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Risk of herbivory negatively correlates with the diversity of volatile emissions involved in plant communication

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Plant-to-plant volatile-mediated communication and subsequent induced resistance to insect herbivores is common. Less clear is the adaptive significance of these interactions; what selective mechanisms favour plant communication and what conditions allow individuals to benefit by both emitting and responding to cues? We explored the predictions of two non-exclusive hypotheses to explain why plants might emit cues, the kin selection hypothesis (KSH) and the mutual benefit hypothesis (MBH). We examined 15 populations of sagebrush that experience a range of naturally occurring herbivory along a 300 km latitudinal transect. As predicted by the KSH, we found several uncommon chemotypes with some chemotypes occurring only within a single population. Consistent with the MBH, chemotypic diversity was negatively correlated with herbivore pressure; sites with higher levels of herbivory were associated with a few common cues broadly recognized by most individuals. These cues varied among different populations. Our results are similar to those reported for anti-predator signalling in vertebrates.

1. Introduction

Many organisms perceive reliable cues that indicate an increased risk of being attacked and adjust their behaviour in response to these cues. It is well established that animals including ants, birds and mammals emit alarm cues that conspecifics and other co-occurring species use to evaluate the risk of predation [1,2]. These cues involve olfactory, acoustical and visual modes of information exchange. Animal behaviourists debate whether the emission of these cues represents intentional communication on the part of the sender or eavesdropping by the receiver. The alarm cues of species that co-occur, such as mixed-species flocks of birds, have often converged such that all species recognize and respond to the alarm calls of the other co-occurring species [3–5].

When plants are attacked by herbivores, they emit a complex blend of volatile organic compounds (VOCs) into the surrounding environment [6]. These damage-induced VOCs contain information regarding the emitter's condition, including the severity and location of damage and the identity of the attacker (reviewed in [7]). Undamaged tissues of the emitting plant perceive these volatile warning cues and respond by increasing defences to reduce subsequent damage [8–10]. Nearby plants can 'eavesdrop' on these cues and induce or prime their own resistance responses [11]. Perceiving and responding to publicly available chemical information may give neighbouring plants a competitive advantage; this eavesdropping may represent a costly consequence of within-plant communication mediated by volatiles.

Plant-to-plant communication is common; over 50 species across diverse taxonomic groups respond to volatile cues [12,13]. The adaptive significance of these volatile-mediated interactions is not well understood. The benefits

for receiver plants that perceive and respond to reliable cues is intuitive and has been supported by a few empirical studies (e.g. [9,14,15]). This benefit to neighbours raises the question—why would emitters provide this information to their neighbours with whom they probably compete? Indeed, the selective mechanisms favouring the emission of volatile cues are less obvious. It is possible that emitting volatile cues is a non-adaptive consequence of damage or that the cues mediate other interactions such as repelling herbivores [16,17] or attracting the predators and parasites of herbivores [18,19]. Volatile cues convey information over relatively short distances and may primarily function to allow individual plants to coordinate and integrate their own defences [20]. Two adaptive hypotheses have been proposed to explain the conditions that could favour emission of informative volatile cues to other individuals in the population and the diversity of those cues: the kin selection hypothesis (KSH) [21] and the mutual benefit hypothesis (MBH) [22,23].

Plants may avoid the consequences of alerting neighbours by using relatively private communication channels that can be perceived most effectively by individuals that are closely related (kin). Under the KSH, information exchange is improved or even exclusive to related individuals through the private channels of communication where informative signals have a genetic basis; consequently, emitters benefit by increasing their inclusive fitness [24]. Decades of experimental work with sagebrush (*Artemisia tridentata*) have shown it to be a model system for studying volatile-mediated induced resistance [8,25–28] and have important implications for plant fitness [15]. Recent field studies of sagebrush found that plants were able to distinguish volatile cues from itself or closely related individuals, a form of kin recognition [21]. It was later determined that related individuals often shared the same non-plastic chemotype and that chemotypes were highly heritable [29]. Additionally, it was found that the efficacy of communication and subsequent strength of induced resistance were dependent on the chemotypes of the emitter and receiver plants [29]. Receiver plants exposed to the induced volatiles of emitter plants of the same chemotype experienced less herbivory compared to cues from a different chemotype than the receiver. Here, the ‘private-channels’ are represented by chemotype-dependent communication used to privatize information exchange so as to only benefit kin and minimize the interception of signals by competitors. When herbivore pressure is relatively low, the costs of providing information to non-kin should favour the evolution of private communication channels.

