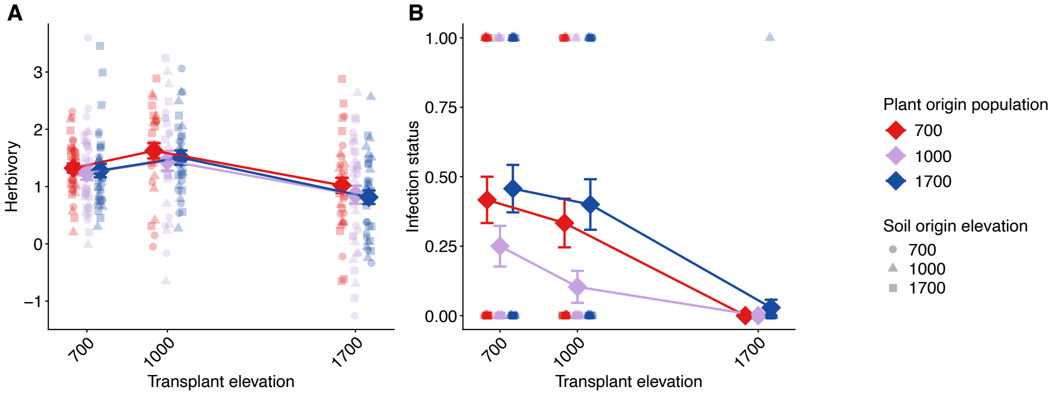

Figure 2. Variation in plant-consumer interactions across transplant elevations and plant populations in a reciprocal transplant experiment. Log-transformed herbivory (A) and proportion of powdery mildew infected plants (B) of *Plantago lanceolata* populations

originating from three elevations (700, 1000, and 1700 m) grown across the transplant elevations. Colours indicate the plant population of origin (red = 700 m, light purple = 1000 m, blue = 1700 m). Symbol shapes indicate the elevation of soil origin (circle = 700 m, triangle = 1000 m, square = 1700 m). Transparent symbols represent individual plants, whereas opaque symbols and connecting lines show mean trait values of each origin population across transplant elevations. Error bars indicate ± SE of the mean.

Table 1. Drivers of intraspecific trait variation, herbivory and fungal infection. Summary table of ANOVA results of the linear models testing the drivers of trait variation, herbivory and fungal infection. Coefficients represent Wald χ^2 values of each predictor. Degrees of freedom are given in the footnote. Significant terms are shown in bold and significance levels are indicated by asterisks (˙: p <= 0.1, *: p <= 0.05, **: p <= 0.01, ***: p <= 0.001).

Trait	Elevation (E)	Plant origin (PlO)	Soil origin (SoO)	E:PlO	E:SoO	PlO:SoO	E:PlO:SoO
Nr. leaves	$1.505_{(1)}$	$\mathbf{27.093_{(2)}}$***	$6.490_{(2)}$	$3.548_{(2)}$	$0.695_{(2)}$	$2.241_{(4)}$	$9.417_{(4)}$
Leaf width	$\mathbf{8.209_{(1)}}$**	$\mathbf{24.756_{(2)}}$***	$0.109_{(2)}$	$0.924_{(2)}$	$0.294_{(2)}$	$2.451_{(4)}$	$2.227_{(4)}$
Leaf length	$\mathbf{5.006_{(1)}}$˙	$\mathbf{20.278_{(2)}}$***	$5.884_{(2)}$	$1.167_{(2)}$	$0.109_{(2)}$	$1.352_{(4)}$	$1.419_{(4)}$
IG conc.	$2.084_{(1)}$	$0.062_{(2)}$	$\mathbf{8.677_{(2)}}$˙	$0.028_{(2)}$	$1.188_{(2)}$	$8.206_{(4)}$	$0.862_{(4)}$
SLA	$0.001_{(1)}$	$\mathbf{13.888_{(2)}}$**	$4.372_{(2)}$	$1.028_{(2)}$	$2.833_{(2)}$	$4.387_{(4)}$	$4.805_{(4)}$
Chlorophyll	$2.530_{(1)}$	$\mathbf{19.872_{(2)}}$***	$\mathbf{26.785_{(2)}}$***	$0.488_{(2)}$	$3.038_{(2)}$	$4.961_{(4)}$	$6.655_{(4)}$
Herbivory	$1.940_{(1)}$	$2.770_{(2)}$	$4.419_{(2)}$	$0.256_{(2)}$	$7.729_{(2)}$	$1.857_{(4)}$	$3.000_{(4)}$
Powdery Mildew	$\mathbf{10.043_{(1)}}$*	$\mathbf{9.984_{(2)}}$**	$3.014_{(2)}$	$1.055_{(2)}$	-	$3.420_{(4)}$	-

