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Plant adaptation to different climates shapes the strengths of chemically mediated tritrophic interactions

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Abstract

1. How plant traits evolve along geographical and climatic gradients has recently received increased attention because of anticipated climate change and associated shifts in insect distribution, whether they are herbivores or predators. This issue is particularly relevant for traits related to growth and anti-herbivore defence of plants, because both sets of traits are closely tied to fitness, and because being sessile organisms, plants tend to experience strong local selection. Despite widespread recognition that the abiotic environment imposes selection on plant traits, how temperature and water availability independently select for allocation to growth and defence against herbivores is not well-resolved, and even more so, when considering under-ground herbivory and tritrophic interactions involving plant herbivores and their predators.
2. To address heritable, climate-driven variation in root traits mediating tritrophic interactions, we performed a common garden experiment with four populations of common red fescue (*Festuca rubra*) encompassing the four corners of a precipitation by temperature gradient matrix.
3. We found that plants originating from wetter and warmer conditions, in addition to producing more biomass, also produced a blend of volatile organic compounds more attractive for predatory nematodes of root insect herbivores. Moreover, across populations, variation in nematode attraction was mediated by balancing the emissions of attractive and repulsive volatile compounds.
4. Our work builds towards better understanding how plant adaptation to climate interacts with adaptations to herbivores and their predators.

KEYWORDS
ecological gradients, entomopathogenic nematodes, indirect plant defences, multi-trophic interactions, plant–herbivore interactions, root herbivore, terpenoids volatile compounds

1 | INTRODUCTION

How climatic conditions shape plant phenotypes through local adaptation has long been a central question in ecology. For instance, when moving from warm and more stable environments to colder and harsher conditions, plants tend to evolve to produce smaller seeds, have earlier phenologies, slower growth rates and display greater investment into clonal reproduction (e.g. Chapin & Chapin, 1981; Körner, 2003; Moles et al., 2007; Montague, Barrett, & Eckert, 2008; Pellissier, Litsios, et al., 2016; Pilon, Santamaria, Hootsmans, & Vierssen, 2003). In a broader ecological context, climatic variation may also have an effect on interspecific interactions. Specifically, Dobzhansky (1950) postulated that the intensity of biotic interactions increases at the warmer and more stable tropical latitudes and this in turn should select for higher values of traits mediating these interactions (Schemske, Mittelbach, Cornell, Sobel, & Roy, 2009). Accordingly, tropical (Bolser & Hay, 1996; Coley & Aide, 1991; Coley & Barone, 1996; Moles, Wallis, et al., 2011; Rasmann & Agrawal, 2011) and low-elevation (Dostálek et al., 2016; Kergunteuil, Röder, & Rasmann, 2019; Pellissier, Roger, Bilat, & Rasmann, 2014; Scheidel & Bruelheide, 2004; Zehnder et al., 2009) plants should be selected for producing higher values of defence-related traits. Nonetheless, exceptions from this pattern exist (Moles, Bonser, Poore, Wallis, & Foley, 2011; Moles, Wallis, et al., 2011). Meta-analyses of latitudinal (Moles, Bonser, et al., 2011) or altitudinal (Rasmann, Pellissier, Defossez, Jactel, & Kunstler, 2014) gradients of plant defences fail to show clear support of the prediction, and suggest that other unaccounted factors, such as abundance of predators, might influence the overall defence patterns along the gradients (Johnson & Rasmann, 2011).

To defend against herbivores, plants produce physical structures, such as trichomes and spines, or toxins and digestibility reducers (Schoonhoven, van Loon, & Dicke, 2005). In addition, plants have been shown to mediate tritrophic interactions, by for instance releasing volatile organic compounds (VOCs) from their leaves (Turlings, Tumlinson, & Lewis, 1990), and roots (Rasmann et al., 2005) for attracting foraging predators, such as predatory wasps or soil-dwelling entomopathogenic nematodes (EPNs), respectively. While the production of secondary metabolites, such as VOCs, is highly dependent on the genetic make-up of plants, or the type of herbivore attacking the plants, their production is also influenced by abiotic factors such as temperature and humidity (Gouinguené & Turlings, 2002). Along elevation gradients, for instance, the diversity and abundance of VOCs have been shown to vary strongly between low- and high-elevation adapted ecotypes (Kergunteuil, Röder, et al., 2019) or species (Defossez, Pellissier, & Rasmann, 2018). Therefore, elevation patterns in plant defences are tightly bound to variations in climatic conditions per se. Indeed, shifts in climatic conditions along geographical clines can simultaneously modify the energetic ability of plants to produce and release VOCs (in harsher conditions, plants can simply not be able to produce more secondary metabolites), as well as the intensity of biotic interactions, ultimately dictating evolutionary changes in plant chemical defence trait expression (Hunter, 2016). Because reduced investment in one trait liberates energy allocation to other traits, we could postulate that in habitats where investment to direct plant toxicity is reduced (e.g. in colder environment), investment in traits mediating predator recruitment could be enhanced if predators are present (Godschalx, Rodríguez-Castañeda, & Rasmann, 2019).