In contrast with the KSH, information is exchanged freely between individuals through open channels of communication under the MBH. Induced resistance is elicited in the majority of plants in a patch from the damage-induced cues of just one or a few damaged plants regardless of their relatedness. All individuals benefit by sharing universally understandable information about the risk of attack [22,23]. Herbivores are predicted to leave such defended patches [22,30]. Goldenrod (*Solidago altissima*) individuals from populations that had been exposed to herbivores for 12 years converged on a common cue that all individuals could perceive and respond to [23]. Cues from individuals belonging to populations that had been experimentally protected from herbivory were not recognized by all members of the population but were more effective at inducing resistance in kin of the same genotype [23].

Here, we investigated the predictions of the KSH and the MBH using survey data from 15 populations of sagebrush (*A. tridentata* ssp. *vaseyana*) along a 300 km transect. For each population, we estimated herbivore pressure by quantifying leaf damage on a subset of plants and calculated chemotype diversity indices based on the abundance and distribution of chemotypes of the same plants used to estimate the damage. In particular, we addressed the following predictions:

- (i) when the risk of herbivory is low, selection should favour private channels of communication and a divergence of chemotypes predicted by the KSH; and
- (ii) when the risk of herbivory is high, selection should favour open channels of communication converging on fewer chemotypes predicted by the MBH.

Both hypotheses predict that populations which experience higher levels of herbivory should be associated with relatively fewer chemotypes than populations which experience lower herbivore pressure. Finding a negative correlation between these variables would lend support to the hypothesis that different selection processes (i.e. MBH and KSH) are simultaneously operating but at different levels of herbivory, leading to divergent patterns of chemotypic diversity. We discuss our findings in the light of the experimental work by Kalske *et al.* [23], specifically the adaptive potential of plant-to-plant signalling and the underlying selection mechanisms. Because of the limitations of observational studies regarding causal inferences, we also discuss several alternative hypotheses that could explain the observed patterns of chemotypic diversity in relation to herbivore pressure reported here.

2. Methods

(a) Survey of herbivore damage

We estimated herbivory on a single branch from 20 haphazardly selected sagebrush plants from 15 sites along a latitudinal transect, spanning over 300 km (figure 1). Herbivore damage was determined by counting the number of leaves with visible chewing or scraping damage and dividing this value by the total number of leaves on a subsection of the branch. At least 60 leaves were observed for each branch. This method was established previously by the authors to demonstrate plant-to-plant communication and induced resistance in sagebrush [8,21,25] and was shown to positively correlate with leaf area removed [31]. After the damage was estimated, a subset of branches from each site were shipped (in approx. 5 days) to the University of Eastern Finland for volatile collection and chemotype assignment. Previous work by P. Grof-Tisza, D.J. Blande, M. Freeman and R. Karban 2019, unpublished, showed that shipping does not affect chemotype determination.

(b) Chemotype determination

Fresh leaves (0.05–0.15 g) were finely chopped, placed into a 20 ml glass vial (Agilent Technologies, USA) and sealed. Vials were then subjected to direct headspace sampling using an Agilent G1888A network headspace sampler connected to an Agilent 6890 N network gas chromatograph and Agilent 5973 inert mass selective detector (MS; Agilent Technologies, USA). Gas chromatography (GC) conditions and details regarding mass spectrometric analysis and compound identification are provided in the electronic supplementary material. Chemotype assignment methods are described elsewhere [32], but briefly, chemotype assignments were based on motifs of discriminating dominant compounds determined by GC–mass spectrometry

