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Intraspecific and interspecific variation in floral volatiles over time

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Abstract Floral volatile organic compounds (VOCs) are traits that influence plant interactions with pollinators and other species. Interspecific and intraspecific variation in traits can strongly influence community and ecosystem processes. Yet, we lack an understanding of patterns of variation in floral VOCs among individuals of a species and across species at the community-level across years, and the degree to which phylogenetic relatedness among species influences these patterns. Such an understanding is crucial to accurately interpret more complex patterns and predict consequences for pollination services and plant reproduction. We measured floral VOCs within forb populations and across forb species in a subalpine meadow in the Northern Rocky Mountains of USA over 3 years. Forb species varied in their per-flower VOC emissions as well as in the composition, originality (distance from community mean) and uniqueness (distance from nearest neighbor) of their floral VOCs. The originality of a species' floral VOCs tended to be more consistent through time than uniqueness. Although not related to phylogeny, there were species-specific differences in originality and uniqueness which may reflect responses of forbs to differences in environmental conditions among years. Interestingly, while species harbored different amounts of intraspecific variation (dispersion) in floral VOCs, species were relatively consistent in this variation across years, and there was significant phylogenetic signal in intraspecific variation. The implications of this temporal consistency for plant–pollinator interactions deserve further attention. Investigating links between interspecific and intraspecific variation in floral VOCs with pollination services and plant reproductive success will help establish the consequences of variation in this important trait.

Keywords Dispersion · Floral bouquet · Functional trait variation · Native bees · Pollination · Pollinator attraction · Scent

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Introduction

In order to better understand the structure and function of species interactions and the potential effects of

environmental change, ecologists have focused on traits (e.g., Stouffer et al. 2011; Eklöf et al. 2013; Dehling et al. 2016). Interspecific trait variation and accompanying functional diversity are important for community and ecosystem processes (e.g., Díaz and Cabido 2001; Hooper et al. 2005; Cardinale et al. 2012). Species with non-redundant, or specialized, traits can fulfill distinct functional roles in a community (Bellwood et al. 2006; Clavel et al. 2011; Estes et al. 2011; Galetti et al. 2013). The originality (i.e., difference in traits from the community average) and uniqueness (i.e., difference in traits from the most similar species in the community) of a species' traits relative to other species in a community can help describe its functional roles and help assess its redundancy or lack thereof (Laliberté and Legendre 2010; Buisson et al. 2013). Further, phylogenetic relatedness among species in a community may contribute to these patterns if more closely related species share similar traits, and incorporating phylogenetic information can provide insight to community assembly, the consequences of species interactions, and ecosystem processes (e.g., Webb 2000; Cavender-Bares et al. 2009).

Although previously thought to be unimportant for community-level patterns (McGill et al. 2006), intraspecific trait variation (ITV)—regardless of trait heritability (Bolnick et al. 2011)—can strongly influence community and ecosystem processes (meta-analysis in Raffard et al. 2019), including trophic interactions (Post et al. 2008), community assembly (Cornwell and Ackerly 2009; Jung et al. 2010; Paine et al. 2011; Siefert 2012), nutrient cycles (Lecerf and Chauvet 2008), crop resistance to disease (Garrett et al. 2009), and community responses to environmental change (Jung et al. 2014). Conversely, both abiotic and biotic (i.e., competition) environmental stress can affect (increase or reduce) within-population ITV in vegetative traits (Helsen et al. 2017). While some studies have found ITV to be driven by differences among populations (Albert et al. 2010), others have found considerable ITV within populations (Messier et al. 2010; Mitchell and Bakker 2014; Siefert et al. 2015). In a meta-analysis, ITV accounted for 25% of the total trait variation within communities and 32% of the total trait variation among communities (Siefert et al. 2015). More generally, consideration of ITV can improve our understanding of the outcomes of species interactions (Kraft et al. 2014), community responses to environmental gradients (Lepš et al. 2011; Kichenin et al. 2013), and ecosystem functions (Breza et al. 2012). Overall, the effects of intraspecific variation on ecological communities rivals that of interspecific variation (Des Roches et al. 2018; Koricheva and Hayes 2018).

Plant–pollinator interactions are mediated by plant traits (e.g., Stang et al. 2006; Junker et al. 2013; Larue et al. 2016). Thus, intraspecific differences in plant traits may affect pollinator attraction and plant–pollinator interactions (Burkle et al. 2013), with implications for plant reproductive success (Gómez and Perfectti 2012). For example, Schlumpberger and colleagues (2009) found among-population variation in phenotypic floral traits to be associated with the attraction of different groups of pollinators. Relative to other plant traits (e.g., leaf traits and other life-history traits), it has been proposed that floral traits may exhibit less intraspecific variation, potentially because precision in pollen deposition depends in part on trait matching with floral visitors and therefore has important consequences for pollination and plant reproductive success (Berg 1960; Cresswell 1998). Low intraspecific variation in floral traits may be indicative of stabilizing selection by pollinators (Waser and Price 1981). Nevertheless, there is substantial intraspecific phenotypic variation in floral traits of some plants species (e.g., Parachnowitsch et al. 2012; Friberg et al. 2013; Lankinen et al. 2016). Further, generalized pollination systems (Armbruster et al. 2004) and populations experiencing fluctuating environmental conditions may accommodate greater variation in floral traits (e.g., Frazee and Marquis 1994; Elle and Hare 2002).

