Increasing intraspecific plant chemical diversity at plot and plant level affects herbivorous, predatory, and pollinating arthropod communities

Lina Ojeda-Prieto[1], Eliecer L. Moreno[1], Robin Heinen[1*], Wolfgang W. Weisser[1*]

[1] Terrestrial Ecology Research Group, Department for Life Science Systems, TUM School of Life Sciences, Technical University of Munich, 85354 Freising, Germany.
*These authors supervised the project equally and share the last authorship

Author for correspondence
Lina Ojeda-Prieto
Terrestrial Ecology Research Group, Department for Life Science Systems
Technical University of Munich
Hans Carl-von-Carlowitz-Platz 1. 85354, Freising, Germany
lina.ojeda@tum.de

ORCIDs
Lina Ojeda-Prieto: 0009-0003-6069-901X
Eliecer L. Moreno: 0009-0008-3798-3326
Robin Heinen: 0000-0001-9852-1020
Wolfgang W. Weisser: 0000-0002-2757-8959

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Summary

1. Plant chemistry mediates interactions between plants and their environment. While intraspecific chemodiversity at the plant level is well-studied, the effects of groups of plants differing in chemistry on interactions need more attention. We conducted a field experiment to test how intraspecific chemodiversity affects plant-arthropod interactions.

2. We manipulated plots of *Tanacetum vulgare* L., differing in chemotype richness and composition, and monitored four arthropod groups (herbivores, flower visitors, predators, and ants) over three seasons. We hypothesized that higher plot-level chemotype richness enhances occurrence across all studied arthropod groups and that the effect on abundance would be negative for herbivore and ant abundance and positive for flower visitors and predators.

3. Our findings, as revealed by mixed models, show that with increasing plot-level chemotype richness, herbivore abundance decreased, flower visitor abundance increased, and predatory arthropods and ants remained largely unaffected.

4. These results underscore the role of plant chemical diversity in shaping insect communities and contributing to ecosystem dynamics.

Key words: aphids, flower visitors, herbivores, insects, predators, plant-insect interactions, *Tanacetum vulgare* (tansy), terpenoids

Introduction

Biodiversity is recognized as a driver of ecosystem functioning and stability (Mora et al., 2014; Espinosa-García, 2022). Biodiversity studies have focused on species richness, examining how increasing plant community diversity affects ecosystem-level processes (Schulze & Mooney, 1992; Cardinale et al., 2006; Eisenhauer et al., 2011; Weisser et al., 2017). Plant communities with greater species richness are linked to a more diverse community of organisms (Ebeling et al., 2018), alterations in food web structure (Giling et al., 2019), and increased ecosystem process rates (Hertzog et al., 2017; Meyer et al., 2017). While species-level diversity has been well-studied, recent research explores biodiversity within species (Crutsinger et al., 2006; Koricheva & Hayes, 2018; Raffard et al., 2019; Noto & Hughes, 2020; Zerebecki & Hughes, 2023; Govaert et al., 2024; Konefal et al., 2024).

One component of within-species diversity is chemodiversity (Müller et al., 2020; Wetzel & Whitehead, 2020). Chemodiversity refers to the variety of chemical compounds produced by organisms (Whitehead et al., 2021; Walker et al., 2022). These compounds, including terpenoids, alkaloids, and phenolics, play diverse roles in plant defense (Hare, 2011; Wetzel et al., 2023), communication, and reproduction (Hartmann, 2007; Whitehead et al., 2022), potentially altering ecosystem dynamics like herbivory rates and pollinator preferences (Eisenring et al., 2021; Müller & Junker, 2022). Chemodiversity affects ecological interactions, impacting richness, diversity, and community structure (Dyer & Jeffrey, 2021; Fernandez-Conradi et al., 2022; Petrén et al., 2023). Studies have shown cascading chemodiversity effects within food webs (Kos et al., 2011; Bálint et al., 2016; Senft et al., 2019).

Intraspecific chemodiversity can be investigated at different scales, from individual plants to larger groups like plots or populations (Müller et al., 2020; Ojeda-Prieto et al., 2024). Research at the plant level has focused on chemodiversity effects on arthropod-plant interactions (Kos et al., 2011; Senft et al., 2017; Benedek et al., 2019). For instance, field observations show certain compounds influence herbivore preference and performance (Kleine & Müller, 2011; Clancy et al., 2018), as well as natural enemies' behavior and reproductive success (Benedek et al., 2015; Zytynska et al., 2019). Manipulative studies reveal that plants with different chemical compositions differ in attractiveness to aphids (Neuhaus-Harr et al., 2024) and herbivore performance (Jakobs & Müller, 2018), reinforcing the role of chemodiversity in plant-arthropod interactions.

Larger-scale studies in chemodiversity are scarce and predominantly correlative. Studies have examined how local chemotype richness influences arthropod communities (Hauri et al., 2021; Espinosa-García, 2022), but questions remain on the responses of different arthropod groups. Manipulative experiments, directly testing the consequences of a gradient of chemotype richness at the group level, show that increasing chemodiversity correlates with higher herbivore diversity but lower plant damage (Bustos-Segura et al., 2017). By systematically manipulating plot-level chemotype richness (CR), we aim to understand how chemodiversity at plant and plot levels shapes arthropod abundance and occurrence. Due to their distinct ecological roles, chemodiversity's effects are expected to vary among arthropod groups. This complexity has not been fully addressed, highlighting the need for comprehensive experimental approaches on arthropod groups and their interactions with plants.

Different plant-interacting groups, such as herbivores, flower visitors, predators, and ants, may share different co-evolutionary histories with – and offer different selective pressures to - the plant that have likely shaped its chemical composition by selecting chemical profiles that serve optimal plant fitness (Dyer & Jeffrey, 2021; Schneider et al., 2021; Whitehead et al., 2021, 2022). Arthropod **abundance** is influenced by plant attractiveness and resource suitability, but it is also shaped by a complex interplay of factors, including predator-prey dynamics, trophic cascades, and habitat structure. However, conceptually, these relationships are best understood from a plant-centered perspective. For herbivores, plants may benefit from having a diverse bouquet of chemicals to deter herbivores and reduce their abundance and impact on the plant (Glassmire et al., 2019; Kariñho-Betancourt, 2020; Zu et al., 2020; Rabelo et al., 2023). For predatory arthropods, plants may benefit from their presence as predators may control herbivore populations (Barbosa et al., 2009; Turlings & Erb, 2018). Therefore, it is likely that more diverse blends of compounds may have evolved in part to attract predatory arthropods (De Boer et al., 2004, 2008; Clavijo McCormick et al., 2012). Similarly, many flower visitors play a crucial role in pollination (Jacobsen & Raguso, 2018; Dantas et al., 2020). Plants may evolve specific compounds to attract more flower visitors, and more diverse profiles attract more visitors. Ants may have positive, negative, or no effects on plants (Yamawo et al., 2021; Ramos et al., 2022). Given that many ants engage in mutualisms with herbivorous aphids, it may be beneficial for plants to evolve repellant compounds. On the other hand, if ants engage in protective mutualisms with plants, it may be beneficial for plants to evolve attractant compounds. Therefore, hypotheses regarding relationships between plant chemodiversity and ant abundance will likely depend on the role of the ants in the study system. Concerning