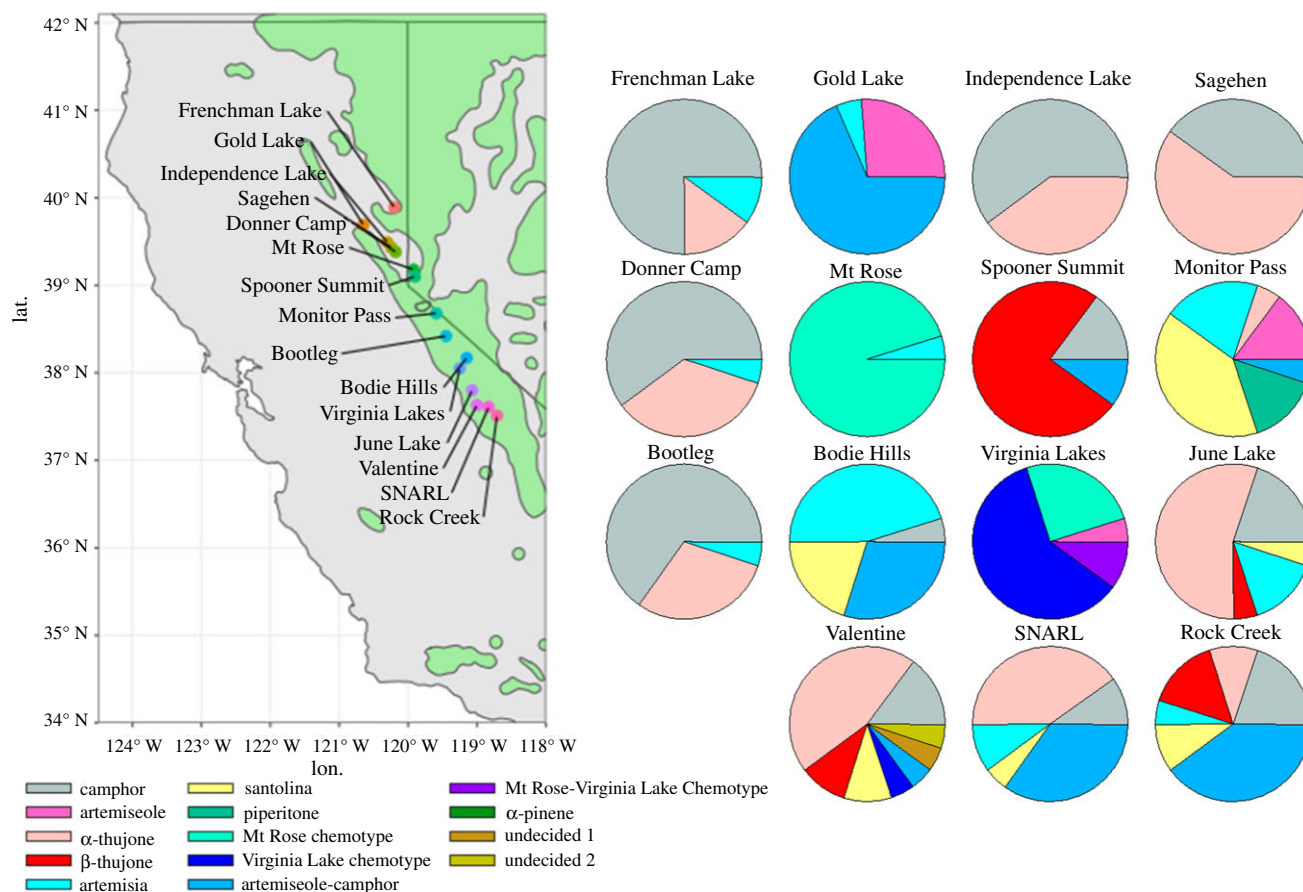


Figure 1. Latitudinal transect of sites and populations ($n = 15$) where sagebrush plants ($n = 20$, except Gold Lake, where $n = 19$) were used for chemotype assignment and to assess herbivore pressure. Shading represents the distribution of *A. tridentata*, including the focal subspecies *A. tridentata* spp. *vaseyana*. Pie charts show the abundance and distribution of chemotypes within each population. (Online version in colour.)

(GC–MS) in the overall emission blend. For example, plants that emitted β -thujone or α -pinene as the dominant compound by the percentage of total emitted compounds were assigned to the β -thujone and α -pinene chemotype, respectively (electronic supplementary material, figure S1). These data ($n = 202$) were combined with those from a pilot study ($n = 98$), where a subset of the populations was sampled in 2016 (electronic supplementary material, table S1). For this earlier study, we used dynamic headspace sampling in the field (described in [29]) and did not estimate leaf damage. Details of this pilot study are included in the electronic supplementary material. Chemotype assignment was not affected by the method used.