Floral volatile organic compounds (VOCs) are plant traits that influence plant interactions with pollinators and other species. Angiosperm flowers produce and emit complex blends of VOCs that are dispersed by air currents and offer long-distance cues to foraging insects, especially pollinators (Raguso 2008; Junker 2016). These olfactory cues provide information to foraging pollinators about the location, identity, and status of the emitting plant, and typically function in concert with visual cues to affect discrimination, landing, and to initiate feeding by flower visitors (Kunze and Gumbert 2001; Dötterl and Vereecken 2010). Some pollinators, especially bees, instinctually prefer certain floral odors but quickly learn and preferentially respond to odors of flowers

containing abundant and nutritious rewards (Wright and Schiestl 2009; Milet-Pinheiro et al. 2013). Recent progress has been made in understanding patterns in the total emissions and composition of floral VOCs among individuals of a species (Parachnowitsch et al. 2012; Klatt et al. 2013; Kuppler et al. 2016; Lenardis et al. 2017), among species in a community (e.g., Junker et al. 2010; Kantsa et al. 2018; Burkle and Runyon 2019), under different environmental conditions (e.g., Farré-Armengol et al. 2014; Burkle and Runyon 2016; Glenny et al. 2018), and the phylogenetic signal in some of these patterns (e.g., Raguso et al. 2006; Steiner et al. 2011; Delle-Vedove et al. 2017).

Intraspecific variation in floral scent has been associated with attractiveness to floral visitors in crop (Klatt et al. 2013; Lenardis et al. 2017) and native plant species (Kuppler et al. 2016; Burkle and Runyon 2019). Across native forb species in a community, higher intraspecific variation in floral scent was related to greater species richness of floral visitors (Burkle and Runyon 2019). Intraspecific variation in floral scent may also be associated with intraspecific differences in plant reproductive success (Kuppler et al. 2016). Yet, we still lack an understanding of whether basic patterns of variation in floral VOCs among individuals and across species at the community level are consistent across years. Such an understanding is crucial to be able to accurately interpret more complex patterns and predict consequences of such patterns for pollination services and plant reproduction. This study provides a first community-level, multi-year assessment of intraspecific and interspecific variation in floral VOCs.

Over 3 years, we measured headspace floral VOCs within forb populations and across forb species in a subalpine meadow in Montana, USA. We aimed to investigate inter-annual variation in floral VOCs within populations and among species, and whether phylogenetic relatedness among species (Fig. S1) contributed to these patterns. Specifically, we tested patterns within and among species and among years in (1) total emissions in floral VOCs per flower, (2) composition of floral VOCs, (3) intraspecific variation (i.e., dispersion) and interspecific variation (i.e., originality and uniqueness) in floral VOCs, after testing for evidence of phylogenic signal. We were interested in whether forb species exhibited different amounts of intraspecific and interspecific variation in floral VOCs, and whether VOC emission varied uniformly among forbs across years, i.e., the degree to which variation in floral VOCs of the majority of species in a community rose and fell together over time. An effect of year could indicate that the environmental conditions in that year, for instance, influenced biochemical pathways similarly across species. Additionally, we were interested in how consistent forb species were in any variation they exhibited across years. Species-specific differences in patterns of floral VOCs among years could indicate species-specific responses to environmental conditions (Glenny et al. 2018).

Methods

Study system

We sampled the floral VOCs of 132 individuals of 47 naturally growing forb species in 2012, 96 individuals of 20 species in 2015, and 224 individuals of 37 species in 2016, for a total of 52 species (47 native species and 6 non-native, weedy species) (Table S1). This sampling took place in a ca. 20 ha portion of a diverse montane meadow near Bozeman, Montana USA at the base of Mt. Ellis (45.625° -110.963°; 1600–1750 m elevation) (Fig. S2). The meadow community contains over 50 forb species, and floral visitors in this system are primarily bees (Burkle and Runyon 2019).

The 3 years varied in their environmental conditions. In 2012, there was a relatively snowy, cold winter, warming quickly to an early hot, dry summer (i.e., relatively extreme weather in both winter and summer), while 2015 and 2016 were more similar to each other and more moderate compared to 2012, though spring came early in 2015 compared to either of the other years and spring was particularly late in 2016 (Table S2).

Quantifying floral volatiles

Floral VOCs were collected at the field site from intact plants and analyzed following the methods detailed in Burkle and Runyon (2017, 2019). Throughout the growing season (late April-early August) in 2012, 2015 and 2016, we regularly visited (approximately weekly, dependent on weather) the Mt. Ellis

community and sampled VOCs from species that were in peak flower. The flowering phenologies of many forb species overlap with each other, though no species maintain peak flower across the entire growing season (see Burkle and Runyon 2019 for more details on phenologies). Plants that appeared healthy (i.e., no signs of physical damage, herbivory, etc.) were haphazardly selected and their newly opened flower(s) enclosed in 950 mL clear polyethylene cups with dome lids (Dart Container Corporation, Mason, MI, USA). Air was pulled out of the cups for 1 h at 0.5 L min^{-1} through volatile traps containing 30 mg of the adsorbent HayeSep-Q (Restek, Bellefonte, Pennsylvania) using portable volatile collection systems (Volatile Assay Systems, Rensselaer, New York). Cotton was used to surround the stem or peduncle where it enters the dome lid to fill the airspace, protect plants from damage, and minimize outside contaminants entering the system. Since collection times were short, filtered air was not pushed into the cups. VOCs were collected from empty cups and cotton near focal plants to identify and exclude contaminants. Floral VOCs were sampled on days of calm sunny weather during peak hours of pollinator activity (1000–1400) (Gibson et al. 2011). For each species in each year, sampled plants were generally in the same part of the meadow but separated by at least 5 m (usually greater than 10 m); for each species, the area within the meadow sampled usually varied across years. VOCs were usually sampled from one flower per plant, however, differences in plant architecture (e.g., presence of clusters or umbels of many small flowers) resulted in variation among forb species in the number of flowers from which VOCs were collected (range: 1–378, median: 1, mean: 21), but emission rates were standardized by the number of flowers in the sampling cup. For Asteraceae species, we counted each capitulum (flower head) as a single flower. We attempted to enclose only flowers in cups, but oftentimes green bracts and tips of peduncles or pedicels that were closely associated with flowers were included in collections. For most forb species in a given year, floral VOCs were collected from three (2012) or six (2015 and 2016) replicate individuals of each forb species, during peak bloom. The floral VOCs of all replicates of each species were collected simultaneously or at a similar time of day.