the **occurrence** of arthropods, higher chemodiversity likely favors arthropod occurrence by increasing the likelihood that a specific compound can be used as a host recognition cue (Lampert et al., 2010; Dyer, 2018; Jacobsen & Raguso, 2018). As a chemical profile is, by definition, a result of cumulative selection processes that have taken place over evolutionary history, compounds may serve unique or dual purposes depending on the interactions. Understanding how plant chemodiversity impacts arthropod communities will provide insights into the evolutionary forces shaping it.

Despite extensive research on plant chemodiversity's effects on arthropod communities, gaps remain. Studies often test only one arthropod group, focus on short-term effects, or compare high vs. low chemodiversity without examining a gradient. Our study addresses these gaps by manipulating the chemodiversity gradient and observing the responses of different arthropod groups over several seasons.

We used *Tanacetum vulgare* L. (tansy), an herbaceous plant with high intraspecific variation in terpenoids, to investigate how variation in the number of tansy chemotypes in a plot affects associated arthropod communities. In a field experiment with 84 plots (six plants each), we manipulated plot-level chemotype richness (CR; i.e., 1, 2, 3, or 6 chemotypes present in a plot) and studied its effects on herbivores, flower visitors, predators, and ants (Fig. 1). We examined the effects of chemodiversity on arthropod occurrence and abundance at the plot level, recognizing that responses may differ across groups due to their distinct ecological roles and interactions with plants. Additionally, we investigated the effects of each of the six chemotypes on arthropod communities, anticipating differential responses based on compound attractiveness or repellence.

We specifically tested the following hypotheses:

H1: Plots with higher chemotype richness will have increased probabilities of arthropod occurrence across groups.

H2: Plots with higher chemotype richness will have decreased herbivore and ant abundances but increased predator and flower visitor abundances.

H3: The presence of certain chemotypes in a plot will have specific effects on herbivores, predators, flower visitors, and ants, potentially influencing their abundance and occurrence patterns.

Materials and Methods

Experimental design

Tansy chemotypes were characterized based on their leaf terpenoid compositions. We selected six chemotypes ('Athu-Bthu', 'Bthu-high', 'Bthu-low', 'Chrys-acet', 'Mixed-high', and 'Mixed-low‘) with three biological replicates each (Fig. S1-1). These chemotypes were propagated via stem cuttings and utilized in a field experiment at the Jena Experiment site in Germany in 2021. The experiment consisted of 84 1m^2 plots, each containing six tansy plants. The plots were designed to vary in chemotype richness levels ranging from 1 to 6 (Fig. S1-2), with 12, 30, 30, and 12 replicate plots, respectively, for each level. Each plot's chemotype composition was pre-assigned, ensuring biological replication of each chemotype combination across the experiment. Plots were distributed equally among six randomized blocks, with specific numbers of plots allocated per

chemotype richness level within each block (more detail in: Ojeda-Prieto et al., 2024)

Insect sampling

From 2021 to 2023, we assessed herbivores, flower visitors, predators, and ants. Specific sampling dates are shown in Table S1-1. Each year, herbivore communities were monitored by counting individual aphids on the plants from their first appearance until nearly none were found. Although the focus was on aphids, other herbivores were scarce. Therefore, the generalization to herbivores here reflects predominantly aphids. Counts were conducted 13 times from June to August 2021, eight times from May to August 2022, and three times from June to August 2023. Each count, executed within a day between 7h and 19h, involved a meticulous scan of each plant, which started from the tip of each stem and proceeded to the end, examining both sides of each leaf. Identification of aphid species followed the key provided in Supplementary Information 1 (S1). When multiple aphid species were present on a plant, we recorded the total number of each. In cases of high aphid densities (>100), we estimated the total by counting aphids on 1 cm of stem or 1 cm^2 of leaf three times in different stems and leaves for each plant, then multiplying the average by the estimated lengths of stems (in cm) or the estimated areas of leaves (in cm^2) colonized by the aphids. We used plot-level occupancy and cumulative plot-level number of aphids to analyze occurrence and abundance.

Flower visitors were assessed by counting the flower heads of individual plants during the flower-visiting recording. Flower visitors were counted three times in July 2021 and once in August 2021. Surveys lasted three minutes per plot and were conducted in random block order from 9h to 15h under optimal weather

conditions (no gusts of wind or precipitation). Flower visitors were identified at the order level. We used presence absence data to analyze the effects of CR and chemotype presence on occurrence. However, as CR and individual chemotypes influence reproductive traits in our system (Ojeda-Prieto et al., 2024), flower visitor abundance per flower head (visitation rate) assessed effects on abundance.

Predatory arthropods and ants on individual plants were recorded during herbivore counting for 2021 and 2022 and the day after in 2023. Predators were classified into taxa/feeding guilds (Araneae, Coleoptera, Dermaptera, Diptera, Hemiptera, and Hymenoptera), specifying aphid parasitoids and parasitized aphids (counted as mummies found). Ant presence on plants, but not abundance, was noted. Predator and ant occurrences and parasitized aphid abundance were used for analyses for the three seasons. In 2023, predator and ant abundances were also analyzed.

Statistical analyses

Statistical analyses were conducted using R version 4.1.2 and RStudio 2023.09.1 (R Core Team, 2021). All statistics were performed at the plot level. The effects of chemotype presence and CR on the occurrence of herbivores, flower visitors, predators, and ants were assessed through binomial Generalized Linear Mixed-effect Models (GLMM) using the '*lme4*' package (Bates et al., 2015). Linear Mixed-Effect Models (LMM) and Zero-Inflated Negative Binomial Models (ZINB), using the "*glmmTMB*" package (Brooks et al., 2017), modeled the effect on abundances. P-values were estimated by type II Wald-Chi-Squared tests using the Anova() function ('*car*' package; Fox & Weisberg, 2019). Data visualization used academic-licensed Biorender® and '*ggplot2'* (Wickham,

2009), *'grid'* (R Core Team, 2021), *'gridExtra'* (Auguie et al., 2017), *'ggpubr'* (Kassambara, 2020), and *'DHARMa'* (Hartig, 2022) packages.