(c) Chemotype diversity indices

We calculated two chemotype diversity indices, the Shannon–Wiener index and richness, for leaves from 20 bushes of each population. Our adaptation of the Shannon–Wiener diversity index reflected the number of unique chemotypes and how evenly chemotypes were distributed among those individuals [33]. Richness was measured as the number of chemotypes identified within each population.

(d) Historic surveys of herbivore damage

To demonstrate the relative temporal consistency of herbivore pressure across populations, we included damage estimates across several years for three sites: Mt Rose, Sagehen and SNARL. We estimated the proportion of leaves on each plant that showed any signs of chewing damage. Over this time frame, chrysomelid leaf beetles (*Trirhabda pilosa* and *Monoxia grisea*), caterpillars (particularly *Aroga websteri*), many generalist grasshoppers and mule deer (*Odocoileus hemionus*) caused most

of this damage. *Trirhabda pilosa* have a tendency to outbreak and are capable of killing sagebrush plants through defoliation [34] (electronic supplementary material, plate S1). Several outbreaks have occurred within the surveyed populations [25]. Even in non-outbreak years, insect herbivores can reduce the fitness of sagebrush plants [35]. Damage by herbivores of other feeding guilds was not included in these estimates because their damage was more cryptic or ephemeral. Our estimates of chewing damage varied in terms of the number of plants analysed, the number of total leaves counted and the researcher involved. Owing to this variation in how these data were collected, they provide a qualitative measure of the risk experienced by plants at each population, but they were not used for statistical analysis.

(e) Statistical analysis

We assessed the influence of chemotypic diversity on the proportion of damaged leaves using generalized linear models (GLMs) in R (v. R-4.0.3) [36]. Specifically, we used a log-linked gamma GLM to account for the truncated Shannon–Wiener diversity index, which only contained positive numbers. We used a negative binomial error distribution with a log-link to model richness, based on the counts of chemotypes at each site. To account for spatial autocorrelation of herbivory, we used site-level averages of plant damage. Chemotype frequencies within the sampled populations of sagebrush, a long-lived plant (greater than 100 years), were unlikely to change between sampling events. Consequently, we did not include time in our model to account for the pilot study and main sampling events occurring in separate years. Because both hypotheses predict that herbivory would be negatively correlated with the diversity indices, we performed a one-tailed test for the regression coefficient and provided the corresponding prediction interval.