VOCs were eluted from traps using 150 µL of dichloromethane; 500 ng of *n*-nonyl-acetate was added as the internal standard. Samples were analyzed using an Agilent 7890A gas chromatograph (GC) coupled with a 5975C mass spectrometer and separated on a HP-1 ms column (30 m × 0.25 mm inside diameter, 0.25 µm film thickness). Helium was used as the carrier gas. The GC oven was maintained at 35 °C for 3 min and then increased by 5 °C min^{-1} to 125 °C, then 25 °C min^{-1} to 250 °C. Quantifications were made relative to the internal standard using ChemStation software (Agilent Technologies, Wilmington, DE, USA). Identifications of compounds were made using NIST 08 Mass Spectral Search Program (National Institute of Standards and Technology, Gaithersburg, MD, USA) and confirmed by comparing mass spectra and retention times with commercial standards, when available. If commercial standards were not available, compounds were assigned a name if spectral match in NIST software was $> 80\%$ and it was previously reported as a floral VOC (Knudsen et al. 2006) otherwise compounds were assigned to a group or class (e.g., benzenoid, monoterpenoid, etc.) based on their putative biosynthetic origin following Knudsen et al. (2006). The presence of unidentified compounds across species and years was verified by comparing retention times, mass spectra, and by using the NIST 08 Mass Spectral Search Program.

Analytical methods

Estimating potential phylogenetic signal in floral VOCs

For each of our analyses to estimate phylogenetic signal in floral VOCs (below), we used the angiosperm supertree of Zanne et al. (2014), trimmed to include a single tip for each of the 52 species sampled (Fig. S1).

To estimate phylogenetic signal in *floral VOC emission rates*, we calculated the *K* statistic (Blomberg et al. 2003) using phylosig in the phytools package (Revell 2012) in R, incorporating intraspecific variation (i.e., as SE) following Ives et al. (2007). The *K* statistic uses the variance of standardized phylogenetically independent contrasts to measure how well the tree fits the data (i.e., floral VOC emission rates), assuming a Brownian motion model of trait evolution. The *K* statistic ranges from 1 to 0, with high values indicating stronger phylogenetic signal (i.e., high similarity in traits among closely related species). We determined the significance of *K* by permuting the

data (nsim = 1000) across the tree and recalculating K from the simulations (Blomberg et al. 2003). Because phylogenetic signal is difficult to detect with fewer than 20 species (Blomberg et al. 2003), we calculated the mean (and SE) total, aliphatic, benzenoid, and terpene per-flower VOC emission rates (log + 1 transformed) for each forb species (N = 52) across all individuals and years.

We investigated the potential phylogenetic signal in *floral VOC composition* among species (N = 52) by calculating pairwise phylogenetic distances among species and testing the correlation between this distance matrix and a Bray–Curtis dissimilarity matrix of VOCs using a Mantel test. In this case, the Bray–Curtis matrix was based on mean emissions of each compound across all individuals and all years for each species.

To estimate phylogenetic signal in *within-population intraspecific dispersion in floral VOCs*, we calculated the K statistic as above using the mean (and SE) dispersion of each forb species (N = 52) across all individuals and years.

To determine the degree to which phylogenetic originality was related to the *originality of floral VOCs*, we first calculated the phylogenetic originality of each species (i.e., having few closely related species; Pavoine et al. 2017) using the quadratic-entropy (QE)-based index (Pavoine et al. 2005) with the originality function in the ade4 package, which calculates the distance of each pair of species on the tree by summing the branch lengths that separate them and then measures the frequency distribution that maximizes quadratic entropy. We calculated the mean originality of floral VOCs of each species (N = 52) as the mean distance of the species centroid from the community centroid across individuals in each year, averaged across years. That is, originality measures how a species' floral VOCs differ from the community average VOCs. We tested the correlation between phylogenetic and functional originality (ln-transformed for normality) across forb species.

To investigate the degree to which phylogenetic uniqueness was related to the *uniqueness of floral VOCs*, we calculated the mean uniqueness of floral VOCs of each species (N = 52) as the mean distance to the nearest neighbor species (centroid) in each year, averaged across years. Phylogenetic uniqueness for each species was calculated as the minimum phylogenetic distance between each species and the single closest other species of the 52 that we sampled using the cophenetic.phylo function in the ape package. A species with highly unique floral VOCs has a scent unlike its nearest neighbor, and conceptually, uniqueness is the opposite of functional redundancy (Walker 1991, Buisson et al. 2013). Of note, while the originality (above) and uniqueness of a species' floral VOCs may be related, it is also possible for a species to have original but non-unique floral VOCs if its bouquet is far from community average in trait space but similar in scent to another community member. We tested the correlation between phylogenetic and functional uniqueness (ln-transformed) across forb species.

Total emission rates of floral VOCs

For the 14 species for which we had 3 years of data and within-species replication in each year, we calculated the total per-flower per-hour emission rates of floral VOCs for each individual, as well as the per-flower per-hour emission rates of each of the three main groups of compounds (aliphatics, benzenoids, and terpenes). We tested for differences in mean total, aliphatic, benzenoid, and terpene emission rates (log + 1 transformed for normality) among species, years, and the interaction between species and year using two-way ANOVAs. In this and other analyses involving year, we set year as a categorical explanatory variable because we were interested in annual variation but had no reason to expect directional patterns across years. Here, and below, where we employ multiple comparisons, we follow the guidelines of Moran (2003) and Gotelli and Ellison (2004) and report unadjusted significance values. Nevertheless, we also investigated significance after applying Bonferroni corrections to significance levels; significance was confirmed in all cases except one (see Table 1).