Table 2. Trait-herbivory and trait-fungal infection relationships. Results of Type II ANOVA Wald χ^2 tests from linear models of trait effects on herbivory and powdery mildew infection. The main trait effects and trait × treatment interactions are shown. Significant terms are shown in bold and significance levels are indicated by asterisks (˙: p <= 0.1,*: p <= 0.05, **: p <= 0.01, ***: p <= 0.001).

	Traits	Trait	Trait:E	Trait:PlO	Trait:SoO
Herbivory:	Nr. Leaves	$\mathbf{14.375_{(1)}}$***	$1.714_{(1)}$	$0.540_{(2)}$	$1.821_{(2)}$
	Leaf width	$0.208_{(1)}$	$6.305_{(1)}$	$0.530_{(2)}$	$1.203_{(2)}$
	Leaf length	$3.614_{(1)}$	$1.872_{(1)}$	$0.147_{(2)}$	$5.966_{(2)}$
	IG conc.	$0.993_{(1)}$	$1.329_{(1)}$	$0.011_{(2)}$	$1.915_{(2)}$
	SLA	$\mathbf{13.370_{(1)}}$***	$1.212_{(1)}$	$2.141_{(2)}$	$4.220_{(2)}$
	Chlorophyll	$1.963_{(1)}$	$0.103_{(1)}$	$0.018_{(2)}$	$6.311_{(2)}$
Powdery mildew infection:	Nr. Leaves	$0.813_{(1)}$	$0.245_{(1)}$	$0.467_{(2)}$	$0.051_{(2)}$
	Leaf width	$\mathbf{9.388_{(1)}}$*	$1.230_{(1)}$	$1.905_{(2)}$	$1.858_{(2)}$
	Leaf length	$\mathbf{5.263_{(1)}}$˙	$0.045_{(1)}$	$3.470_{(2)}$	$1.108_{(2)}$
	IG conc.	$0.190_{(1)}$	$0.523_{(1)}$	$0.264_{(2)}$	$1.195_{(2)}$

	SLA	$3.274_{(1)}$	$0.331_{(1)}$	$3.479_{(2)}$	$0.195_{(2)}$
	Chlorophyll	$0.230_{(1)}$	$0.463_{(1)}$	$0.395_{(2)}$	$1.618_{(2)}$

4 Discussion

Using a reciprocal transplant experiment along an environmental gradient with *P. lanceolata*, including the reciprocal transplantation of soils, we aimed to disentangle the determinants of intraspecific functional trait variation and to test how this variation relates to plant-consumer interactions. Traits differed markedly between the study populations, whereas phenotypic plasticity was less common and genotype-by-environment interactions were absent. Herbivory showed little variation among populations or along the gradient, whereas fungal infection differed both among populations and across transplant sites. Several of the differentiated traits were consistently associated with consumer damage across populations and transplant environments. Our findings suggest that trait differentiation may contribute to population-level variation in susceptibility to herbivores and pathogens. Overall, our results provide additional evidence that intraspecific trait variation matters for biotic interactions and that investigating the sources of variation in functional traits enhances our understanding of how infectious disease and pest dynamics may be affected by a changing climate.

4.1 Patterns and sources of intraspecific variation in traits

Several traits varied between the origin populations of plants, with the high-elevation population showing a clear morphological differentiation. This pattern is consistent with widespread evidence that environmental heterogeneity along elevation gradients imposes strong divergent selection and drives phenotypic divergence in plants (Halbritter et al., 2018; Körner, 2016; Pellissier et al., 2010; Read et al., 2014). In our study, high-elevation plants produced more leaves that are shorter and wider, indicating a distinct high-elevation ecotype (*sensu* Turesson, 1922) in *P. lanceolata*. While both leaf width and leaf length decreased with increasing elevation, high-elevation plants had the shortest, yet widest leaves. In other words, trait differentiation covaried positively with elevation for leaf length and negatively for leaf width. Such a pattern corresponds to co- and counter gradient variation (Conover & Schultz, 1995; Levins, 1968, 1969) for leaf length and width respectively, which potentially reflects a cryptic form of local adaptation (Conover et al., 2009; Sparks et al., 2022). A sole focus on leaf area would obscure this pattern, highlighting the value of preserving more simple morphological features for analysis. Jointly these findings illustrate how subtle shifts in trait combinations can arise along environmental gradients even within widely distributed and ecologically flexible species (Smith et al., 2020).