Effects of chemotype richness and chemotype presence on arthropod taxa occurrence and abundance

Binomial GLMMs assessed the effect of CR and chemotype presence on occurrence. LMMs and ZINB tested the effects on abundance. Data were analyzed at the arthropod group and lower taxonomic levels (when indicated). Data were analyzed cumulatively for each year and for each independent sampling time. Detailed model conditions and transformations for each group are given in Supplementary Information 1 (S1).

Results

During our sampling campaigns, we registered the following arthropod numbers: For 2021, 166.630 herbivores in total for 13 sampling dates (58.550 *Aphis fabae* (Scopoli, 1763), 22.691 *Brachycaudus cardui* (Linnaeus, 1758), 382 *Macrosiphoniella tanacetaria* (Kaltenbach, 1843), 62.055 *Metopeurum fuscoviride* (Stroyan, 1950), and 22.952 *Uroleucon tanaceti* (Linnaeus, 1758)), 974 flower visitors in four sampling dates (316 Coleoptera, 236 Diptera, 134 Hemiptera, 237 Hymenoptera, and 51 Lepidoptera), and 4.233 parasitized aphids in 10 sampling dates. For nine sampling dates in 2022, 11'171.066 herbivores (1.610 *A. fabae,* 3.321 *B. cardui*, 35.902 *Ma. tanacetaria*, 37.196 *Me. fuscoviride*, and >1.1 Mio *U. tanaceti*), and 341 parasitized aphids. For three sampling dates in 2023, 234.386 herbivores (249 *A. fabae,* 217 *B. cardui*, 0 *Ma. tanacetaria*, 9.535 *Me. fuscoviride*, and 224.385 *U. tanaceti*), 9.940 predators (1.573 Araneae, 4.770 Coleoptera, 508

Dermaptera, 1.032 Diptera, 531 Hemiptera, 5.309 Hymenoptera) and 3.783 ants (*Lasius niger* (Linnaeus, 1758)).

Seasonal patterns in the herbivore community

Phloem feeders heavily dominated the free-living insect herbivore community in the tansy model system, whereas chewing herbivores were largely absent. We observed two generalist aphid species in our field study (*A. fabae* and *B. cardui*) and three tansy-specialist aphid species (*Ma. tanacetaria, Me. fuscoviride,* and *U. tanaceti)*. Our observations revealed the species-specific seasonal pattern of aphid populations. Populations grew exponentially during the warmer months of June and July and collapsed in August each year (Fig. S1-2). However, the timing and height of peak abundance varied among the species. The two generalist species (*A. fabae* and *B. cardui*) exhibited a similar pattern; they were the first to colonize the tansy plants and reached peak abundance in early July 2021 (Fig. S1-2a). However, they were much less abundant in 2022, with a peak occurring at the end of May. Conversely, the specialist species were less abundant in 2021, reaching their peak in mid-June for *Ma. tanacetaria* and in mid-July for *Me. fuscoviride* and *U. tanaceti.* In 2022, these species were more abundant, displacing the generalist species, and reached peak abundance in mid to late June (Fig. S1-2b). Generalist aphid species were even less common in the field in 2023, while *U. tanaceti* dominated the plots with increased abundance in July (Fig. S1-2c).

Effects of chemotype richness and chemotype on herbivore occurrence and abundance

Our study first investigated the effect of CR on plot-level I) herbivore occurrence and II) herbivore abundance across samplings

in each experimental year. All plots were occupied by at least one herbivore each year, but the herbivore species-specific occurrence in plots varied. For instance, *Me. fuscoviride* was present in all plots in 2021 (Table S1-2), for *U. tanaceti* this was the case in 2022 (Table S1-3) and 2023 (Table S1-4). The only significant effect of CR on aphid occurrence was observed for *Me. fuscoviride* in 2023, which decreased when CR increased (X^2_1=9.42, P=0.002).

We then examined how specific tansy chemotypes influenced herbivore occurrence at the plot level using individual models for each chemotype (S1). Certain chemotypes were associated with higher or lower likelihoods of colonization, i.e., occurrence, and higher or lower herbivore abundance, depending on the year and herbivore species (Table S1-11). *A. fabae* occurrence in 2022 was higher when 'Bthu-low' (X^2_1=4.50, P=0.034) or 'Mixed-high' was in the plot (X^2_1=6.68, P=0.010), but lower when 'Mixed-low' was in the plot (X^2_1=4.89, P=0.027). In 2023, it was lower when 'Bthu-low' (X^2_1=4.50, P=0.034) or 'Mixed-low' (X^2_1=4.89, P=0.027) was present and higher when 'Mixed-high' was present (X^2_1=6.68, P=0.010). Certain chemotypes within the plot affected *B. cardui* occurrence in 2022; 'Bthu-high' increased *B. cardui* occurrence (X^2_1=4.16, P=0.041), while 'Bthu-low' decreased it (X^2_1=6.42, P=0.011). *Ma. tanacetaria* occurrence was not affected by any chemotype. *Me. fuscoviride* occurrence in 2023 decreased when 'Athu-Bthu' (X^2_1=5.23, P=0.022) or 'Mixed-high' (X^2_1=9.42, P=0.002) was present in the plot. *U. tanaceti* occurrence in 2021 decreased when 'Mixed-high' was present (X^2_1=7.47, P=0.002).

Concerning abundance, there was no effect of CR on cumulative aphid abundance across all species (X^2_1=0.29, P=0.588) nor within each of the five species in the first year (*A. fabae:* $X^2_{1=}$0.03, P=0.870; *B. cardui:* X^2_1=1.51, P=0.219; *Ma. tanacetaria:* $X^2_{1=}$1.13,

349 P=0.288; *Me. fuscoviride:* X^2_1=0.52, P=0.471; *U. tanaceti:* X^2_1=0.38,
350 P=0.536; Fig. 3a, Table S1-2). However, increasing CR negatively
351 affected herbivore abundance in the following years (2022:
352 X^2_1=7.63, P=0.006; 2023: X^2_1=4.39, P=0.036; Fig. 2a, Tables S1-3,
353 S1-4), mainly driven by the negative effect of CR on *U. tanaceti*
354 populations in 2022 (X^2_1=5.93, p=0.015) and on *U. tanaceti*
355 (X^2_1=4.44, P=0.035) and *B. cardui* abundances in 2023 (X^2_1=5.56,
356 P=0.018; Fig. 3a). Notably, *Ma. tanacetaria* aphids were not
357 observed in the field in 2023 at all. Plot-level chemotypic diversity
358 had little effect on whether a plot was occupied by aphids during the
359 year, mainly because all plots were occupied. However, there were
360 negative effects on the abundance of several herbivore species.