To determine the degree to which forb species within the community were relatively consistent in their mean total, aliphatic, benzenoid, and terpene per-flower per-hour VOC emission rates (log + 1 transformed) from year to year, we used correlations across species for each year-pair, including all of the species that were measured in each year-pair (N = 20 species measured in both in 2012 and 2015, N = 32 in 2012 and 2016, and N = 17 in 2015 and 2016). Thus, a benefit of these analyses (and similar correlational

Table 1 ANOVA results of the effects of forb species, year, and their interaction on total VOC emissions, aliphatic emissions, benzenoid emissions, and terpene emission rates (nanograms per- flower per-hour)

Source	DF	Total VOC emissions		Aliphatics		Benzenoids		Terpenes	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Species	13,156	31.41	**< 0.0001**	2.78	**0.014***	83.64	**< 0.0001**	63.07	**< 0.0001**
Year	2,156	32.61	**< 0.0001**	46.39	**< 0.0001**	25.71	**< 0.0001**	14.24	**< 0.0001**
Species × Year	26,156	3.27	**< 0.0001**	3.59	**< 0.0001**	6.10	**< 0.0001**	3.43	**< 0.0001**

All log + 1 transformed

Bold indicate *P*-values at significance levels of alpha less than 0.05

**P*-value that did not meet significance criterion under conservative Bonferroni correction for multiple comparisons

analyses described below) is the ability to expand our inference by including species for which we measured floral VOCs in at least 2 years (i.e., not restricted to the 14 forb species which were measured in all 3 years).

Composition of floral VOCs

To test the degree to which species and year explained variation in the composition of floral VOCs among individuals of 14 species sampled over 3 years, we used PERMANOVA (adonis in the vegan package in R, Oksanen et al. 2019), including species and year as main effects and their interaction. We visualized the differences among individuals, species, and years using non-metric multi-dimensional scaling (NMDS) based on Bray–Curtis dissimilarities. We also fit vectors from each group of floral VOCs onto the NMDS in order to investigate the maximum correlations of each group of compounds to the projections of individuals in floral VOC space and to visualize which groups of compounds were most strongly associated with differences among species. To further investigate which specific compounds, if any, were driving the observed patterns in total floral VOC emissions and in floral VOC composition among years, we used similarity percentage analysis (simper in the vegan package in R).

Within-population intraspecific variation in floral VOCs (dispersion)

There were 14 species for which we had 3 years of data with intraspecific replication in each year. Using dispersion distances to centroid in floral VOCs for individuals of each species in each year (calculated using betadisper in the vegan package in R based on Bray–Curtis dissimilarities), we tested the effects of species, year, and their interaction on within-year intraspecific dispersion in floral VOCs (square-root transformed for normality) with a two-way ANOVA.

To determine the degree to which forb species within the community were relatively consistent in their within-year intraspecific variation in floral VOCs from year to year, we correlated mean dispersion values across species for each year-pair, including all of the species that were measured in each year-pair.

Originality

There were 17 species for which we could calculate originality of floral VOCs in each of the 3 years. Within-year originality was calculated as the distance of a species centroid from the community centroid (considering those 17 species only) in each year. We tested the effects of species, year, and their interaction on within-year originality (ln-transformed for normality) with a two-way ANOVA. To determine the degree to which species within the community were relatively consistent in their mean originality in floral VOCs from year to year, we used a correlation across species for each year-pair, including all species that were measured in each year-pair and the corresponding assemblage centroid (which was relatively invariant among years, see Discussion).

Uniqueness

There were 17 species for which we could calculate the uniqueness of floral VOCs in each of the 3 years. Within-year uniqueness was calculated as the distance

of an individual in floral VOC trait space to its nearest neighbor of a different species in the same year (considering those 17 species only). We tested the effects of species, year, and their interaction on within-year uniqueness (log-transformed for normality) using a two-way ANOVA. To determine the degree to which species within the community were relatively consistent in their mean within-year uniqueness in floral VOCs from year to year, we calculated nearest neighbors based on species centroids (cube-root transformed) and used a correlation across species for each year-pair, including all species that were measured in each year-pair. For all tests here and above, assumptions were checked and met, and transformations made if necessary.

Although originality and total emission rate were consistently correlated, there were few other significant correlations between emission rates, dispersion, originality, or uniqueness of floral VOCs across species in each year (Table S3). Therefore, we report the results of all above analyses, but use appropriate caution when interpreting patterns involving originality and total emission rate.

Results

Overview

Across the 52 sampled forb species, we detected floral emissions of aliphatics (32 compounds), benzenoids (29 compounds), terpenoids (56 monoterpenoids, 5 sesquiterpenoids, and 3 irregular terpenes), 4 nitrogen containing compounds, 2 miscellaneous cyclic compounds, and 2 C5-branched chain compounds (Fig. S2).

Phylogenetic signal in floral VOCs

Across all 52 forb species, we found no significant evidence of phylogenetic signal in total ($K = 0.28$, $P = 0.22$), aliphatic ($K = 0.39$, $P = 0.66$), benzenoid ($K = 0.33$, $P = 0.08$), or terpene ($K = 0.13$, $P = 0.71$) per-flower per-hour floral VOC emission rates. Phylogenetic distance between forb species was also not significantly correlated to their similarity in floral VOC composition (Mantel: $r = 0.07$, $N = 52$ species, $P = 0.23$). There was evidence of phylogenetic signal in the within-population intraspecific dispersion in floral VOCs ($K = 0.63$, $P = 0.002$, Fig. S3); phylogenetic signal in within-population intraspecific dispersion was also detected when including only the 14 forb species sampled in all 3 years ($K = 0.82$, $P = 0.041$). Phylogenetic originality and originality of floral VOCs were not correlated across species ($r = -0.18$, $P = 0.21$). Phylogenetic uniqueness and uniqueness of floral VOCs were not correlated across species ($r = -0.005$, $P = 0.97$).

