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Floral volatiles structure plant–pollinator interactions in a diverse community across the growing season

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Abstract

1. While the importance of floral odours for pollinator attraction relative to visual cues is increasingly appreciated, how they structure community-level plant–pollinator interactions is poorly understood. Elucidating the functional roles of flowering plant species with respect to their floral volatile organic compounds (VOCs) and how those roles vary over the growing season is an initial step towards understanding the contribution of floral VOCs to plant–pollinator interaction structure.
2. We sampled the floral VOCs, phenologies and bee visitors of naturally growing plants in a montane meadow in the Northern Rocky Mountains of USA in order to acquire a base understanding of how floral VOCs and other plant traits may structure plant–pollinator interactions across the growing season. We expected forb species with floral VOCs that were original (far from the community mean) and unique (far from the nearest neighbour) would have few pollinating partners (i.e. specialists), while forbs with non-original or highly variable floral VOCs would form the generalist core of interactors, thereby contributing to network nestedness (specialists interacting with nested subsets of generalists). Network modularity (patterns of distinct, highly connected subnetworks) could be influenced by groups of pollinators that are attracted to or repelled by certain floral bouquets.
3. Species blooming in early spring emitted similar floral VOC blends containing generalist attractants, whereas floral VOC complexity was highest in mid to late summer. Forb species varied in the originality, uniqueness, and intraspecific variation (i.e. dispersion) of their floral VOCs, indicating the potential for different functional roles in plant–pollinator networks. Specifically, the originality, uniqueness and dispersion of forb species' floral VOCs increased across the growing season.
4. Floral VOCs influenced forb interactions with pollinators. Floral VOCs contributed to the nested structure, but not modular structure, of community-level plant–pollinator network structure. Forb species with more original floral VOCs were less connected, while forb species emitting more compounds and with higher intraspecific variation in floral VOCs were more connected to pollinators.
5. These findings show that floral scent plays important roles in structuring bee–forb interactions and guiding seasonal patterns in complex communities. Understanding seasonal patterns in floral VOCs may have important implications for plant–pollinator interactions among communities differing in species composition, or as shifts occur in suites of co-flowering species due to climate change.

KEYWORDS
floral scent, floral traits, functional diversity, interspecific trait variation, intraspecific trait variation, native bees, plant–pollinator network structure, pollination services

1 | INTRODUCTION

To date, pollination biology has largely focused on the role of visual cues for pollinator attraction (Raguso, 2008a), including floral colour, size and shape, and these traits are known to contribute to community-level patterns in plant–pollinator interaction networks (e.g. Vazquez, Chacoff, & Cagnolo, 2009). The importance of floral odours for pollination is increasingly appreciated (Raguso, 2008b; Schiestl, 2015), yet how they structure plant–pollinator interactions is less well understood (Larue, Raguso, & Junker, 2016). Floral odours are predicted to be important determinants of interaction network structure because they are among the most important cues used by pollinators to locate pollen and nectar rewards. For example, the odour plume emitted by flowers can function over long distances to attractant or repel pollinators and at short distances can stimulate landing and feeding (Dötterl & Vereecken, 2010; Junker, 2016; Raguso, 2008b). Although bees are known to possess innate preferences for some floral scents, they can quickly learn odours associated with flowers containing the most abundant and nutritious rewards (Milet-Pinheiro et al., 2013; Raguso, 2008b). However, floral volatiles are not expected to fully explain network structure since they usually function in tandem with other floral cues (e.g. flower colour; e.g. Junker & Parachnowitsch, 2015; Kantsa et al., 2017). Two ways that we can approach the structure of plant–pollinator interactions in order to better understand the role of floral volatile organic compounds (VOCs) is (a) community-level structural properties (nestedness and modularity) and (b) the roles of species within these networks.