361 If there was an effect of a specific chemotype present in a plot on
362 herbivore abundance in the year 2021, it was always positive.
363 However, all significant effects of particular chemotypes observed
364 in 2022 or 2023 were negative (Table S1-11). Herbivore abundance
365 was lower in 2022 in either 'Chrys-acet' or 'Mixed-high' presence
366 and lower in 2023 when 'Athu-Bthu' or 'Mixed-low' was in the plot
367 (Tables S1-3 and S1-4). When investigating species-specific effects,
368 we found that *A. fabae* abundance in 2021 increased when 'Mixed-
369 high' was present (X^2_1=6.77, P=0.009), *B. cardui* when either
370 'Bthu-high' (X^2_1=3.97, P=0.046) or 'Chrys-acet' were present
371 (X^2_1=6.16, P=0.013), and *U. tanaceti* when 'Bthu-high' was in the
372 plot (X^2_1=5.98, P=0.014). Lower *A. fabae* abundance was observed
373 in 2022 when 'Bthu-low' was in the plot (X^2_1=3.91, P=0.048) and
374 in 2023 when 'Athu-Bthu' (X^2_1=7.39, P=0.006) or 'Chrys-acet'
375 (X^2_1=19.14, P<0.001) were part of the community. *Me. fuscoviride*
376 abundance in 2022 was negatively associated with 'Bthu-low'
377 (X^2_1=5.85, P=0.016), and *U. tanaceti* abundance in 2022 was
378 negatively associated with either 'Chrys-acet' (X^2_1=12.77, P<0.001)

379 or ‘Mixed-high’ (X^2_1=5.58, P=0.018). In 2023, *B. cardui* was lower
380 when ‘Athu-Bthu’, ‘Bthu-high’, or ‘Mixed-high’ was present (Athu-
381 Bthu: X^2_1=4.42, P=0.035; Bthu-high: X^2_1=40.71, P<0.001; Mixed-
382 high: X^2_1=79.26, P<0.001), and *U. tanaceti* abundance was
383 negatively associated to the presence of ‘Athu-Bthu’ (X^2_1=5.08,
384 P=0.024) or ‘Mixed-low’ (X^2_1=3.92, P=0.048). The effects of
385 specific chemotypes on herbivore abundance varied across different
386 years, with positive impacts observed in 2021 and predominantly
387 negative impacts in 2022 and 2023.

388 *Effects of chemotype richness and chemotype identity on flower*
389 *visitors*

390 We first analyzed the effect of CR on flower visitor occurrence.
391 Higher CR increased the occurrence of Lepidoptera, i.e., adult
392 butterflies (X^2_1=3.87, P=0.049), but not other taxa. Hymenoptera
393 and Lepidoptera flower visitor occurrences increased when ‘Bthu-
394 low’ and ‘Athu-Bthu’ were in the plot, respectively (Tables S1-5,
395 S1-11).

396 We evaluated the effect of CR on the visitation rate of flower
397 visitors. We found a positive effect on all orders (X^2_1=10.71,
398 P=0.001, Fig. 2b), and specifically for Coleoptera (X^2_1=16.78,
399 P<0.001), Hymenoptera (X^2_1=11.56, P<0.001), and Lepidoptera
400 (X^2_1=8.80, P=0.003, Fig. 3b). Concerning the presence of particular
401 chemotypes within plots, ‘Chrys-acet’ (X^2_1=5.98, P=0.014) and
402 ‘Mixed-high’ (X^2_1=6.95, P=0.008) positively affected the visitation
403 rate across all the orders. While Diptera and Hemiptera abundances
404 were not influenced by the presence/absence of any chemotypes,
405 Coleoptera was influenced by the presence of ‘Bthu-low’ and
406 ‘Chrys-acet’ (Table S1-5); Hymenoptera by ‘Bthu-low’ (X^2_1=7.58,

407 P=0.006), and Lepidoptera by 'Athu-Bthu' (X^2_1=7.53, P=0.006,
408 Table S1-12).

409 Analysis of the effect on the total number of individuals (not the
410 visitation rate) is in Table S1-6. We found positive effects on total
411 number of individuals of all orders (X^2_1=10.71, P=0.001),
412 Coleoptera (X^2_1=16.78, P<0.001), Hymenoptera (X^2_1=11.56,
413 P<0.001), and Lepidoptera (X^2_1=8.80, P=0.003), as found by the
414 analysis of CR on visitation rate. However, when using the total
415 number as the response variable, particular chemotypes had
416 different effects on different groups. The abundance of all orders
417 was affected by the presence of any of the chemotypes except for
418 'Chrys-acet', 'Athu-Bthu' affected the number of flower visitors
419 belonging to Coleoptera and Lepidoptera, 'Bthu-low' to Coleoptera
420 and Hemiptera, and 'Bthu-high' and 'Mixed-low' to Coleoptera
421 (Table S1-6).

422 *Effects of chemotype richness and chemotype on predators and ants*

423 Predatory arthropods occurred in all plots in all years (Tables S1-7
424 to S1-9), and ants (*L. niger*) occurred in all plots in 2023 (Table S1-
425 10). The only effect of CR on predator taxa/feeding guild occurrence
426 was observed in predatory Hemiptera in 2022 (X^2_1=6.54, P=0.010),
427 which increased with CR. For chemotype identity effects, the
428 occurrence of parasitized aphids in 2021 decreased when 'Mixed-
429 low' was in the plot and in 2022 when 'Chrys-acet' was present
430 (2021: X^2_1=4.71, P=0.030; 2022: X^2_1=5.55, P=0.018, Tables S1-7,
431 S1-8).

432 Increasing CR did not increase predator abundance (overall -Fig. 2c-
433 nor by taxa/feeding guild -Fig. 3c-). However, there was a positive
434 effect of 'Chrys-acet' presence on the number of parasitized aphids

435 in 2021 (X^2_1=6.30, P=0.012, Table S1-7) and ant abundance in 2023
436 (X^2_1=6.58, P=0.010, Table S1-8), but a negative effect on total
437 predator abundance in 2023 (X^2_1=4.16, P=0.041) and on abundance
438 of predatory beetles in 2023 (Coleoptera: X^2_1=3.85, P=0.050, Table
439 S1-9). A positive effect on Dermaptera abundance in 2023 was
440 found when 'Athu-Bthu' was present (X^2_1=8.51, P=0.004).