Total emission rates of floral VOCs

For 14 forb species, differences in per-flower per-hour emission rates of total VOCs (Fig. 1a), aliphatics (Fig. 1b), benzenoids (Fig. 1c), and terpenes (Fig. 1d) among species depended on year (i.e., species × year interaction), with main effects of species and year (Table 1). Total VOC emission rates and emission rates of aliphatics were observed to be lowest in 2016, intermediate in 2015, and highest in 2012. Benzenoid emission rates were lower in 2016 compared to 2012 or 2015, while monoterpene emission rates were lower in 2012 and 2016 compared to 2015. *Rosa woodsii* and *Monarda fisulosa* flowers had the highest total emission rates (Fig. 1a) and highest terpenes (Fig. 1d; notably *cis*- and *trans*-geraniol, eugenol, and geranyl acetate in *R. woodsii*; *p*-cymene, gamma-terpinene, and carvacrol in *M. fistulosa*), while *Fritillaria pudica* flowers had the lowest emission rates of total (Fig. 1a) and monoterpene VOCs. Flowers of *Rosa woodsii*, *Delphinium bicolor*, and *Cerastium arvense* emitted greater amounts of aliphatics than *F. pudica* (Fig. 1b). *Rosa woodsii* flowers emitted the highest amounts of benzenoids (especially phenyl ethyl alcohol), followed by *Dodecatheon pulchellum*, *Erythronium grandiflorum*, etc.; *Geranium viscosissimum* flowers emitted the lowest (Fig. 1c). Some forb species (e.g., *Rosa woodsii*) were very consistent in total floral VOC emission rates across years, while others (e.g., *Erythronium grandiflorum*) emitted different total amounts of floral VOCs in each year, and still others (e.g., *Balsamorhiza sagittata, Cerastium arvense*) were similar in just 2 of the 3 years (Fig. 1a).

Including the forb species for which we measured floral VOCs in two or more years, mean per-flower per-hour total emission rates, benzenoid emission rates, and terpene emission rates of forb species were positively correlated across species in all year-pairs,

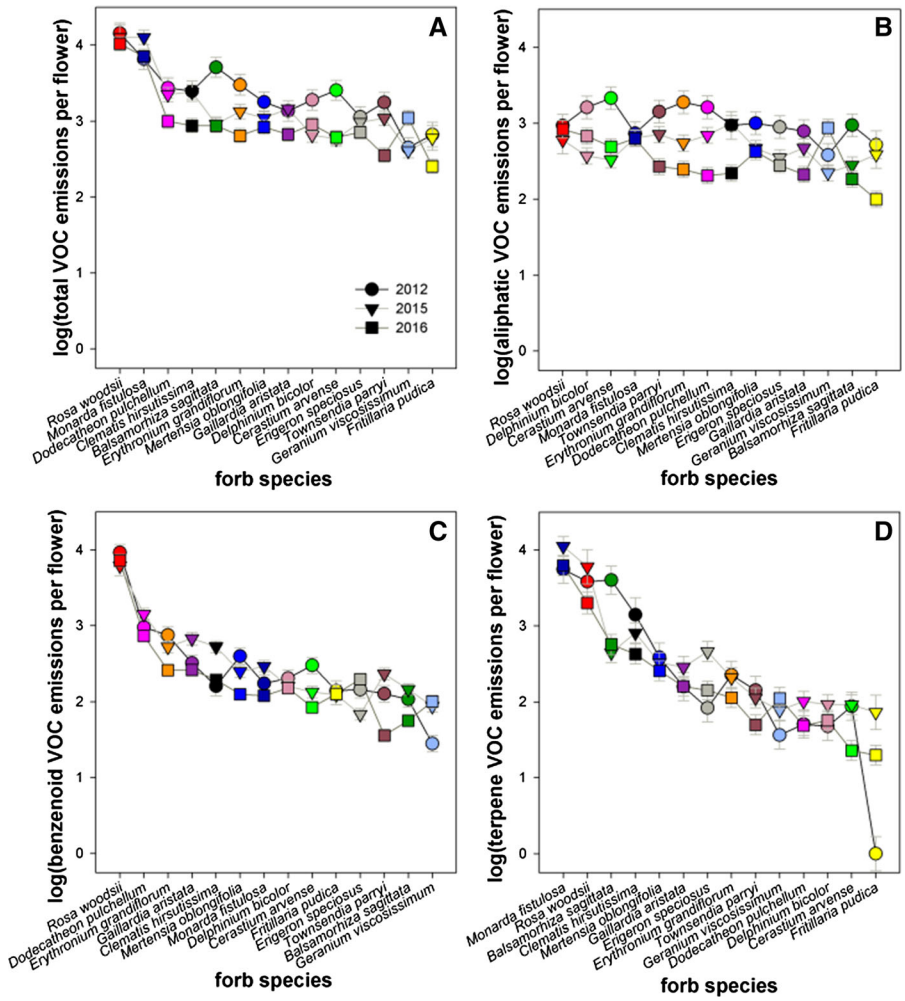

Fig. 1 Least-square mean total (**a**), aliphatic (**b**), benzenoid (**c**), and terpene (**d**) VOC emission rates (nanograms per flower per hour, log-transformed) of each forb species in each year. Error bars are ± SE. Forb species are arranged in rank order in each panel. See Fig. S4 for back-transformed values

Table 2 Correlations between year-pairs in emission rates (ng per-flower per-hour) of total floral VOCs, aliphatics, benzenoids, and terpenes (all log + 1 transformed) across forb species

Comparison	*N*	Total emissions		Aliphatics		Benzenoids		Terpenes	
		r	*P*	*r*	*P*	*r*	*P*	*r*	*P*
2012 vs 2015	20	0.76	**0.0001**	0.051	0.83	0.87	**< 0.0001**	0.74	**0.0002**
2012 vs 2016	32	0.79	**< 0.0001**	0.18	0.31	0.70	**< 0.0001**	0.86	**< 0.0001**
2015 vs 2016	17	0.83	**< 0.0001**	0.018	0.95	0.84	**< 0.0001**	0.91	**< 0.0001**

N is the number of forb species included in the analyses

Bold indicate *P*-values at significance levels of alpha less than 0.05

while there were no relationships across species in any year-pairs for aliphatic emission rates (Table 2).