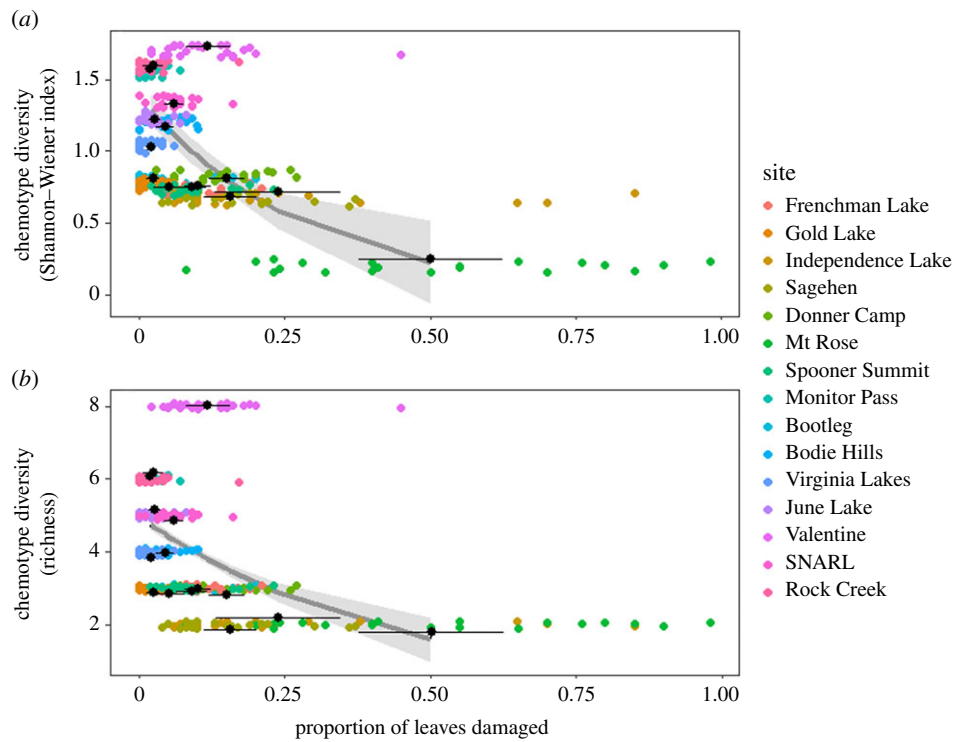


Figure 2. The relationship between the proportion of leaves damaged by herbivores and chemotype diversity indices, including (a) the Shannon–Wiener diversity index and (b) richness of chemotypes identified within the population. Black circles and error bars represent the mean and 95% confidence interval of damage for each site. The shaded area represents the 95% confidence interval of the regression model. (Online version in colour.)

3. Results

Previously, two chemotypes had been characterised for this subspecies [29,37]. We found 11 chemotypes across the latitudinal transect in addition to those that had previously been reported (figure 1). This increased the known number of chemotypes in this subspecies of *A. tridentata* by 450%. A more detailed description of these chemotypes is provided in the electronic supplementary material, figure S1. Two undetermined chemotypes were identified in the Valentine population. These chemotypes were included as unique chemotypes in the calculation of the diversity indices. This was a conservative measure designed to ensure that chemotypic diversity was not underestimated at this site. One sample at Gold Lake resulted in a poor-quality chromatogram and was subsequently omitted.

We found a strong negative relationship between the proportion of damaged leaves in our surveys and both chemotype diversity metrics (Shannon–Wiener index: GLM gamma (log), $\beta = -3.62$, 95% confidence interval (CI) $(-4.76, -2.35)$, $T = -5.17$, $p < 0.001$; richness: GLM nbinom (log), $\beta = -2.13$, 95% CI $(-3.58, -0.64)$, $T = -2.34$, $p < 0.001$; figure 2). Sites with high levels of chewing damage by herbivores had low diversity of volatile chemotypes. Sites with relatively low levels of damage had relatively higher diversity of volatile chemotypes. Plants at the Mt Rose site had the lowest chemotypic diversity and experienced the highest levels of damage from *T. pilosa* beetles. To assess the influence of this site on our parameter estimates, we omitted Mt Rose and refitted the models. Although the strength of the relationship decreased without this site, it remained significant (Shannon–Wiener index: GLM gamma (log), $\beta = -2.71$, 95% CI $(-4.96, -0.35)$, $T = -1.94$, $p = 0.03$; richness: GLM nbinom (log), $\beta = -3.43$, 95% CI $(-6.48, -0.30)$, $T = -1.88$, $p = 0.03$).

Historical surveys indicated that levels of herbivory among populations have remained relatively consistent over time (figure 3). While levels of chewing damage varied among individual plants within each population and among the different populations of this subspecies, the relative rates of damage experienced by plants of the three populations for which we have estimated damage were consistent over multiple years. The populations at Mt Rose, Sagehen and SNARL generally received higher, intermediate and lower levels of chewing damage by herbivores, respectively.

4. Discussion

Emission of volatiles by plants is analogous to alarm calls associated with some animal systems insofar as it elicits responses in eavesdropping individuals leading to reduced risk. For example, the emission of volatiles by damaged sagebrush causes other branches on the damaged plant as well as branches on neighbouring plants to induce resistance to herbivory [8]. Alarm calls in animals are thought to have evolved through kin selection [38,39]. The cost to the emitter by exposing itself to a predator is outweighed by the benefit of alerting close relatives that share genes. Several studies with disparate species have demonstrated that individuals will only signal the presence of a threat if kin are nearby [40,41]. Often the intensity of signalling is proportional to the risk [42,43]. For example in primates, the low risk may be conveyed by non-verbal eye movement, where only a nearby receiver such as a mate or kin will receive the message; high risk is conveyed through loud vocalizations that alert a broader audience including unrelated conspecifics and heterospecifics [42,44]. Many animal species can perceive and respond to anti-predator signalling of heterospecifics