441 *Temporal effects*

442 Analyses at independent sampling times, available in
443 Supplementary Information 1 (S1), revealed that while relationships
444 between chemotype richness and the occurrence of various
445 ecological groups were generally weak, the temporal patterns in
446 abundance were clear. Effect on abundance showed a shift in slope
447 from positive to negative for herbivores over time (particularly in
448 specialist aphids); while it remained mostly positive relationships
449 for flower visitors, ants, and predators (Supplementary Information
450 2).

451 **Discussion**

452 Intraspecific chemodiversity is a key driver of interaction variation
453 within plant species. Our understanding mainly comes from
454 observational and correlative studies, with controlled studies in
455 natural or semi-natural settings limited due to the challenges of
456 manipulating plant chemistry. In this study, we manipulated plant
457 chemical diversity at the plot level by selecting plant chemotypes
458 with varying chemical blends and manipulating the number of
459 chemotypes within plots (i.e., plot-level chemotype richness -CR-).
460 Using tansy (*Tanacetum vulgare* L.), we explored the effect of
461 chemodiversity on natural arthropod communities. Our study
462 provides evidence that intraspecific chemodiversity affects

processes at the plot level. We showed that CR had many negative effects on herbivores but positive effects on flower visitors, with minimal effects on predators or ants. Additionally, there were strong effects of chemotype identity, i.e., the composition of the plots, on plant-arthropod interactions at the plot level, an effect also often found in biodiversity experiments (e.g., Scherber et al., 2010). Our study thus highlights the role of individual chemotypes in shaping interactions, contributing to our understanding of the ecological significance of chemical diversity in plants.

Effects of chemotype richness on the occurrence of arthropod groups

Contrary to our expectations, we did not find strong evidence that CR affects plot-level arthropod occurrences **(H1)**. While some significant relationships between CR and specific taxa occurrence were observed, most were weak. One reason may be that many arthropod taxa occurred in all plots or were absent during certain samplings, limiting the variation needed to test hypotheses. Another reason is that specialized herbivore populations build up over the season before they decline, and in years when aphids are abundant, total population sizes are very high, and almost all plants are infested. We observed significant positive relationships for polyphagous aphid species such as *A. fabae* and *B. cardui* in the individual samplings during the first sampling year. These species only feed on tansy for several weeks. Significant negative relationships were observed for monophagous species, particularly in *Me. fuscoviride* in 2023, suggesting that polyphagous and monophagous species may respond differently to chemical cues in their host-seeking behavior (Gripenberg et al., 2010; Benedek et al., 2015; Ziaja & Müller, 2023). It also emphasizes the strong shift from polyphagous to monophagous herbivores in the system over

the season. It could be that during the establishment phase, polyphagous herbivores were more abundant in the surrounding grassland and that monophagous species required time to colonize from the nearest tansy hosts. All specialized tansy aphids overwinter on or next to the host plant; hence, once the field plots are colonized, local overwintering and early colonization in the season by the specialized aphids are possible.

For flower-visiting taxa, we consistently observed positive relationships between CR and occurrence, indicating the role of specialized chemistry in these mutualists (Silva et al., 2018; Farré-Armengol et al., 2020; Sasidharan et al., 2023). In contrast, the relationship between CR and other groups' occurrence was weak. These findings suggest that plant chemistry differentially affects arthropod groups based on their interaction with the plant. While plant chemistry significantly influences directly interacting organisms like flower visitors, it does not show a similar significant impact on indirectly interacting organisms such as predators and ants (Ali et al., 2023).

Effects of chemotype richness on the abundance of arthropod taxa

We found strong support for CR affecting the abundance of herbivores and flower-visiting arthropods but not predatory arthropods and ants, partially in line with **(H2)**. Higher CR plots supported fewer herbivores in 2022 and 2023, although this relationship varied between aphid species. In general, the effects of CR on herbivore abundance were driven by its effects on the dominant monophagous aphid species, *U. tanaceti*, for both years and *B. cardui* for 2023. An interesting observation is that the slope between CR and herbivore abundance, despite the relationships not always being significant, started consistently positive in 2021 but

turned increasingly negative over the first season and across the years. It might be that the shift towards monophagous aphids over time emphasized the negative effect of CR on herbivore abundance. Since *U. tanaceti* had not yet successfully colonized the experiment in the first year, and polyphagous species were more common, this may explain the lack of CR effects in the first year. Monophagous herbivores may be more strongly affected by chemical defenses in high CR (Ziaja & Müller, 2023) in concordance with the neighborhood-mediated associational resistance hypothesis (Randlkofer et al., 2010).

Higher CR plots had more flower visitors, with significant positive effects observed for Coleoptera, Hymenoptera, and Lepidoptera but not for Diptera and Hemiptera, suggesting that CR may differentially affect flower visitors (Sasidharan et al., 2023). Chemotypes exhibit variations in their phenology, influenced by the chemical diversity of their growth environment (Ojeda-Prieto et al., 2024). These variations can extend the flowering period within a plot containing a greater number of different chemotypes. Consequently, CR will affect the occurrence and abundance of flower visitors.

Our study revealed that the chemodiversity of the plot did not affect predator or ant abundance. The precise reasons underlying these findings remain unclear. However, it is plausible that additional factors, such as prey availability, which may be influenced by herbivore-host chemical composition (Benedek et al., 2019), or alternative foraging strategies (Wäschke et al., 2013), contribute to shaping these patterns. Further research is warranted to elucidate the interplay between these factors and their collective impact on predator and ant abundance in response to chemodiversity.

Effects of chemotype presence on arthropod communities

We found chemotype-specific impacts on plot-level occurrence and abundance across arthropod taxa, in line with our hypothesis **(H3)**. In herbivores, patterns were rather incongruent and differed strongly with the year of sampling. Herbivore occurrence data showed few chemotype-specific effects in 2021, the first season after establishment. Different chemotypes positively and negatively affected the species observed in the following two years. This suggests that most aphids seem to respond to plant-chemical cues as expected (Mehrparvar et al., 2014; Clancy et al., 2018). Herbivore abundance data show a clear pattern, where in 2021, chemotype effects were typically positive, which may suggest that colonizers were using specific terpenoid cues initially. Interestingly, in the subsequent years, chemotype-specific effects, when significant, were always negative. A possible scenario suggests that chemotypes may serve as a mosaic that partly regulates aphid densities, which aligns with the idea that specialized chemistry evolved with a defensive function (Fox, 1981; Wolf et al., 2011). This idea is further reinforced by the fact that the overall effect of chemotypes on herbivore abundance tends to be neutral to negative.