Across systems, plant–pollinator interactions are very often observed to have a nested structure, meaning that specialists interact with subsets of increasingly more generalist species (Bascompte, Jordano, Melian, & Olesen, 2003). This nested structure is thought to be important because it can confer robustness to perturbations like extinctions, invasions and disturbances (e.g. Memmott, Waser, & Price, 2004). Numerous factors are known to contribute to nestedness, including morphology and size-related traits, phenology and abundance (e.g. Stang, Klinkhamer, & van der Meijden, 2006; Vazquez, Bluthgen, Cagnolo, & Chacoff, 2009; Vazquez, Chacoff, et al., 2009). One factor that has received insufficient investigation as a contributor to network nestedness is the VOCs emitted by flowers. Pollinators are known to exhibit preferences for certain combinations, or 'bouquets', of volatile compounds (Dobson, 2006; Wright, Lutmerding, Dudareva, & Smith, 2005), and these preferences can correlate with patterns of visitation (Junker, Hocherl, & Bluthgen, 2010; Kantsa et al., 2018). We might expect generalist pollinators to be attracted, in part, to many forb species with a range of floral VOCs, and specialist pollinators to be attracted to fewer forb species that emit similar, specific suites of floral VOCs that are nested subsets of generalist bouquets.

Though not as well-studied as the nested structure of plant–pollinator interactions, these interaction networks can also be modular (contain compartments; e.g. Olesen, Bascompte, Dupont, & Jordano, 2007). Pollination systems (i.e. floral syndromes and the pollinator functional groups that visit them; Faegri & Van Der Pijl, 1979; Fenster, Armbruster, Wilson, Dudash, & Thomson, 2004) have been found to be associated with the modular structure of plant–pollinator interaction networks (e.g. Carstensen, Sabatino, & Morellato, 2016; Danieli-Silva et al., 2012; Dicks, Corbet, & Pywell, 2002). While floral scent is often mentioned in a general sense as a contributor to pollination syndromes and has been tested in some groups (e.g. Dobson, 2006; Knudsen & Tollsten, 1993; Knudsen, Tollsten, Groth, Bergström, & Raguso, 2004; Kantsa et al., 2019), the degree to which floral VOCs contribute to the modular structure of plant–pollinator interactions is unknown. If certain pollinator groups are attracted to (or repelled by) specific floral bouquets, then we would expect to observe these groups associating within modules, thereby influencing the structure of interaction networks. While these previous studies have considered widely divergent pollinator groups, including butterflies, bees and flies, where a strong signal of floral scent syndromes may be expected among these groups, it is not known whether finer-scale, within-group (e.g. bees only) modules are related to bouquets of floral VOCs.

Within plant–pollinator interaction networks, each plant species has traits that influence the roles of that species in its interactions with pollinators. Floral bouquets can signal to pollinators in several ways. First, the floral VOCs of an individual or a species may be *unique* if no other individuals or species in the community have a similar scent profile (i.e. no near neighbours in floral scent trait space; sensu Buisson, Grenouillet, Villéger, Canal, & Laffaille, 2013; Coux, Rader, Bartomeus, & Tylianakis, 2016; Walker, 1992). Second, the floral VOCs of an individual or species may be *original* if its scent profile is distinct compared to the scent of the average member of the community (sensu Buisson et al., 2013; Coux et al., 2016; Laliberté & Legendre, 2010). Likewise, if the flowers of an individual or species emit compounds that are similar to many other species in the community, its floral VOCs would be unoriginal. Third, the floral VOC profiles of the individuals of a species in the community may be consistent (low *dispersion* and intraspecific variability) or highly variable (high dispersion) (sensu, e.g. Bolnick et al., 2011; Kuppler, Höfers, Wiesmann, & Junker, 2016; Siefert, 2012). These metrics are not static properties of the individual or species because they depend on community context (i.e. the composition of the other individuals and species in the community and their floral VOCs). Therefore, these metrics have potential implications for the functional roles of

floral VOCs for pollinator attraction. For instance, we might expect forbs with unique or original floral VOCs to be visited by specialist pollinators, while forbs with unoriginal VOCs might be visited by core generalist pollinators. We might also expect forb species with consistently similar floral VOCs (i.e. low intraspecific dispersion) to be visited by a more consistent pollinator community compared to species with high intraspecific dispersion of their floral VOCs. This framework may be useful for considering the potential implications of shifts in flowering phenologies due to climate change that result in changes in the suites of species with which a focal plant species co-flowers, given the context-dependent nature of these metrics in representing the uniqueness, originality and dispersion of floral VOCs *relative* to other co-flowering members of the community.