Soil origin influenced both chemical defense and physiological traits. Plants growing in mid-elevation soils produced higher concentrations of iridoid glycosides compared to plants growing in high-elevation soils, and chlorophyll content was reduced in plants growing in low- and mid-elevation soils relative to those in high-elevation soils. Variation in soil nutrients is known to influence leaf iridoid glycoside concentrations in *P. lanceolata* (Prudic et al., 2005), suggesting that the soil effects observed here may reflect differences in nutrient availability among soils. Consistent with this interpretation, chlorophyll content - a proxy for plant nutritional status - also varied across soil origins. More broadly, soil properties such as salinity (Busoms et al., 2015), quartz content (Ellis & Weis, 2006), or heavy metal concentrations (Antonovics, 2006; Arnold et al., 2016) are known to drive trait variation and local adaptation in other systems, highlighting the importance of edaphic conditions for plant phenotypes. In addition to abiotic soil properties, several soil-mediated processes may influence plant chemical composition and nutritional status, including interactions with mycorrhizal fungi (Delavaux et al., 2017), plant–soil feedbacks (van der Putten et al., 2013), and other soil biota (Brussaard, 1997).

While several traits differed among populations, we found little evidence for genotype-by-environment interactions across transplant environments. Populations therefore differed mainly in their mean trait values, but their responses to transplant elevation and soil origin were largely parallel. Jointly, our results suggest that trait variation in *P. lanceolata* along this elevational gradient reflects a combination of population differentiation and environmental effects mediated by soil conditions. However, some of the observed differences may reflect early environmental influences or maternal effects associated with the conditions experienced by the source plants (Baskin & Baskin, 1973; Roach & Wulff, 1987). Consequently, while our results are consistent with population differentiation along the elevational gradient, they do not allow us to fully separate genetic differentiation from transgenerational phenotypic plasticity (Höckerstedt et al., 2020).

4.2 Variation in biotic interactions

Multiple studies show that species interaction intensity decreases with increasing elevation (Descombes et al., 2017; Hargreaves et al., 2019; Pellissier et al., 2018; Rasmann et al., 2014; Roslin et al., 2017; Schemske et al., 2009; Zvereva & Kozlov, 2022). In line with this pattern, we found infection prevalence to sharply decline with increasing elevation. Because pathogen infection and herbivory can impose fitness costs in hosts, spatial variation in enemy pressure could generate spatially variable selection for defence. However, the differences in powdery mildew infections among plant populations did not follow the same elevational pattern. This suggests that infection risk does not necessarily translate to into differences in host resistance, as disease outcomes emerge from a complex interplay between environment, hosts, and pathogens (McNew, 1960). On the other hand, field transplant experiments may mask genetic variation in resistance for example if infection patterns are generated by few highly infectious pathogen clones (Laine, 2007), and thus an elevational gradient in resistance cannot be ruled out with certainty.

In terms of herbivory, contrary to previous work carried out in the Swiss Alps, we did not observe a reduction towards higher elevations (Descombes et al., 2017; Pellissier et al., 2014). One possible explanation is that herbivore activity may be less tightly constrained by environmental gradients than pathogen infection. While pathogen dynamics often depend strongly on local microclimatic conditions such as temperature and humidity, many herbivores are mobile and can behaviourally track suitable host plants across heterogeneous environments (Gripenberg et al., 2010). As a result, herbivore pressure may be buffered against elevational variation and instead shaped more strongly by local ecological factors, such as herbivore and plant community composition or microhabitat structure (Halliday, Cappelli, et al., 2023). Interestingly, in Pellissier et al. (2014), a correlation between herbivory and elevation was detected, with high-elevation ecotypes experiencing lower herbivory and exhibiting reduced chemical defence. However, this pattern was not driven by plastic responses: iridoid glycoside concentrations showed no genotype-by-environment interaction and remained largely unchanged across temperature treatments, in contrast to growth-related traits such as biomass, which were plastic. This lack of plasticity in defence chemistry suggests that elevational differences in herbivory may not readily emerge under experimental or local field conditions.