For flower-visiting arthropods, chemotype-specific patterns were most common in abundance data. Most flower visitors are highly mobile and do not linger in the same plot for long (Burdon et al., 2020; Knauer et al., 2021), suggesting that specific chemotypes lead to higher abundance in certain plots. Significant chemotypes positively affected flower visitors, with low-concentration B-thujone chemotypes having the most robust and consistent effects on different taxa, aligning partially with previous results (Sasidharan et al., 2023). Mixed chemotypes had few effects, and high-concentration B-thujone chemotype did not affect flower

visitors. Although B-thujone can signal nectar or pollen rewards (Metcalf & Kogan, 1987), its effects depend on the overall blend of volatile compounds and the preferences of local flower-visiting species. We found stronger effects of chemotype identity on the total number of individuals than on the visitation rate (Tables S1-5 and S1-6). CR and individual chemotypes influence reproductive traits in our system (Ojeda-Prieto et al., 2024). These effects might be confounded by the influence of CR and chemotype on reproductive traits rather than reflecting true effects on flower visitors.

Fewer and weaker chemotype-specific effects were found for predators and ants, suggesting that these groups could be influenced by different mechanisms, including modified behaviors, such as predation activity or aphid-tending in ants (Senft et al., 2017; Mehrparvar et al., 2018; Hauri et al., 2022).

Future perspectives for chemodiversity research

Exploring several key areas of chemodiversity will deepen our understanding. Scaling up experiments to entire landscapes will elucidate how chemodiversity influences ecosystems and biodiversity across diverse habitats. Assessing its effect on plant-insect interactions should include ecosystem functions like predation rates and herbivore performance. Studying how chemodiversity influences herbivore behavior, including responses from generalist and specialist species, will offer insights with potential applications in pest management. Further exploring the interplay between plant chemistry and arthropod communities will advance our understanding of ecosystem functioning and guide conservation and management practices.

Conclusion

Previous studies have focused on intraspecific variability in ecosystem functioning. Our research demonstrates that plot-level chemotypic diversity impacts arthropod colonization patterns. Our results emphasize the role of intraspecific chemodiversity in shaping arthropod communities on plants. Our work shows that plots with higher intraspecific chemodiversity accumulate fewer herbivores and attract more flower visitors. The presence of specific chemotypes within a plot exerted highly variable impacts on abundance but also on occurrence patterns of various arthropod groups, suggesting that specific chemotypes, and potentially specific components they produce, may be a driver of the occurrence of arthropod taxa.

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Competing interests

All authors declare no conflict of interest to disclose.

Author contributions

WWW conceived the original idea and designed the experiment. Research conducted by: RH prepared the field experiment and propagation of plants. LOP, RH, and WWW planted the field experiment. LOP and ELM collected all data and maintained the field experiment. LOP analyzed ecological data with input from RH and WWW. LOP wrote the manuscript with input from ELM, RH, and WWW. All authors contributed to the final version and approved the final submission.

Data availability

Data and R code scripts supporting the results are archived in Dryad.