The challenges in using ecological gradients for addressing the factors driving variation in plant defences are multiple. First, along large-scale geographical clines, variation in temperature and precipitation often co-vary. For instance, alpine ecosystems are clearly characterized by colder temperatures and shorter growing seasons, but at the same time, they also experience higher levels of precipitation and humidity than low-elevation habitats (Körner, 2007). Therefore, addressing the independent and relative contribution of both humidity and temperature on plant defences remains challenging when working along one linear ecological gradient. We took advantage of a natural precipitation by temperature gradient matrix in order to infer plant adaptation in communities exposed to climate change with increasingly warm and dry periods. Second, as mentioned above, variation in climates modifies plant growth parameters (Körner, 2003). Therefore, variation in plant defence traits can also result from variation in allocation to plant growth. Classically, it has been postulated that because carbon accumulation is slower in resource-poor environments, it is more cost-effective for these plants to allocate to defence than to regrowth (Coley, Bryant, & Chapin, 1985). However, such effects vary according to different scales of organization (Anstett, Nunes, Baskett, & Kotanen, 2016; Hahn & Maron, 2016). For instance, the observations that climatic conditions imposing slow growth (e.g. in cold habitats) select for higher levels of defences have been mainly highlighted when comparing species (Defossez et al., 2018; Fine, Mesones, & Coley, 2004), but not when analysing intraspecific variation (Kergunteuil, Röder, et al., 2019; Pellissier et al., 2014), in which a decline in defence in colder habitats has been mostly associated with lower herbivore pressure (Kergunteuil, Röder, et al., 2019; Pellissier et al., 2014).

We here used an integrative approach that combines behavioural assay and chemical analysis of VOCs to address the relative contribution of temperature and precipitation regimes on ecotypic trait differentiation for recruiting natural enemies under different herbivore treatments (Woods, Hastings, Turley, Heard, & Agrawal, 2011). Specifically, we addressed how plant growth and defence traits of the widely-distributed red fescue (*Festuca rubra* L.) have adapted to climatic gradients. To assess between-population differences in the ability to produce root VOCs for attracting EPNs, we performed climate- and herbivore-controlled below-ground olfactometer bioassays using clones of *F. rubra* originating from a natural environmental grid combining precipitation and elevation gradients (Knappová et al., 2018; Münzbergová, Hadincová, Skálová, & Vandvik, 2017).

We asked whether populations originating from different climatic conditions differ in (a) their ability to produce VOCs either constitutively or when damaged by generalist root herbivores (larvae of *Melolontha melolontha* F.), and (b) in the ability to attract EPNs. Finally, we asked (c) whether differences in VOC production and nematode recruitment are related to differences in root growth-related traits. We predicted that plants from colder regions (a) produce lower amounts of VOCs in relation to a potential relaxation of herbivore pressure at these sites and (b) attract less EPNs. Due to our experimental design, it is further possible to test for a humidity effect on plant–predator interactions independent of temperature, but we had no specific prediction for the direction of these effects. Finally, we predicted that (c) VOC production and root growth traits are correlated to form habitat-specific growth-defence strategies. With this work, we aim at extending previous research in clinal adaptation to below-ground tritrophic interactions, and unravelling the factors shaping covariations in plant defence and plant growth traits along ecological gradients.

2 | MATERIALS AND METHODS

2.1 | Studied species and field collection sites

Festuca rubra L. is a common perennial grass species of temperate and alpine grasslands in Europe. To address our questions, we took advantage of a fully crossed sampling design of *F. rubra* spp. *rubra* ecotypes growing along a natural climatic grid established in western Norway (the SeedClim Grid, Klanderud, Vandvik, & Goldberg, 2015). Out of the original 12 grassland localities (Klanderud et al., 2015), we selected the four most extreme localities in terms of precipitation and temperature, representing two levels of summer temperature combined with each of two levels of mean annual precipitation (Table S1, Figure S1): ALPINE 1 (cold–dry) – 1,208 m above sea level (asl), 596 mm of mean annual precipitation and 6.17°C mean summer temperature; ALPINE 4 (cold–wet) – 1,088 m asl, 2,725 mm and 6.58°C; BOREAL1 (warm-dry) – 589 m asl, 600 mm and 10.3°C; and BOREAL 4 (warm–wet) – 346 m asl, 2,923 mm and 10.78°C. In order to mainly focus on climatic variation across populations, the four initial sites were selected specifically to ensure that grazing regime and grazing history, bedrock, slope, aspect and vegetation types are as similar as possible. The geographical distance between sites is on average 15 km (Klanderud et al., 2015). While for methodological difficulties of sampling in the soils we do not have data on actual herbivore pressure along the climatic grid, we could speculate that herbivory varies with temperature and precipitation according to the most common pattern recorded world-wide. Several studies have showed that herbivore pressure decreases with elevation (i.e. with decreasing temperature and increasing precipitation), whether in Norway (Hill & Hodkinson 1995), Central Europe (Pellissier et al., 2014), Central Asia (Rokaya, Dostálek, & Münzbergová, 2016) or North America (Galen, 1990).

For the experiment, we used 10 genotypes from the initial set of 25 individual genotypes per population (Münzbergová et al., 2017) that were grown and maintained for two seasons in a common garden at the Botanical Institute, Czech Academy of Sciences (350 m asl, mean of the four warmest months, 16.5°C) with regular watering during the vegetation season. In a previous study (Münzbergová et al., 2017), on the same genotypes, we measured a wide range of functional traits related to the production of above- and below-ground biomass. These data were measured in four different growth chambers for each genotype, representing the four climatic extremes of the model system. Averages of these traits across growth chambers provide information on the performance of the genotypes. These data were used as additional plant growth-related explanatory variables in the current study. Using mean values of the growth traits from the previous study is justified as the differences among genotypes were generally stronger than the genotype × environment interactions (Münzbergová et al., 2017) and we use values integrated across four different environments to describe the performance of each genotype.

2.2 | Olfactometer experiments

All the olfactometer bioassays were performed according to a common garden procedure with homogeneous controlled conditions regarding temperature, water availability and herbivory. Any significant differences among plant populations for nematode recruitment reveal genetic differentiation of defensive phenotypes (Cheplick, 2015). In May 2017, 40 days before olfactometer experimentation, each individual genotype was separated into two equally sized tufts and potted in the glass cylinders of the olfactometer device (see Figure S2) using potting soil (Ricoter Erdaufbereitung AG and sand; 2:1) and later was transferred into a climate-controlled chamber (16-hr light 24°C: 8-hr dark 18°C and 55% RH). Plants were watered twice a week during acclimation prior experimentation. In total, we tested 7–8 genotypes per climatic site of origin with two herbivore treatments (‘healthy’ and ‘infested’) ($N = 60$ individual plants tested).