Using this framework, we assembled a comprehensive dataset of the floral VOCs of naturally growing plants across the growing season and explored relationships between patterns in those floral VOCs and plant–pollinator interactions, after testing whether controlling for phylogenetic signal was useful. Specifically, we first investigated how floral VOCs might fundamentally structure plant–pollinator interactions by testing how floral VOCs contributed to the nestedness and modularity of community-level forb–bee interaction networks. We hypothesized that if floral VOCs contributed to nestedness, then core generalist forb species in the forb–bee interaction network (i.e. visited by numerous bee species) would also emit core generalist floral VOCs in the plant-VOC emissions network. Further, we hypothesized that if floral VOCs contributed to modularity, then forb species within the same module would emit more similar floral bouquets than those in different modules. Second, for forb species within the interaction network, we investigated how their floral VOCs differed in richness of compounds, originality, uniqueness and dispersion across the growing season. Given patterns of increasing forb and bee diversity over the growing season in this system, we hypothesized that if blending in with neighbouring forbs early in the season when floral abundances and diversity are low facilitated pollinator visitation, while standing out from neighbours is beneficial later in the season when floral abundances and diversity are high, then originality, uniqueness and dispersion may increase over the season. Third, we determined how these potential predictors of the functional roles of floral VOCs were related to patterns of bee visitation to forb species. We hypothesized that forbs with original or unique floral VOCs to be visited by a limited suite of bees, and forbs with high intraspecific dispersion in floral VOCs to be visited by a broad suite of bees.

2 | MATERIALS AND METHODS

2.1 | Study system

In 2012, we sampled the floral VOCs, phenologies and pollinator visitors of 47 species of naturally growing plants in a diverse montane meadow near Bozeman, Montana USA at the base of Mt. Ellis (45.625°–110.963°; 1,600–1,750 m elevation) in order to acquire an understanding of how floral VOCs and other plant traits structure plant–pollinator interactions across the growing season. The meadow supports over 50 plant species and 75 bee species (Figure 1). The area utilized in this study covers ca. 20 ha.

2.2 | Quantifying floral volatiles

Methods used to capture and quantify floral VOCs from intact plants are detailed in Burkle and Runyon (2017). Throughout the growing season (late April-early August), we regularly visited (approximately weekly) the Mt. Ellis community and sampled VOCs from species that were in peak flower. Plants that seemed healthy (no signs of damage, herbivory or other stressors) were haphazardly selected and their flower(s) enclosed in 950 ml clear polyethylene cups with clear dome lids (Dart Container Corporation) and portable volatile collection systems (Volatile Assay Systems) were used to pull air out of the cups for 1 hr (0.5 L/min) through volatile traps containing 30 mg of the adsorbent HayeSep-Q (Restek). Floral VOCs were sampled on days of calm sunny weather during hours of peak pollinator activity (1,000–1,400). The number of flowers from which VOCs were sampled varied among forb species, but VOC emissions were standardized by the number of flowers in the cup. On each 1-hr sampling period, VOCs were collected from an empty cup near focal plants to quantify any ambient compounds in the air and were subtracted from corresponding chromatograms to remove background contaminants from each VOC profile. Floral VOCs were collected from three replicate individuals of each forb species, during peak bloom.

Volatile organic compounds were eluted from traps with 150 μl of dichloromethane, and 500 ng of *n*-nonyl-acetate was added as an internal standard. Samples were analysed using an Agilent 7890A gas chromatograph (GC) coupled with a 5975C mass spectrometer and separated on a HP-1ms 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 to 125°C, then 25°C/min to 250°C. Quantifications were made relative to the internal standard using ChemStation software (Agilent Technologies). Compounds were identified using NIST 08 Mass Spectral Search Program (National Institute of Standards and Technology) and confirmed by comparing mass spectra and retention times with commercial standards, when available. Volatile compounds were assigned to a group or class (e.g. benzenoid, monoterpenoid, etc.) based on their inferred biosynthetic origin following Knudsen, Eriksson, Gershenzon, and Ståhl (2006).