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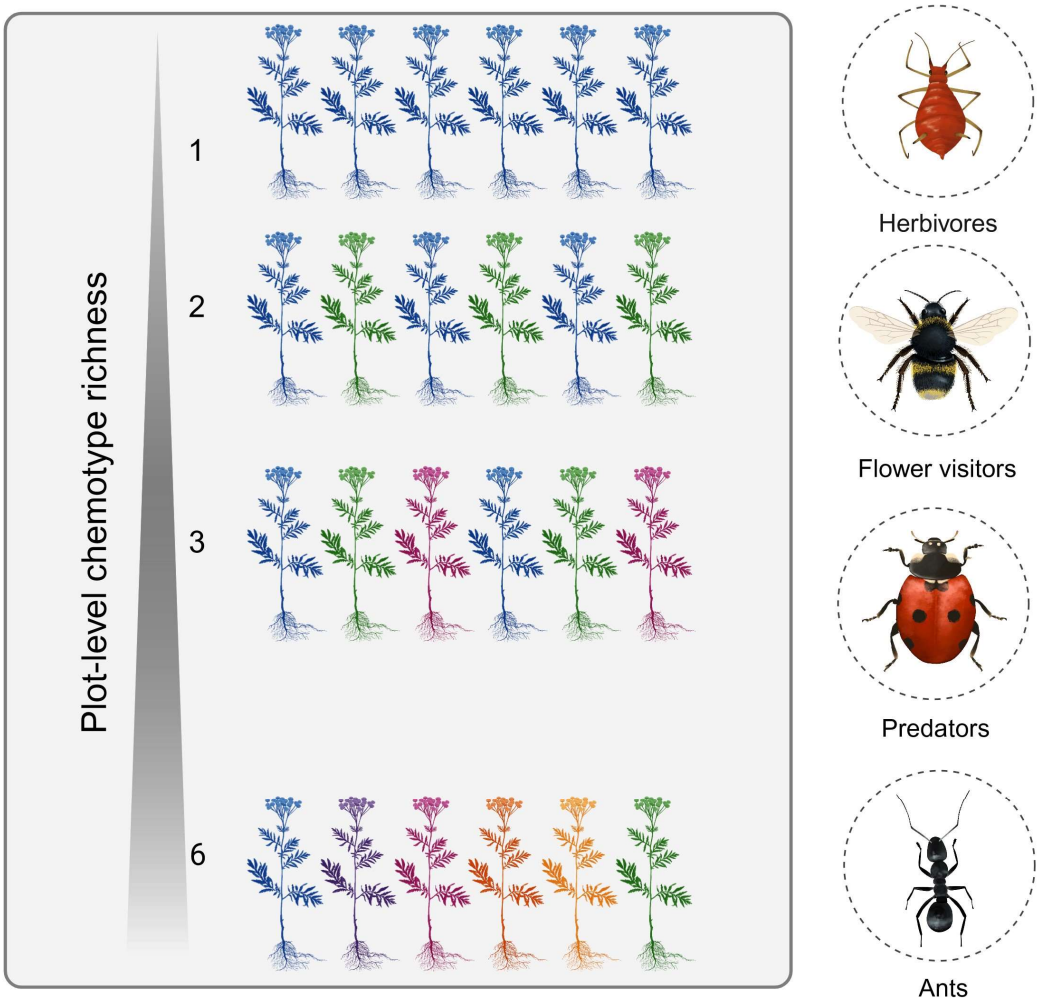
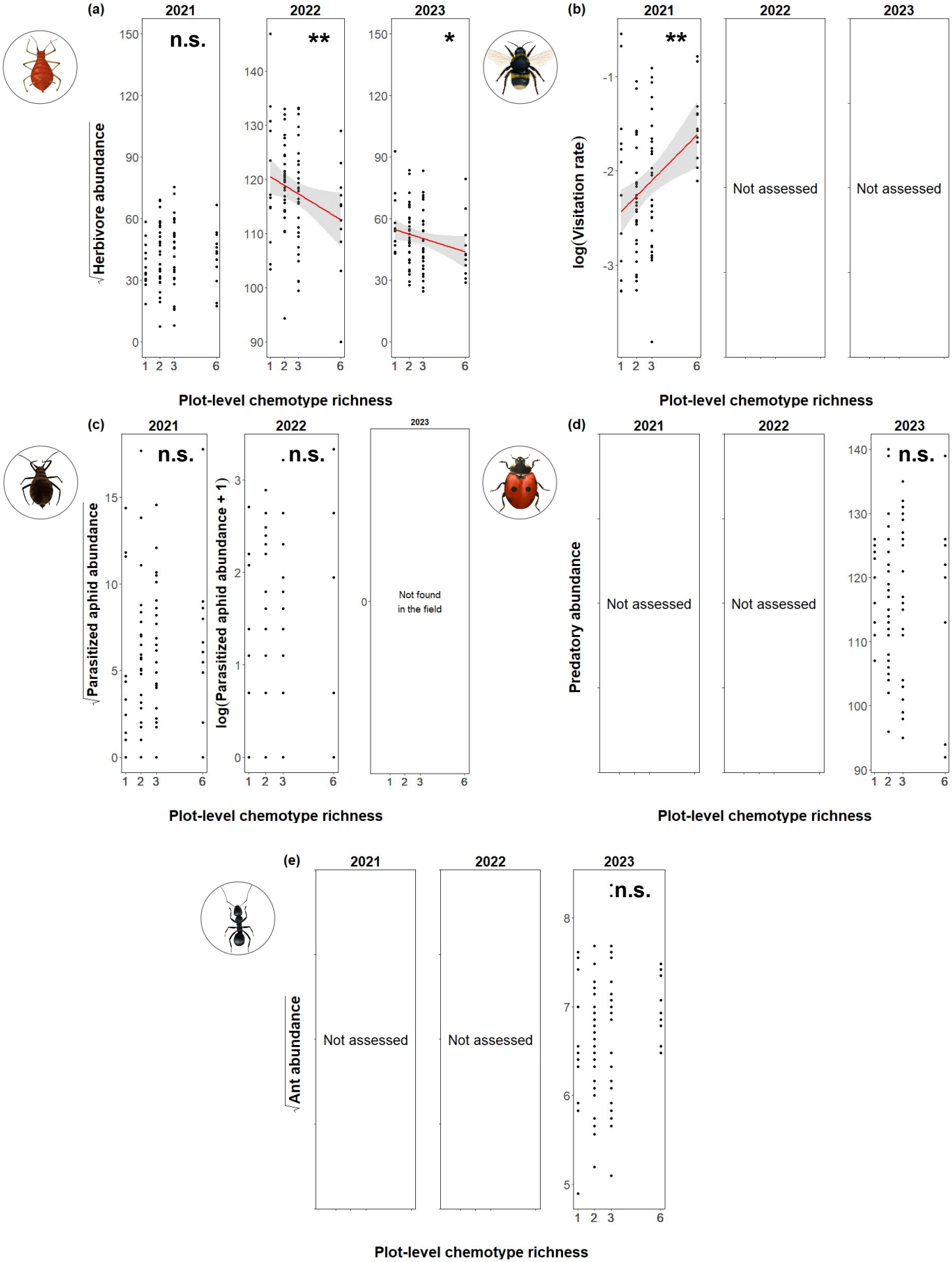
Main Figures

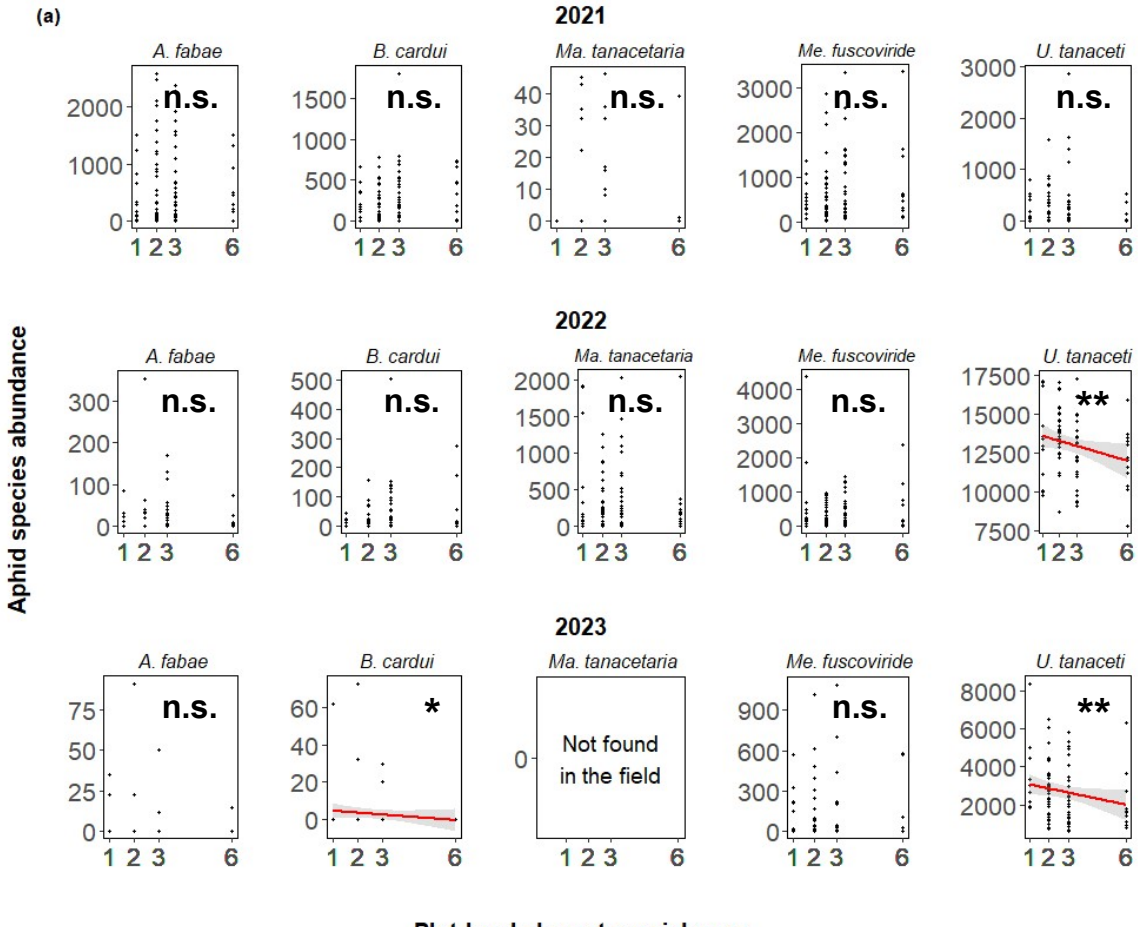
Figure 1. Influence of *Tanacetum vulgare* intraspecific chemodiversity on arthropod communities. The left panel illustrates the gradient of plot-level chemotype richness, with each color symbolizing a specific chemotype of *Tanacetum vulgare* in a six-plant community. From levels 1 to 6, the chemodiversity increases, indicating an increase in different chemotypes. The right panel presents the evaluated arthropod communities: herbivores, flower visitors, predators, and ants, which are expected to be influenced by intraspecific chemodiversity. Created with Biorender®. Agreement number: FE271K6HDD.