For each pair of plants originating from the same genotype, the ‘infested’ plant was inoculated with one 2nd instar larvae of common cockchafers (*M. melolontha* F., Coleoptera; Scarabaeidae). While adults of *M. melolontha* are all generalist leaf eaters, larvae are obligate root feeders of a wide range of plants, including species in the Poaceae family such as *Festuca* spp. (Gyawaly, Koppenhöfer, Wu, & Kuhar, 2016). Three days later, the olfactometers were assembled as shown in Figure S2, with the connecting arms filled with white sand (10% humidity (Rasmann et al., 2005)), and 24 hr later, the middle of the two-arm olfactometers was inoculated with 2,000 individual *Heterorhabditis megidis* (Rhabditida: Heterorhabditidae) EPN-infective juveniles. We used *H. megidis* because they are generally widespread, they have been shown to rely on host–plant cues for several systems such as coniferous plants, graminoids and other angiosperms (Rasmann, Ali, Helder, & Putten, 2012), and their infection generally results in relatively fast larval mortality (i.e. after 7 days) for different Scarabaeidae species (Koppenhofer & Fuzy, 2004). In order to limit behavioural bias in plant-mediated interactions, all the behavioural assays were carried out with a single laboratory-reared strain collected in Switzerland (i.e. nematodes were naïve regarding any plants originating from the four studied localities). One day after EPN inoculation, nematodes were extracted from the sand of the side arms using the Baermann funnel method (Rasmann et al., 2005). Finally, roots were carefully water-washed, ground to powder in liquid nitrogen and placed in 20-ml glass headspace vials for VOC analysis.

2.3 | Chromatographic analyses of VOCs

The root material collected following the olfactometer tests was stored at −80°C before solid-phase microextraction (SPME) analysis. Samples were added with 20 ng of tetralin (CAS # 522651; Sigma-Aldrich) as internal standard (IS), and incubated for 3 min at 35°C, after which a 100 μm polydimethylsiloxane (PDMS)-coated fibre (Supelco) was inserted into the vial for 20 min. Compounds were thermally desorbed from the fibre during 210 s (splitless mode, 250°C, 6.5 psi pressure, 210 ml/min purge flow, helium carrier gas) and immediately injected onto a GC column (HP-5MS columns [30 m length × 0.25 mm i.d., and 0.25 μm film thickness, Agilent]). The initial column temperature in the oven (Agilent 7890A) of 50°C was ramped at a rate of 6°C/min until 250°C (hold time 1 min) and finally for 3 min post-run at 260°C. The helium constant flow rate was 0.9 ml/min. Peak detection was performed on a mass detector (Agilent 5975C) with transfer line temperature at 280°C, ion source and quadrupole temperatures at 230°C and 150°C, respectively, and with electron impact (EI) mode over the mass range of 33–250 m/z. Compounds were identified using pure standards, or tentatively, using the NIST library in comparison with well-resolved plant species (e.g. corn). Peak area for each detected compound was divided by the peak area of the internal standard, and root emissions of volatiles were finally given as tetralin equivalent nanograms of compound released by gram (fresh weight) of root biomass.

2.4 | Statistical analyses

Volatile organic compounds and plant growth trait analyses – We assessed the effect of site of origin (four levels) and herbivory (two levels), and their interactions on the amount and composition of the VOCs produced by *F. rubra* plants using permutational multivariate ANOVA (PERMANOVA). We used the *adonis* function in the *VEGAN* package (Oksanen et al., 2013) in R (R Development Core Team, 2017) to calculate dissimilarities among samples using the Bray–Curtis metric. Similarly, we assessed the effect of site of origin on plant growth trait matrix (rhizome biomass, total root biomass, shoot biomass, root-to-shoot ratio, plant height, number of ramets) using multivariate PERMANOVA (*adonis* function in VEGAN). The growth trait dissimilarity matrix was calculated using the Bray–Curtis metric. Next, we assessed the strength of the correlation between the plant growth trait matrix and the VOC matrix with a coinertia analysis (*coinertia* function in the package (Dray & Dufour, 2007)). The significance of the shared variance was assessed using a Monte Carlo test as implemented in *ADE4*. In other words, we here sought for a correlated structure of plant growth and chemical defences across sites (Defossez et al., 2018; Pellissier, Moreira, et al., 2016), in which plant genotypes could vary in the simultaneous expression of VOCs and plant growth traits. The correlation between root growth traits and VOCs is meaningful since the amount of VOCs analysed was calculated on a per unit of biomass (mg) basis, therefore independent of the size of the roots. Because the coinertia analysis indicated a significant correlation between the VOCs and growth trait matrices (see results), we further extracted the most important traits driving such correlations using the *envfit* function in VEGAN and plotted them on a NMDS graph. In other words, here we sought to determine whether larger sized plants also produced more VOCs, independently of their total root biomass.

Nematode recruitment analyses – We assessed the effect of site of origin (four levels), herbivore damage (two levels) and their interaction on the number of nematodes collected in the olfactometer arms using a generalized linear model (function *glm* in R) with quasi-Poisson distribution in order to take into account overdispersion (Rasmann et al., 2005). Significant differences were estimated with likelihood-ratio tests, and pairwise comparisons across sites of origin were performed using post hoc tests (*glht* function in the *MULTCOMP* package (Hothorn, Bretz, & Westfall, 2008)).

Correlation between VOC production and root growth – We further sought to explain nematode recruitment by the production of VOCs and overall root growth parameters. In order to do that, we performed linear regressions between the main axis of the coinertia analysis representing the shared covariation between VOCs and plant growth (see above) and the number of EPNs recruited. The strength of the correlation was tested using mixed-effect models, by including site as random effect on the regression analysis between the number of nematodes and the first coinertia axis (*lme* function in the package *NLME* (Pinheiro, 2012)).