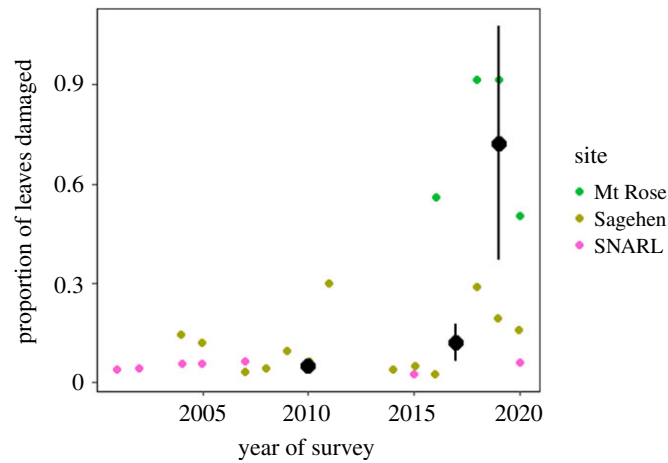


Figure 3. Historical herbivore damage estimates for three sites demonstrating the temporal consistency of herbivore pressure. Black circles represent the mean and 95% confidence interval of damage for each site. (Online version in colour.)

[1–4]. This is in part owing to the convergence of warning signals. For example, the acoustic similarity of mobbing calls in passerine birds enables naive individuals to correctly interpret calls of other species [5].

Our survey of 15 sagebrush populations revealed that those populations which experienced high levels of herbivory had lower diversity of chemotypes while those populations which experienced low levels of herbivory had higher diversity of chemotypes. There are several possible causal explanations for the pattern that we observed. First natural selection could favour convergence of signals when the risk of herbivory is great and divergence of signals when risk is low; we will explore this causal hypothesis first. Alternatively, causation could proceed in the opposite direction and the diversity of emissions could cause differences in rates of herbivory and we will consider this hypothesis later.

There are at least two mechanisms that have been proposed in the plant–herbivore literature by which the risk of herbivory can shape signal diversity and both predict the pattern that we observed [21–23]. The MBH predicts that at high risk, plants should converge on a few signals that all or most individuals can recognize [22,23]. The KSH predicts that at low risk, plant signals should diverge so that only kin can benefit from private communication [21]. Our results were consistent with both hypotheses. Because we do not know the frequencies of chemotypes of these populations over an evolutionary time-scale, we have no direct evidence of population-level convergence of chemotypes; this limits our ability to make inferences. It is interesting to note that the MBH makes predictions about reducing high signal diversity at high herbivory levels and the KSH makes predictions about increasing signal diversity at low herbivory levels. These two hypotheses are thought to operate at different spatial scales [21–23]. The MBH primarily operates between patches, where patches comprised resistant individuals deter herbivores or cause them to abandon the patch. The KSH operates at smaller within-patch scales, where only the emitter and nearby relatives capable of responding to emitted cues benefit.

Sagebrush plants respond most effectively to volatiles from plants of the same chemotype [25,29,44]. We found that all but one plant sampled from the Mt Rose population (19 out of 20), had the Mt Rose chemotype. Most individuals in those populations like Mt Rose that have experienced high levels of damage are probably able to perceive and respond

to the few distinct VOC cues found at these sites. However, the particular chemical nature of the cues was different for different populations that experienced high herbivory. For example, at Mt Rose, most individuals had a volatile profile dominated by grandisol, while at nearby Spooner Summit, most had a profile dominated by β -thujone. One possible explanation for this pattern is that individuals in these at-risk populations have not settled on a cue because it is the most effective for repelling the herbivores or because it travels most effectively in that environment. Rather, this pattern suggests frequency-dependent selection of cues so that most individuals share the same cue and are, therefore, able to exchange information with a majority of their neighbours. In the future, it would be interesting to test this hypothesis and to examine the changes in the spatial distribution and frequencies of cues in sites where dominant cues turnover (e.g. the area between Mt Rose and Spooner Summit).