2.3 | Quantifying plant–pollinator interactions

On calm, sunny days, we quantified the identity and frequency of plant–pollinator interactions by walking a nonlinear transect through the meadow and capturing any insects observed visiting the reproductive parts of flowers between 0900 and 1600 hr. These floral visitors were 91% bees, and we restricted our analyses to this group. Observations were performed once or twice per week, weather permitting, over the growing season (late April-early

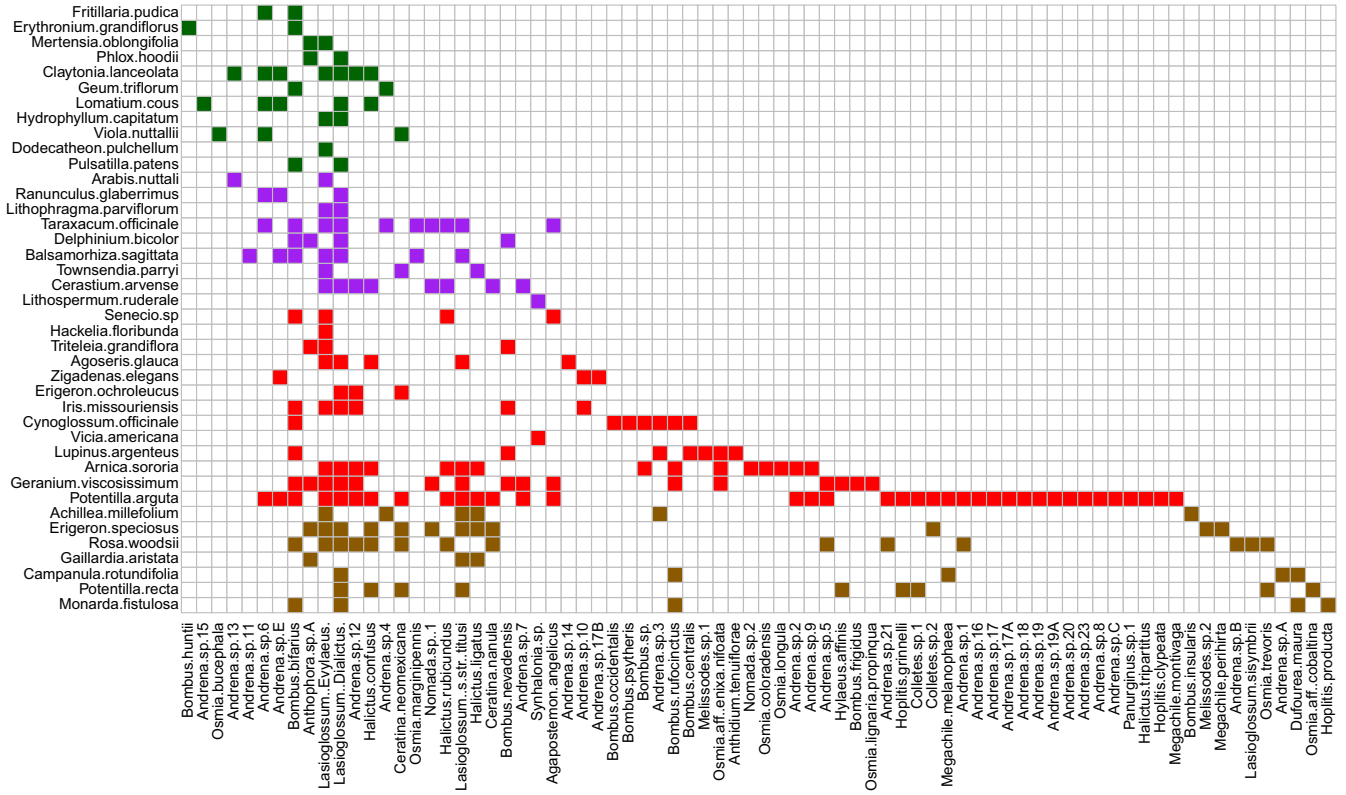

FIGURE 1 Matrix illustrating forb–bee interactions as filled boxes. Forbs are rows and ordered according to their peak flowering date, with early-blooming species (green) closer to the top and later-blooming species (brown) closer to the bottom. Bees are columns. Some bee species are active across the whole flowering season, visiting plants in each of the 4 seasonal periods (colours). Bee species richness increases over the growing season, peaking in mid to late summer (see also Figure 3)