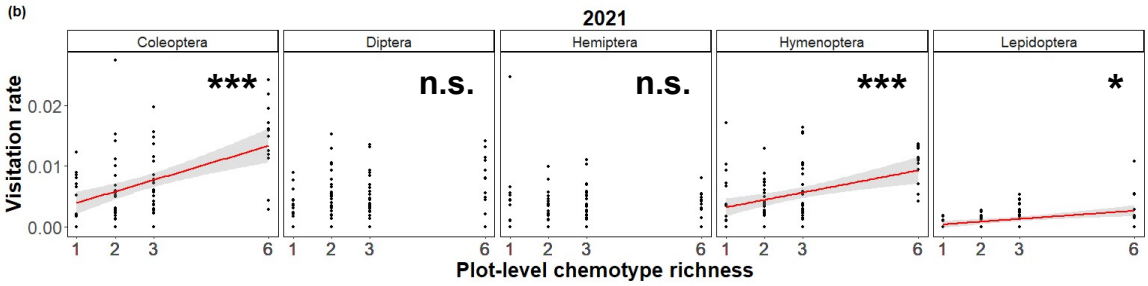
Figure 2. Effect of plot-level chemotype richness on the abundance of different arthropod communities over three years (2021–2023). (a) Effect on herbivore abundance, represented by five aphid species each year. **(b)** Effect on flower visitor abundance (i.e., visitation rate), calculated as the cumulative count of flower-visiting insects divided by the sum of flower heads counted during each assessment date. **(c)** Effect on parasitized aphid abundance (aphid mummies). **(d)** Effect on predator abundance. **(e)** Effect on ant abundance. Significance is indicated as follows: n.s.=not significant, * $P<0.05$, ** $P<0.01$, and *** $P<0.001$. Degrees of freedom, Wald's Chi-square statistics, and p-values are reported in Tables S1 – S8.

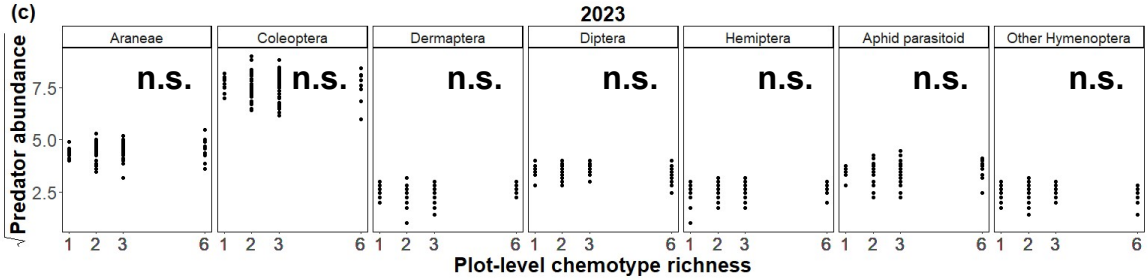
1076 **Figure 3. Effect of plot-level chemotype richness on specific**
1077 **group abundances within each guild of arthropod communities**
1078 **over three years (2021–2023). (a)** Effect on herbivore abundance
1079 of *Aphis fabae*, *Brachycaudus cardui*, *Macrosiphoniella*
1080 *tanacetaria*, *Metopeurum fuscoviride*, and *Uroleucon tanaceti* each
1081 year. **(b)** Effect on flower visitor abundance of Coleoptera, Diptera,
1082 Hemiptera, Hymenoptera, and Lepidoptera. **(c)** Effect on predator
1083 abundance of Araneae, Coleoptera, Dermaptera, Diptera,
1084 Hemiptera, Aphid parasitoids, and Other Hymenoptera for 2023.
1085 Significance is indicated as follows: n.s.=not significant, * $P<0.05$,
1086 ** $P<0.01$, and *** $P<0.001$. Degrees of freedom, Wald's Chi-
1087 square statistics, and p-values are reported in Tables S1 – S7.


Plot-level chemotype richness
1
2
3
6
Herbivores
Flower visitors
Predators
Ants


(a)
2021
2022
2023
n.s.
**
*
√Herbivore abundance
(b)
log(Visitation rate)
Not assessed
Not assessed
Plot-level chemotype richness
(c)
n.s.
n.s.
√Parasitized aphid abundance
log(Parasitized aphid abundance + 1)
Not found
in the field
(d)
n.s.
Predatory abundance
Not assessed
Not assessed
Plot-level chemotype richness
(e)
n.s.
√Ant abundance
Not assessed
Not assessed
Plot-level chemotype richness


(a)
2021
A. fabae
B. cardui
Ma. tanacetaria
Me. fuscoviride
U. tanaceti
n.s.
2022
**
2023
*
Not found in the field
Aphid species abundance
Plot-level chemotype richness


(b)
2021
Coleoptera
Diptera
Hemiptera
Hymenoptera
Lepidoptera
***
n.s.
*
Visitation rate
Plot-level chemotype richness


(c)
2023
Araneae
Coleoptera
Dermaptera
Diptera
Hemiptera
Aphid parasitoid
Other Hymenoptera
n.s.
Predator abundance
Plot-level chemotype richness