Composition of floral VOCs

Across 14 species and 3 years, the main effects of species and year and the species × year interaction explained 77% of the variation among individuals in their floral VOC composition (Table 3, Fig. 2). Several compounds were strongly associated with these patterns in total floral VOC emissions and composition across species: high levels of (*Z*)-3-hexenyl-acetate, limonene, phenylethyl-alcohol, *n*-hexanal, (*Z*)-beta-ocimene, and alpha-pinene were observed in 2012; high levels of carvacrol in 2015; and high levels of decanal in 2016 (Table S4).

Within-population intraspecific variation in floral VOCs

For individuals of 14 forb species, we found that within-year intraspecific dispersion in floral VOCs differed among species, but not among years (Table 3, Fig. 3a). There was no significant interaction between species and year (Table 3). The floral bouquet of *Erigeron speciosus, Balsamorhiza sagittata,* and *Erythronium grandiflorum* had the highest dispersion, while *Rosa woodsii* had the lowest (Fig. 3a). Including forb species for which we measured intraspecific variation in floral VOCs in two or more years, mean dispersion in floral VOCs of species was weakly positively correlated between years (Table 4), though these relationships were marginally significant at best.

Originality

For 17 species, floral VOC differences in mean within-year originality among species varied by year (species × year interaction), with main effects of species and year (Table 3, Fig. 3b). Mean originality in floral VOCs [of individuals across species] was lowest in 2015, intermediate in 2012, and highest in 2016. Floral VOCs of *Rosa woodsii* and *Monarda fistulosa* consistently had the highest originality, while *Delphinium bicolor* and *Cerastium arvense* VOCs had the lowest (Fig. 3b).

Across forb species for which we measured floral VOCs in two or more years, mean originality of a species in one year was positively associated with its originality in another year (Table 4).

Uniqueness

For 17 species, differences in mean within-year uniqueness among species in floral VOCs varied by year (species × year interaction), with main effects of species and year (Table 3, Fig. 3c). Mean uniqueness of floral VOCs [of individuals across species] was higher in 2012 compared to 2015 and 2016. Floral scent of *Claytonia lanceolata, Erythronium grandiflorum, Clematis hirsutissima,* and *Townsendia parryi* had greater uniqueness than *Arabis nuttali* (Fig. 3c). Across forb species for which we measured floral VOCs in two or more years, mean uniqueness of a species in 1 year was not associated with its uniqueness in another year in any year-pair comparisons (Table 4).

Discussion

This study provides a first assessment of within-population intraspecific and interspecific variation in floral VOCs across species in a community over several years. We found that although forb species differed from each other in their per-flower per-hour

Table 3 The effects of forb species, year, and their interaction on floral VOC composition (based on PERMANOVA), intraspecific variation (i.e., dispersion), originality, and uniqueness (separate ANOVAs)

Source	DF	Composition			Dispersion			Originality		Uniqueness	
		F	r^2	*P*	*F*	*P*	DF	*F*	*P*	*F*	P
Species	13,156	24.52	0.49	**0.001**	2.64	**0.0023**	16,176	32.57	**< 0.0001**	2.42	**0.0026**
Year	2,156	34.16	0.11	**0.001**	1.77	0.17	2,176	9.29	**< 0.0001**	6.04	**0.0029**
Species × year	26,156	4.13	0.17	**0.001**	1.18	0.26	32,176	2.60	**< 0.0001**	2.15	**0.0009**

Bold indicate *P*-values at significance levels of alpha less than 0.05

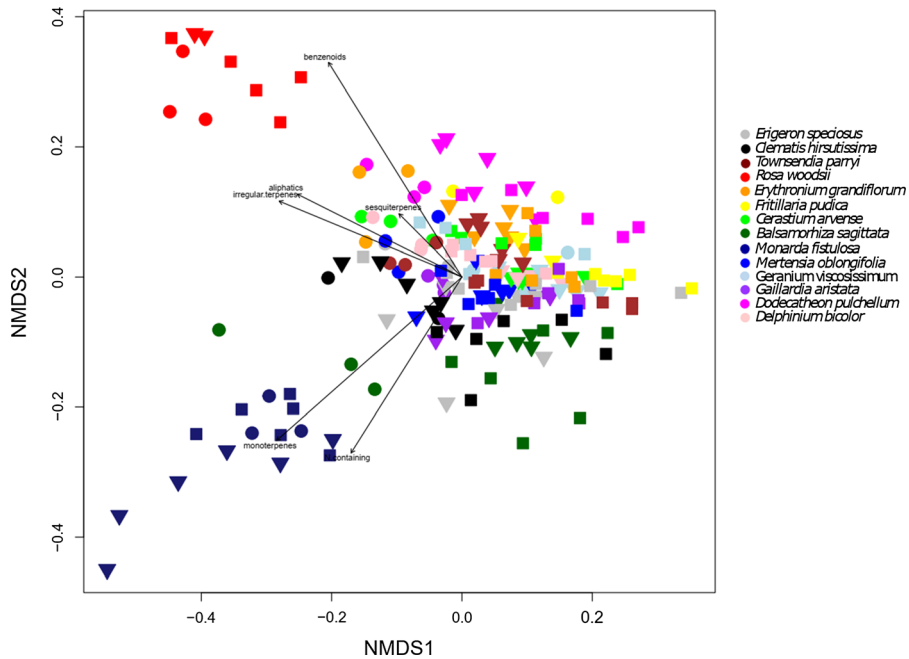

Fig. 2 NMDS illustrating the floral VOCs of individuals of 14 forb species (colors) in each of three years: 2012 (circle), 2015 (triangle), 2016 (square). Vectors show the significant fitted main compound classes