Our survey results corroborated the experimental study by Kalske *et al.* [23]; in populations of goldenrod exposed to herbivores, selection favoured open channels of communication, converging on fewer VOC signals universally recognized by all individuals as predicted by the MBH [22]. Goldenrod individuals benefited more by eavesdropping on the damage that all neighbours were experiencing relative to the costs of providing this information to their competitors. Conversely, in populations of goldenrod experimentally protected from herbivores, selection favoured private channels of communication and a divergence of VOC signals as predicted by the KSH. Under these conditions, goldenrod individuals presumably benefited less by sharing information with neighbours compared to the costs of eavesdropping by competitors.

Both the MBH and the KSH assume that herbivore intensity causally influenced chemotypic diversity, but the inverse is equally plausible. High variability (diversity) in plants can reduce herbivory [45,46]. A population of sagebrush individuals that share a single chemotype are likely to have low diversity of defensive and nutritional traits, producing conditions allowing herbivores to flourish [47]. In addition, many of the volatile compounds emitted by sagebrush [29,37,48] deter attacking arthropods [49,50] and are known to specifically repel those that feed on sagebrush [51]. Moreover, greater volatile diversity may correlate with higher in-leaf concentrations of these compounds, potentially reflecting their level of defence. Previous work in other systems with

volatile chemotypes found a large overlap between in-leaf and headspace compounds, except for those that do not readily volatilize (e.g. sesquiterpenes) and those that are biosynthesized in response to damage [52].

Manipulative experiments are needed to distinguish between these alternative causal explanations that are independent of volatile-mediated plant communication (i.e. KSH and MBH) for the relationship between chemotype diversity and herbivory. Long-term experimental suppression of herbivores could be established across populations that differ in levels of chemotypic diversity to test the hypothesis that herbivore pressure drives the diversity of volatile chemotypes and not the reverse. For example, if pesticide applications increased chemotypic diversity at Mt Rose relative to controls, this would be evidence of the KSH. Similarly, generating conditions leading to high densities of *T. pilosa* (and accordingly, high herbivory) in sagebrush populations historically associated with low levels of herbivory would test the MBH. Here, we would expect a decrease in chemotypic diversity associated with experimentally elevated levels of herbivory relative to a control. Complementary experiments would test the specificity of chemotypes at eliciting communication between emitting and receiving plants of different chemotype combinations. Under the MBH and the open communication model, we would expect to see widespread recognition of emitted VOCs. Under the KSH and the private communication model, we would expect to see selective recognition, such that the strongest response should occur between genetically related individuals with the same chemotype. These experimental manipulations over an appropriate time-scale to affect changes in chemotypic frequencies across populations of long-lived sagebrush plants are not easily accomplished. Identifying plant–herbivore systems more amenable to experimentation would provide a more tractable means to rigorously test the effects of herbivore risk on induced volatiles used in plant-to-plant signalling and to identify the drivers of warning signal diversity.

In conclusion, there are parallels between our finding of a negative association between the diversity of volatile chemotypes and levels of herbivory and anti-predator signalling in

animals. As has been found in some animal systems, the privacy of alarm signals used is dependent on risk level and relationship between emitter and receiver [2–5,41–44]. Warning signals may be as subtle as gestures between kin or as public as loud vocalizations that are perceived by conspecifics and heterospecifics alike in cases of substantial threat [42,44]. In this latter case of high risk, alarm signals may converge as seen in mixed flocks of birds [2–5]. In sagebrush, this may be analogous to the reduction of chemotypic diversity as seen in populations that were associated with the highest levels of herbivory. This work suggests that regardless of kingdom, when risk is high and equally shared among individuals, selection may favour cooperative interactions via open channels of communication mediated by universally recognized warning signals. Conversely, when risk is low and not equally shared, selection may favour private channels of communication and diversification of warning signals.

Data accessibility. Data and code are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.nk98sf7vc> [53].

Authors' contributions. P.G.-T.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, supervision, visualization, writing—original draft, writing—review and editing; R.K.: conceptualization, data curation, writing—original draft, writing—review and editing; M.U.R.: data curation, visualization, writing—review and editing; A.S.: data curation, writing—review and editing; J.D.B.: conceptualization, funding acquisition, project administration, resources, supervision, writing—review and editing. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Competing interests. We declare we have no competing interests.

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