4.3 Trait-consumer relationships

Our results demonstrate that intraspecific variation in plant functional traits can shape interactions with herbivores and pathogens by influencing plant palatability, growth strategy, and exposure to natural enemies. First, we found that variation in SLA was positively associated with arthropod herbivory. This suggests that individuals with a faster growth strategy (higher SLA) experience greater herbivory, potentially due to increased palatability. In contrast, the number of leaves showed a negative relationship with herbivory, indicating that larger plants may accumulate proportionally less damage. These contrasting effects suggest that, in *P. lanceolata,* SLA and leaf number capture different axis of the functional trait space. Further, we detected no relationship between herbivory and the content of iridoid glycosides, which may be surprising as higher iridoid glycoside concentrations reduce herbivory on *P. lanceolata* in caterpillar feeding assays (Darrow & Bowers, 1999; Pellissier et al., 2014). However, feeding assays and natural herbivory measurements are often weakly correlated, which may explain the absence of a relationship in our field observations (Descombes et al., 2020). Or, alternatively, herbivory was driven primarily by specialist herbivores, which are less sensitive to variation in iridoid glycoside concentrations than generalist herbivores (Reudler et al., 2011). Elevation gradients can further complicate trait-herbivory relationships, as shifts in community composition of herbivores along elevation can favour generalists at higher elevations and specialists at lower elevations (Fernandez-Conradi et al., 2022).

In the case of powdery mildew infection, the width of the longest leaf emerged as a surprisingly strong predictor, exceeding the effect of leaf length. Because powdery mildews are primarily wind-dispersed, this result may reflect on the importance of the width of *P. lanceolata* leaves for the effective leaf area exposed to airborne propagules, thereby linking plant biomechanics and epidemiology (Tack et al., 2014). Taken together, trait-consumer relationships were consistent across environments, but plant origin populations varied in all traits involved in plant-consumer relationships, indicating that ecotypic differentiation may mediate plant-consumer relationships.

4.4 Conclusion

Our results show that intraspecific variation in plant functional traits can arise from both population differentiation and environmental effects, and that this variation can translate into differences in interactions with herbivores and pathogens. By combining a reciprocal transplant of plants and soils with measurements of multiple functional traits and consumer damage, we were able to uncover the ecological drivers of trait variation and link them to plant-consumer dynamics. Importantly, plant populations differed in several traits associated with herbivory and pathogen infection, suggesting that spatial variation in plant phenotype can mediate consumer interactions even when environmental responses are largely parallel among populations. These findings highlight that intraspecific trait variation can provide a mechanistic pathway linking environmental heterogeneity to variation in biotic interactions. More broadly, our study illustrates how trait-based approaches can improve predictions of species interactions under environmental change. Because climate and soil conditions are shifting across many ecosystems (Bobbink et al., 2010; Parmesan & Yohe, 2003), understanding how these factors generate trait variation within species, and how such variation influences trophic interactions, will be critical for predicting ecological responses to global change.

Acknowledgements

We thank the commune of Chur for allowing us to lease land for the experiment, P. Niklaus for his advice on experimental design, J. Gehler, B. Oberholzer, and L. Zhao for their help with field data, sample collection, and lab processing, J. Moser for her help in negotiating the land lease contract, and N. Zurbuchen and M. Jokinen for dismantling the common gardens. This work was supported by the University of Zürich and a PhD grant from the University Research Priority Program 'Evolution in Action' awarded to A-LL & AW, an Ambizione Grant (PZ00P3_202027) from the Swiss National Science Foundation to FWH, and a SNSF grant 179481 to SR. A-LL acknowledges funding from the 632 European Research Council (ERC AdG; Co-EvoChange 101097545) and the Research Council 633 of Finland (grant 311229) as well as funding from the University of Helsinki.

Author contributions

A-LL, AW, FWH, LADH & MR conceived and designed the study; FWH, LADH & MR installed the field experiment; FWH & MR collected and processed leaf samples; MR collected field data; GG & MR performed chemical analysis; MR analysed the data; MR & ALL wrote the initial version of the manuscript; all authors contributed to the final version of the manuscript.