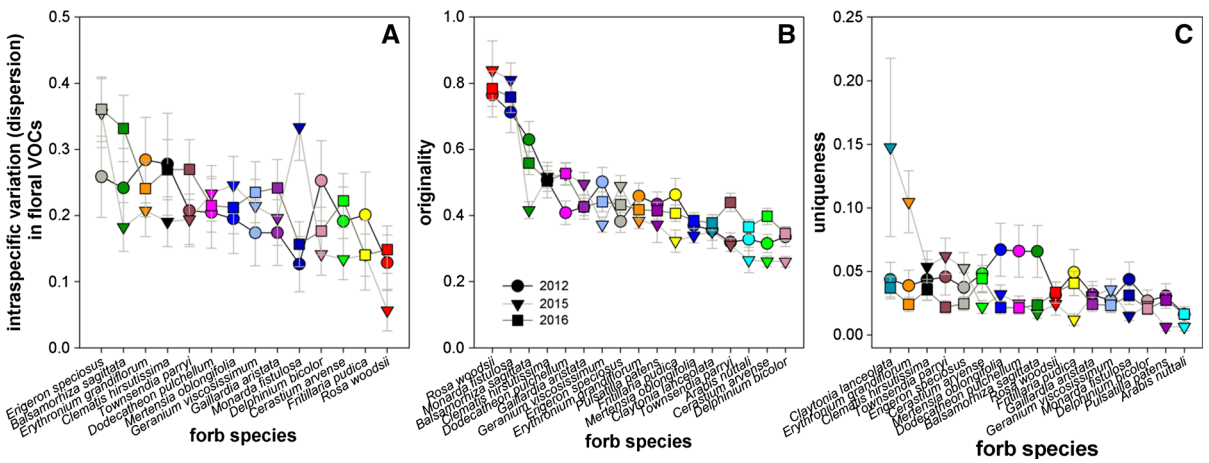

Fig. 3 Back-transformed least-square mean intraspecific variation (i.e., dispersion) (**a**), originality (**b**), and uniqueness (**c**) in floral VOCs of each forb species in each year. Error bars are ± SE

VOC emission rates as well as in the composition, originality (distance from community mean), and uniqueness (distance from nearest neighbor) of their floral VOCs, there was no evidence of phylogenetic signal in these patterns among species. Interestingly, the originality of a species' floral VOCs tended to be more consistent through time (across years) than uniqueness. Nevertheless, the originality and uniqueness of some species' floral VOCs fluctuated with year (i.e., species × year interactions), indicating that beyond the main differences among species and years, there were species-specific differences among years that may reflect responses of forb species to differences in environmental conditions among years. Notably, we also found that while species harbored different amounts of within-population

Table 4 Correlations between year-pairs in intraspecific variation (i.e., dispersion), originality, and uniqueness of floral VOCs across forb species

Comparison	Dispersion			*N*	Originality		Uniqueness	
	N	*r*	*P*		*r*	*P*	*r*	*P*
2012 vs 2015	17	0.38	0.13	20	0.54	**0.015**	0.37	0.11
2012 vs 2016	32	0.32	0.073	32	0.66	**< 0.0001**	0.18	0.33
2015 vs 2016	15	0.51	0.051	17	0.78	**0.0002**	0.12	0.64

N is the number of forb species included in the analyses

Bold indicate *P*-values at significance levels of alpha less than 0.05

intraspecific variation in floral VOCs (dispersion), most species (with a few exceptions) were relatively consistent in this variation across years, possibly because of some degree of phylogenetic conservation of this intraspecific variation among species. Inter-annual consistency in intraspecific variation may result from fairly rigid biochemical pathways or stabilizing selection from pollinators, among other possibilities, and will require additional investigation to understand the causes and consequences. Other critical next steps will be to examine relationships between interspecific and intraspecific variation in floral VOCs among species and over time with community-level patterns of plant–pollinator interactions, pollination services, and plant reproductive success.

Total emission rates and composition of floral VOCs

Not surprisingly, total per-flower per-hour VOC emission rates—as well as the emission rates of main groups of floral VOCs (i.e., aliphatics, benzenoids, and terpenes)—were different among species. That is, like other studies have found, species vary in their floral VOC emissions (e.g., Knudsen et al. 2006; Filella et al. 2013), with some species having flowers that are more fragrant than other species. More interestingly, we found that average total floral VOC emission rates across species in a community can vary from year to year, indicating that ambient environmental conditions may influence some core biochemical pathways similarly across species. For example, warmer temperatures generally have a consistent positive effect on emission of floral scent (Hansted et al. 1994; Sagae et al. 2008; Hu et al. 2013; Farré-Armengol et al. 2014) likely via positive effects on plant physiology (e.g., VOC biosynthesis) and physiochemical properties of individual compounds (e.g., increased volatililty). Although less studied, differences in precipitation or water availability across years can also affect emission of floral VOCs (Burkle and Runyon 2016; Campbell et al. 2019), but the mechanisms are not understood.

However, while some species were very consistent in total floral VOC emission rates across years, others were not, suggesting that environment can influence floral volatile chemistry in species-specific ways (Farré-Armengol et al. 2014; Burkle and Runyon 2017). These findings for interspecific variation in total floral VOC emissions among years were consistent with our findings for floral VOC composition, which illustrated differences among species and years as well as species-specific differences among years (i.e., species × year interaction). Differences among species in their yearly variation in floral VOC emissions and composition were also consistent with species-specific floral VOC responses to experimental manipulations of environmental conditions (Burkle and Runyon 2016; Glenny et al. 2018). Some compounds strongly associated with these year-to-year patterns in floral VOC emissions across species are known to influence pollinator behavior. For example, limonene, ocimene, and alpha-pinene were emitted in relatively greater amounts in 2012, and can each alter foraging behavior of bees (Schiestl and Roubik 2003; Byers et al. 2014). This suggests that across-year variation in floral VOCs could have broader community effects on pollinators and plant reproduction, and highlights the need to better understand how particular aspects of the abiotic environment contribute to variation in floral VOCs and plant–pollinator interactions.