Detection of individual VOC effect – We performed a Random Forest analysis, package *randomForest* (Liaw & Wiener, 2002) on all VOCs to extract individual VOCs that most explain nematode recruitment. The first 6 VOCs together explained 91% of the total variance. Therefore, we performed mixed-effect linear regression analyses (site as a random factor) between each one of these 6 VOCs and nematode recruitment.

3 | RESULTS

3.1 | VOC emissions and plant growth traits

Across the four populations of *F. rubra*, we retained 20 VOCs that were specifically produced either constitutively or induced upon root herbivore damage (Figure 1, Figure S3). The PERMANOVA analysis detected a positive effect of site of origin (Figure 1, Figure S4; $F_{3,77}$ = 3.41, p = 0.003), herbivore treatment ($F_{1,77}$ = 2.74, p = 0.04) and their interaction ($F_{3,77}$ = 1.86, p = 0.06). Beyond the general influence of herbivory on VOC profiles, we reported independent effects of root herbivores on single compounds (Figure S5). Herbivore treatment resulted in a differential increase or reduction in specific compounds. Interestingly, this differential expression depended on the sites of origin (Figure S5). Differences in volatile profiles across plant populations were reflected by variations in total amount of VOCs along the two ecological gradients, that is temperature and precipitation, embedded in our natural system. Contrary to our expectations, plants originating from cold environments released 50% more VOCs than the plant from warm conditions (Figure 2a). On the other hand, plants from wet habitats produced 2.6 times more VOCs as compared to plants from dry habitats (Figure 2b). Plant populations also tended to segregate in the growth parameter space (site effect; $F_{3,77}$ = 2.09, p = 0.06), with populations from the warm and wet environment displaying the highest above- and below-ground biomass.

The coinertia analysis indicated a shared common structure between the VOC matrix and the plant growth trait matrix (r = 0.28, Monte Carlo test on 999 replicates; p < 0.001). Along the principal axis of coinertia, plants' phenotypes change from displaying high root and shoot biomass and height and preferential production of VOCs 8, 9, 11, 16 and 18 (Figure S6), to small plant size, high root-to-shoot ratio and preferential production of VOCs 2, 4, 12, 10, 17 and 20 (Figure S5). The envfit analysis indicated that the NMDS ordination of VOCs is mostly associated with plant shoot biomass

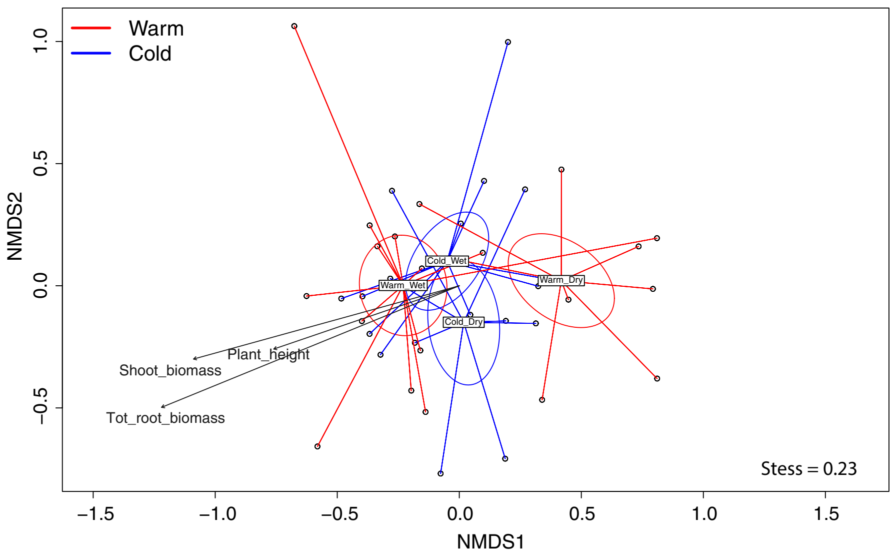

FIGURE 1 Environmental fitting analysis. Shown are the two axes of a non-metric multidimensional scaling (NMDS) ordination of individual VOCs of *Festuca rubra* plants separated by site of origin (i.e. four different climatic populations). Arrows represent significant correlations ($p < 0.05$) of plant growth traits with the ordination. Lines connect all the samples to the centroids of each population, and ellipses indicate 95% confidence intervals around the centroids

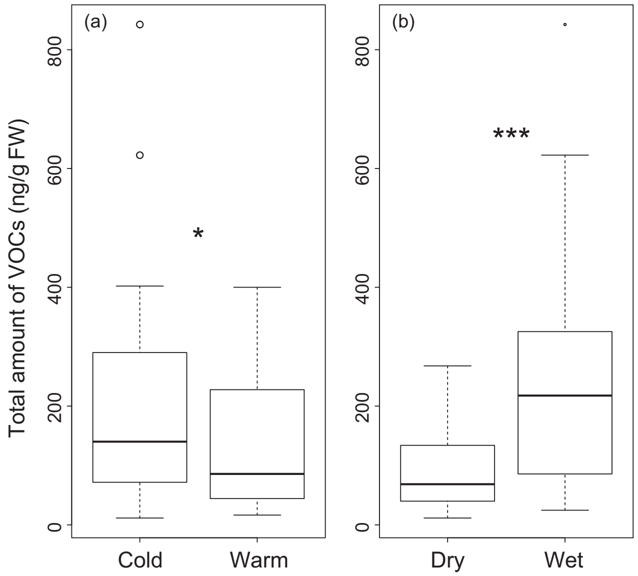

FIGURE 2 Total VOC production across (a) elevation gradient (warm = low-elevation plants; cold = high-elevation plants) and (b) precipitation gradient composing the environmental grid of our natural system. Significant differences were tested with a linear model (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$)

($r^2 = 0.22$, $p = 0.001$), plant height ($r^2 = 0.11$, $p = 0.01$) and belowground biomass ($r^2 = 0.29$, $p = 0.001$) (Figure S4).