Conflict of interest statement

The authors have no competing interests to declare.

Data and code availability

The data and code used to produce the analyses and figures have been submitted to GitHub (https://github.com/MichaelRechsteiner/CalTrans2021).

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Supplementary

Supplementary Table 1. Post-hoc tests of significant effects of plant populations and soil origins on traits, herbivory and fungal infection. Summary table of contrasts derived for the significant effects (see Table 1) in the linear models testing the significant drivers of trait variation, herbivory and fungal infection.

Response	**Contrasts**	**Estimate**	**SE**	**D.f.**	**p.value**
Nr. leaves	Low-elevation population - Mid-elevation population	0.146	0.070	277.052	0.093
Nr. leaves	Low-elevation population - High-elevation population	-0.239	0.070	277.085	0.002
Nr. leaves	Mid-elevation population - High-elevation population	-0.385	0.070	277.093	0.0000002
Leaf width	Low-elevation population - Mid-elevation population	0.047	0.090	277.032	0.862
Leaf width	Low-elevation population - High-elevation population	-0.362	0.090	277.058	0.0002
Leaf width	Mid-elevation population - High-elevation population	-0.408	0.090	277.063	0.00003
Leaf length	Low-elevation population - Mid-elevation population	1.395	0.656	277.011	0.086
Leaf length	Low-elevation population - High-elevation population	2.980	0.658	277.022	0.00003
Leaf length	Mid-elevation population - High-elevation population	1.585	0.658	277.024	0.044
IG conc.	Low-elevation soil - Mid-elevation soil	-2.531	2.400	255.455	0.543
IG conc.	Low-elevation soil - High-elevation soil	4.308	2.411	255.113	0.176
IG conc.	Mid-elevation soil- High-elevation soil	6.839	2.363	255.485	0.011
SLA	Low-elevation population - Mid-elevation population	0.796	0.918	270.017	0.662
SLA	Low-elevation population - High-elevation population	-2.486	0.919	270.023	0.02
SLA	Mid-elevation population - High-elevation population	-3.282	0.922	270.024	0.001
Chlorophyll	Low-elevation population - Mid-elevation population	-1.741	0.608	274.02	0.012
Chlorophyll	Low-elevation population - High-elevation population	-2.708	0.610	274.043	0.00004
Chlorophyll	Mid-elevation population - High-elevation population	-0.967	0.610	274.054	0.253
Chlorophyll	Low-elevation soil - Mid-elevation soil	-0.084	0.604	274.153	0.99
Chlorophyll	Low-elevation soil - High-elevation soil	-2.821	0.616	274.106	0.00002
Chlorophyll	Mid-elevation soil- High-elevation soil	-2.737	0.610	274.425	0.00003
Powdery mildew	Low-elevation population - Mid-elevation population	1.756	1.049	Inf	0.215
Powdery mildew	Low-elevation population - High-elevation population	-0.644	0.638	Inf	0.571
Powdery mildew	Mid-elevation population - High-elevation population	-2.399	1.021	Inf	0.049

Supplementary Table 2. Effects of transplant elevation on traits, herbivory and fungal infection. Summary table of the effect of transplant elevation on the width and length of the longest leaf, and powdery mildew infection.

Response	**Parameter**	**Coefficient**	**95% CI**	**D.f.**	**p-value**
Leaf width	Transplant elevation	-0.371	[-0.651, -0.092]	282	0.009
Leaf length	Transplant elevation	-2.622	[0.073, -1.915]	282	0.057
Powdery mildew	Transplant elevation	-2.267	[-0.609, -2.679]	-	0.007

Supplementary Table 3. Effects of traits on herbivory. Summary table of the effects of the number of leaves and SLA on herbivory.

Response	**Parameter**	**Coefficient**	**95% CI**	**D. f.**	**p-value**
Herbivory	Nr. leaves	-0.016	[-0.036, 0.005]	286	0.136
Herbivory	SLA	0.017	[-0.006, 0.041]	280	0.150

Supplementary Table 4. Effects of traits on powdery mildew infection. Summary table of the effects of the width and the length of the longest leaf on powdery mildew infection.

Response	**Parameter**	**Coefficient**	**95% CI**	**p-value**
Powdery mildew	Leaf width	1.014	[0.428, 1.598]	0.0007
Powdery mildew	Leaf length	0.101	[-0.040, 0.241]	0.160