Within-population intraspecific variation in floral VOCs: dispersion

Species were relatively consistent across years in the amount of dispersion in floral VOCs that their individuals displayed, and there was phylogenetic signal in this variation. Thus, intraspecific variation in floral VOCs seems to be more of a species-level property than a trait that is easily modified by environmental conditions. While sample sizes were small for each plant species in 2012 ($N = 3$), intraspecific variation in floral VOCs was consistent with 2015 and 2016 ($N = 6$), suggesting within-species VOC variation is conserved and regulated by plants. However, some species, such as *Monarda fistulosa*, did not fit this general pattern, displaying particularly high or low intraspecific variance in floral VOCs in a particular year. Despite these exceptions, across forb species, species with high mean dispersion in one year were generally associated with having high mean dispersion in another year, and vice versa for species with low dispersion. Given the weak nature of these correlations, measurements of floral volatiles of additional species across years are needed to clarify the pattern. Our previous work in this community found that forb species with higher dispersion of floral VOCs were more connected to pollinators (i.e., visited by a broader suite of bee species) (Burkle and Runyon 2019), thus greater dispersion may allow plants to attract generalist pollinators and improve the likelihood of pollination. It will be interesting for future studies to investigate the degree to which inter-annual consistency in intraspecific variation in floral VOCs (or lack thereof) has implications for pollinator attraction, given known inherent variation in pollinator community composition among years (e.g., Williams et al. 2001; Petanidou et al. 2008). Specifically, we might expect forb species with consistently low intraspecific variation in floral VOCs across years to be under stabilizing selection, possibly by specialist pollinators.

In this system, there was phylogenetic signal in the amount of within-population intraspecific variation in floral VOCs but not, interestingly, in emissions rates, scent bouquets, or any other aspect of floral VOCs that we measured. Although one might expect Asteraceae species to exhibit high among-individual variation in floral VOCs—a pattern that we observed—simply because flower heads are composed of hundreds of flowers of different types (i.e., ray and disc) at different stages of development, similarity in the amount of variation in floral VOCs in closely related species was widespread across the phylogeny. Assessments of phylogenetic signal in the amount of intraspecific trait variation across species appear to be rare (e.g., Gaudard et al. 2019) and will require additional investigation to understand how widespread such patterns are and their ecological or evolutionary significance.

Interspecific variation in floral VOCs: originality and uniqueness

Forb species displayed strong differences in the originality of their floral VOCs. Despite slightly variable patterns in originality of species in different years, species with high originality in one year generally had high originality in another year and vice versa. By contrast, the uniqueness of forb species' floral VOCs was more variable among years than their originality, and species with high uniqueness in a given year generally did not maintain that high uniqueness in other years. Floral VOC originality may be more constrained by pollinator-mediated selection in some plant species compared to uniqueness, similar to other floral visual traits (Waser and Price 1981). Originality of floral scent could be constrained in some species if there is selection to not deviate too far from the community mean, for example, if it is beneficial to be non-original and smell like many other species, thereby belonging to the core group of generalist forb species that attract generalist pollinators. By contrast, in species with highly unique VOCs, the pressure to emit a consistent floral bouquet might be relaxed because they already stand out in the community. Species with highly unique floral VOCs may rely more on floral scent for pollinator attraction than other plant traits (e.g., floral display). However, whether pollinator species can detect or respond to these year-to-year changes in uniqueness has not been examined. It will be interesting to explore the degree to which other plant traits, like floral color or display, signal to or are under selection from pollinators (Parachnowitsch et al. 2012) in species with unoriginal or non-unique floral VOCs, particularly across plant species that share pollinators. Furthermore, time-of-year (Filella et al. 2013; Burkle and Runyon 2019), pollination status, visual cues, and other ecological

contexts (reviewed in Raguso 2008) could modify the importance of floral VOC originality and uniqueness and contribute to plant–pollinator interaction structure (e.g., Junker et al. 2010; Kantsa et al. 2018; Burkle and Runyon 2019) in different systems.

Considering that we assessed a somewhat different suite of forb species in each year, we found it interesting that the position of the community centroids based on floral VOCs in each year and across all individuals in all years were very similar. As a result, the "overall average floral scent" of this meadow community appears to be relatively consistent from year to year. If this pattern is present in other systems, it could have important implications for predicting how original, and possibly apparent to pollinators, the scent of a potential or recent invasive species may be relative to the resident community. It remains to be seen whether more dramatic fluctuations in environment or in species composition than encapsulated in the three years assessed in this study could alter the community centroid.

Conclusions

In this meadow community over three years, we documented interspecific and intraspecific variation in floral VOCs. Perhaps most interestingly, we found temporal (among-year) consistency in intraspecific variation in floral VOC composition. Additional studies are needed to confirm whether these patterns are present in other systems. In particular, much of the work on floral VOCs has been short term, evaluating floral VOCs as snapshots. Incorporating additional temporal scales in investigations of floral VOCs (e.g., of single flowers, individuals, populations, and communities over days, seasons, and years) will help elucidate the times and contexts in which variation in floral VOCs is expressed. A better understanding of both interspecific and intraspecific patterns in floral VOCs in combination with other plant traits is important for predicting the structure and function of plant–pollinator interactions, particularly as environmental conditions continue to change at a variety of spatial and temporal scales.

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Compliance with ethical standards

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