3.2 | Nematode recruitment

Overall, nematode behaviour was influenced by site of origin (Figure 3, GLM, quasi-Poisson, $X^2 = 50.46$, $df = 3$, p-value < 0.001). Plants from warmer sites recruited 27% more nematodes than cold-adapted plants (Figure 3), and plant populations from wet habitats were more than twice more attractive compared with dry-habitat populations (Figure 3). Contrary to expectations, we did not detect an effect of herbivore treatment on nematode recruitment (herbivore treatment effect: $X^2 = 0.69$, $df = 1$, p-value = 0.41; interaction between site and herbivore treatment: $X^2 = 3.84$, $df = 3$, p-value = 0.28). Across all treatments, we found that nematode recruitment was independent of root biomass (linear mixed-model with plant ecotypes as random factor; $F_{1,83} = 1.89$, $p = 0.18$). However, because herbivore infestation significantly reduced root biomass (LMM, site of origin as random factor, $X^2 = 12.50$, $df = 1$, $p < 0.001$), when comparing infested and non-infested plants, nematode attraction per gram of root was higher for infested plants (GLM, quasi-Poisson, $X^2 = 19.78$, $df = 1$, $p < 0.001$). Therefore, after accounting for root biomass effect (mixed-effect model for root biomass on EPN attraction with ecotypes as random factor, $r = -0.16$, $F = 1.90$, $p = 0.17$), only plants from cold and dry environments tended to be more attractive after herbivore infestation as compared to uninfested plants (Figure S7; GLM, quasi-Poisson, $X^2 = 2.93$, $df = 1$, p-value = 0.09).

Across all plants tested, the first coinertia axis negatively correlated with the number of nematodes recruited (Figure 4; mixed-effect linear regression analysis; $r = -0.79$, $t = -3.03$, $p = 0.03$). These results corroborate an enhanced nematode recruitment for high temperature–high moisture plant growth phenotype (high plant size, high root and shoot biomass) and point to a positive correlation between volatiles released by such ecotypes (VOCs 8, 9, 16 and 18) and the attraction of the third trophic level. On the contrary, cold-habitat plant growth phenotype (small plant size, high root-to-shoot biomass), which was associated with the production of VOCs 2, 10, 12 and 20, recruited fewer nematodes.

3.3 | Effect of VOCs on nematode recruitment

Random Forest analysis showed that α-curcumene (VOC16), nonadecatriene (VOC9), decane (VOC20), α-muurolene (VOC17), 1-undecene (VOC8) and –octanone (VOC4) (Figure S8) best predicted nematode recruitment. Particularly, we found strong attractiveness for two hydrocarbons; 1-undecene (Figure 5a) and nonadecatriene

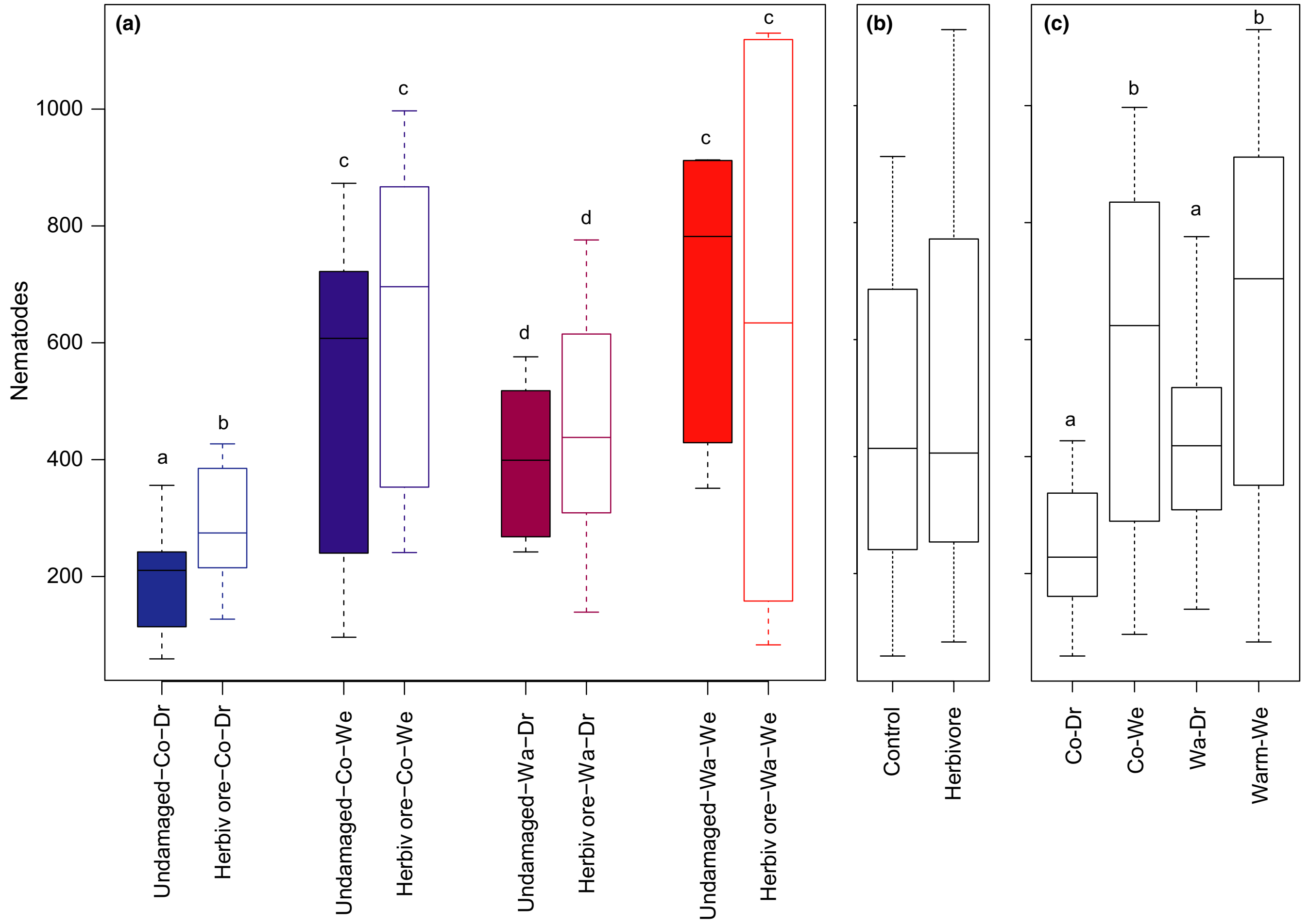

FIGURE 3 Nematode recruitment. Boxplots in panel (a) show the number of entomopathogenic nematodes *Heterorhabditis megidis* recruited near roots that were either undamaged (filled bars) or damaged by *Melolontha melolontha* larvae for 3 days (open bars) ($n = 6$) and across four climatic populations: Co-Dr = cold and dry, Co-We = cold and wet, Wa-Dr = warm and dry, and Wa-We = warm and wet. Different letters above boxes indicate significant differences (post hoc pairwise comparisons, $p < 0.05$). Panels (b and c) show the marginal means for the two herbivore treatments and the four climatic populations, respectively

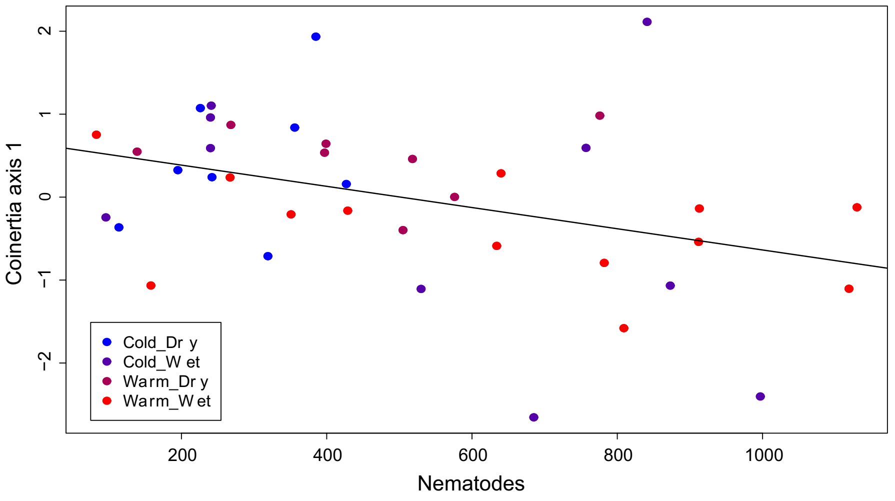

FIGURE 4 Relationship between the first coinertia axis and nematode recruitment. The coinertia axis corresponds to plant phenotypic variation that spans plants that have higher biomass (Figure S5a) and produce a characteristic VOC blend of producing more of VOCs 8, 9, 16 and 18 (see Figure S5b) to smaller plants that produce mainly VOCs 2, 10, 12 and 20 (Figure S5). Linear regression analysis; $r = -0.79$, $t = -3.03$, $p = 0.03$

(Figure 5b), and one sesquiterpene; α-curcumene (Figure 5c), but repulsion for decane (Figure 5d). Generally, nematodes tended to be attracted to plants emitting larger total amounts of VOCs (Figure 5e).

4 | DISCUSSION

We tested for the effect of temperature and humidity on the ecotypic differentiation in below-ground predator recruitment by performing

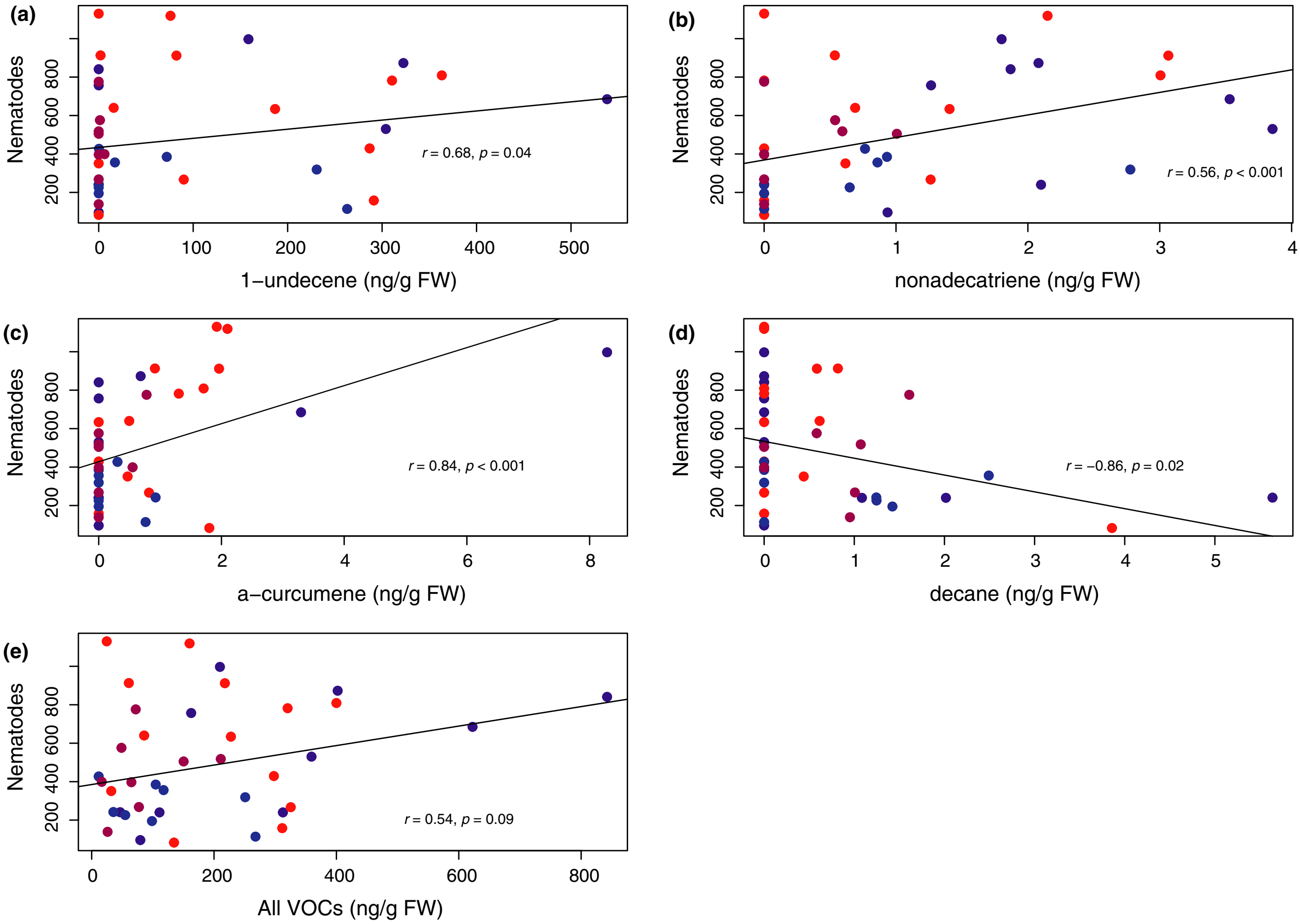

FIGURE 5 Relationship between VOCs and nematode recruitment. Shown are the relationship between (a) 1-undecene and nematodes, (b) nonadecatriene and nematodes, (c) a-curcumene and nematodes, (d) decane and nematodes and (e) the total amount of VOCs produced and nematodes. Colours of dots correspond to different climatic populations of *Festuca rubra* (see legend in Figure 4)

common garden bioassays on clones of plants originating from four contrasting climatic conditions. We found that ecotypes from wetter habitats, independently of temperature of origin, produced more VOCs and attracted more EPNs near their roots, regardless of plants being infested with root herbivore larvae. Overall, the enhanced production of specific blends of VOCs, including aliphatic hydrocarbons and sesquiterpenes, favoured EPN recruitment in wet-habitat originating plants, while the production of other aliphatic hydrocarbons (decane) by plants from colder and dryer sites diminished EPN attraction.

4.1 | VOC production and EPN recruitment

Root production of specific VOC blends has been associated with EPN recruitment in several systems (e.g. see review in Johnson, Benefer, et al., 2016; Rasmann et al., 2012; Turlings, Hiltpold, & Rasmann, 2012). For instance, the production of sesquiterpenoid and other volatile compounds was proven to be the major cues for attracting infective juvenile EPNs near the site of wounding in the roots of corn (Rasmann et al., 2005), citrus and blueberries plants (Ali et al., 2012; Ali, Alborn, & Stelinski, 2011). Through Random Forest analyses, we highlighted several VOCs that best explained EPN recruitment, including a sesquiterpene and two hydrocarbons. Interestingly, we also observed a negative correlation between another hydrocarbon (decane) and EPN recruitment, and plants from dry and cold sites produced more of this compound. Therefore, EPN recruitment, besides a general overall dose-dependence relationship (i.e. more total VOCs is equal to more nematodes recruited), is the results of a delicate balance of the VOCs mixture, which is in turn a result of plants adapting to different climatic conditions (Moore, Andrew, Kulheim, & Foley, 2014). Herbivore-infested plants of cold and dry site recruited more efficiently EPNs as compared to control plants. In line with above, those herbivore-infested plants were the only ones that reduced decane production after herbivore attack, suggesting a strong role of repulsive VOCs in the system and strong dose dependence, which might be under a diffuse selective regime involving other soil-dwelling organisms such as root herbivores (Robert et al., 2012). The ultimate net impact of EPNs on plant fitness (i.e. trophic cascades) was not measured here, but some speculations can be drawn. First, plants from the warmer environments were suffering the most damage in terms of root biomass loss (see

Figure S9), but were also the ones attracting most EPNs, even when undamaged. Therefore, those plants might invest more in indirect defences (i.e. VOCs for attracting predators) than in direct resistance. In a previous study, we showed that *F. rubra* ecotypes attracting more EPNs in olfactometers were those also surviving the best in the field, under herbivory (Kergunteuil, Röder, et al., 2019). Investment in attractive VOC blend production seems thus an efficient strategy for warding off herbivores, even when direct resistance is impaired.

4.2 | Plant growth-defence allocation strategies

We found strong ecotypic variation in plant traits depending on the site of origin of the plants. Overall, plants from wetter habitats produced higher root biomass (Münzbergová et al., 2017), and the highest amount of VOCs per gram of roots. Accordingly, we found that plants from wetter sites attracted the highest number of EPNs. Interestingly, plant chemical and structural traits were correlated at the phenotypic level, suggesting correlations among ecophysiological traits. In other words, this indicates that plant adaptation to a particular environment requires a generalized restructuration of the plant phenotype (Agrawal & Fishbein, 2006). Whether such correlation is driven by genetic linkages between growth-related and defence-related traits (e.g. by controlling antagonistic hormonal pathways (Lowry, Popovic, Brennan, & Holeski, 2019)), or whether traits are correlated because of common responses to local conditions, has yet to be determined. Nonetheless, using these same ecotypes, it was previously observed that growth-related traits are correlated with a range of physiological traits and that such correlated phenotypic and physiological restructuration across habitats is related to genetic differentiation (Stojanova et al., 2018). In line with this, Rokaya et al. (2016) demonstrated that *Salvia nubicola* from higher elevations grew smaller and was better defended against herbivores, despite Dostálek et al. (2016) showing that high-elevation plants contain lower diversity of defensive phenolic compounds. Therefore, it seems that adaptation of *F. rubra* plants to wet habitats facilitates a general below-ground strategy of higher predator-mediated resistance against herbivores, while at the same time also an increased biomass production. On the contrary, results obtained when studying above-ground direct resistance on the same system showed that *F. rubra* clones from colder and wetter sites had the highest amount of phenol-based compounds (in the undamaged state at least), while the highest amount of silica and highest resistance against a leaf-chewing generalist caterpillar were observed on plants from warmer sites (Knappová et al., 2018). In other words, differences in above-ground defences were mainly driven by temperature but not by precipitations in the same system. Taken together, these findings suggest that selection for individual traits related to growth and defences is uncoupled across above- and below-ground organs, and both evolve independently based on the specific selective regimes in the different compartments of the ecosystem.

4.3 | Allocation strategies of VOC production

Theory postulates the existence of trade-offs between different types of defences and defence-deployment strategies (Agrawal, Conner, & Rasmann, 2010). For instance, a trade-off between constitutive defences and their inducibility should exist based on the fact that both defences use the same set of resources (Thaler & Karban, 1997). It was postulated that the patterns of defence induction depend on the probability of attack and the value of the tissues eaten (Zangerl & Rutledge, 1996). Hence, plants or organs that are regularly attacked or that are highly valuable should have greater constitutive defences. In our study, we did not look specifically for trade-offs, but as argued above, we observed that plants of cold and dry origin invest more in inducibility of defences, while particularly plants of warm and wet origin invest more in the constitutive production of VOCs. This is in line with previous work by Rasmann, Buri, et al. (2014) along elevation gradients. It was shown that *Vicia sepium* plants growing at low elevation, where herbivore pressure is strong, produce constitutively a copious amount of VOCs in their above-ground organs for attracting ants, while at the highest elevation end, in environments where herbivores are more haphazardly spread, the inducibility of VOC production is higher. In addition, we can suppose that plants growing in cold and dry environments are exposed to poor-soil resources as compared to plants originating from warm and wet conditions. Although this resource depletion may limit plant defence to inducible strategies (Stamp, 2003), further efforts are required to disentangle the role of nutrient and herbivory gradients in clinal adaptation of plants. For this purpose, the exact amount of annual herbivory these plants experience in their roots remains to be assessed. To date, we do not have specific evidence in how much root herbivory happens along the slopes of the Norwegian fjords. Similar research in the Central Alps has shown a general decline of above-ground herbivore pressure at high elevation (cold and wet habitats) compared with low elevations (warm and dry habitats) (Defossez et al., 2018; Pellissier et al., 2012), and a decrease in soil biodiversity with increasing elevation (Kergunteuil, Campos-Herrera, Sánchez-Moreno, Vittoz, & Rasmann, 2016; Kergunteuil, Röder, et al., 2019). Despite years of research, quantifying herbivory in natural populations remains a major challenge in ecology (Johnson, Bertrand, & Turcotte, 2016; Salazar & Marquis, 2012), and even more, in below-ground systems (Johnson et al., 2007; Johnson & Rasmann, 2015). Therefore, to accurately assess the interactive effect of climate and herbivore pressure, future common garden experiments in the field that manipulate herbivory will be needed.

4.4 | Concluding remarks on plant adaptation to climate change

The observed genetically based variation in *F. rubra* traits from climatically-differentiated populations is indicative of strong climatic selection and sufficiently limited gene flow to allow for local adaptation

(Endler, 1977). Current climate change is modifying the structure of communities, and the selective forces on a broad array of organisms (Parmesan, 2006). Thus, for species with broad distributions along climatic clines, such as *F. rubra*, adaptation to climate change might be possible, thanks to high variation in plasticity and trait expression (Münzbergová et al., 2017), which is determined both genetically and epigenetically (Münzbergová et al., 2017). The current paradigm of increasingly warm and dry periods in places generally cold and wet, such as at high elevations, indicates that alpine communities should experience a reshuffling in composition through low-land adapted invading plant species (Steinbauer et al., 2018), and rapid invasion of novel herbivores (Rasmann, Pellissier, et al., 2014). Therefore, in the near future, plants growing at higher elevation should experience higher levels of competition and herbivory. However, the extent of adaptation necessary to survive such new threats might not be sufficient (Pellissier & Rasmann, 2018), in part because of genetic constraints and barriers to dispersal and gene flow (Aitken, Yeaman, Holliday, Wang, & Curtis-McLane, 2008; Davis, Shaw, & Etterson, 2005; Etterson & Shaw, 2001; Skelly et al., 2007). *F. rubra* has shown strong potential for adaptation over steep climatic gradients, and potential for uncoupled above- and below-ground growth and defence traits' evolution. Therefore, our work contributes to better understanding how plant adaptation to climate change will interact with adaptations to above-ground and below-ground herbivores and predators.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHORS' CONTRIBUTIONS

A.K., S.R. and Z.M. conceived the ideas and designed methodology; A.K. and L.H. collected the data; A.K. and S.R. analysed the data; S.R., A.K. and Z.M. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

All data for this paper are available from Dryad Digital Repository https://doi.org/10.5061/dryad.174v48d (Kergunteuil, Humair, Münzbergová, & Rasmann, 2019).

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