August), and a total of 154 observation hours were completed for this study (see Figure S1 for sampling curve). When forb species were blooming but no pollinators were observed visiting their flowers, this was noted as well. Bees were frozen, pinned and identified to species or morphospecies (Figure 1) using the methods described in Reese, Burkle, Delphia, and Griswold (2018). Specimens were deposited in the Montana State University Pollinator Health Center Collection located in the Burkle Community Ecology Lab in Bozeman, MT.

2.4 | Quantifying floral phenologies and other plant traits

To estimate floral densities and forb species richness over the season, we counted the number of open flowers of each species in ten 2 × 2 m plots that spanned the meadow up to three times per week. We used mean values across plots for each species at peak bloom as their peak floral abundance. To estimate flower colour, which can be a cue of similar (Klahre et al., 2011) or greater (Hirota et al., 2012) importance to floral scent in some pollinator–flower pairings, we took digital photographs of flowers of each species. Because of the potential issues associated with measuring floral colour using spectrometers (Johnsen, 2016) and the benefits of using digital images (Garcia, Greentree, Shrestha, Dorin, & Dyer, 2014; Troscianko & Stevens, 2015), we used the latter approach, aiming to pair the images with processing to objectively measure reflectance and colour (e.g. Troscianko & Stevens, 2015). However, we were unable to complete the necessary processing, so converted colour to wavelength (nm) using academo.org/demos/wavelength-to-colour-relationship/, which does not incorporate UV or differences in how bees see colours relative to humans but does provide general information on variation in flower colour and serves as a proxy for some of the visual information received by bees.

2.5 | Analytical methods

2.5.1 | General seasonal patterns in forb and bee richness

Using floral density data, we tallied the richness of forb species blooming on each day in each plot, and using flower–bee interaction data, we tallied the richness of bee species captured on each observation day. We visually inspected seasonal patterns in mean forb and bee species richness over the growing season. We also tested the relationship between peak flowering date and links per species (i.e. richness of bees visiting a forb species; ln-transformed for normality) across forb species using linear regression.

2.5.2 | Controlling for potential phylogenetic signal

For each of our linear models (below), we first tested whether models incorporating phylogeny improved model fit. We used the angiosperm supertree of Zanne et al. (2014), trimmed to include a single tip for each of the 47 species sampled (Figure S2). We performed each model with and without Phylogenetic Generalized Least Squares (PGLS), which incorporates a variance–covariance error structure based on phylogenetic relationships, thereby taking non-independence among species into account (Symonds & Blomberg, 2014). In each case, the model without phylogeny was supported (Table S1), so we proceeded without PGLS. We used the pez, ape, picante, lmtest, Hmisc and phytools libraries in R.

2.5.3 | Total floral VOCs

For each forb species, we calculated the average per-flower total floral VOC emission rate across individuals as well as average per-flower emission rate of the major groups of floral VOCs defined by biosynthetic origin following Knudsen et al. (2006) (i.e. aliphatics, benzenoids and terpenoids; further subdivision of VOC groups restricted forb sample sizes which precluded analysis). We investigated whether there were patterns across species in total per-flower VOC emission rate and in each group of compounds (transformed for normality) over the growing season (i.e. peak flowering of each species) using separate linear regressions.

2.5.4 | Nestedness

We tested the degree to which (a) the interactions between forb and bee species and (b) the floral VOCs emitted by these same forb species were nested in structure based on within-season subnetworks (i.e. four 3-week periods) using oecosimu and nestedchecker with method quasiswap in the R package vegan 2.5-4. These within-season subnetworks represent four phenologically distinct periods of peak bloom in this system: (a) early spring (late April to mid-May; Julian days 114–134), (b) late spring (mid-May to early June; Julian days 135–155), (c) early summer (early June to late June; Julian days 156–176), and (d) mid-summer (late June to mid-July; Julian days 177–197), based on Ward's hierarchical clustering (Burkle & Alarcón, 2011). Typically, meadows dry in late July and finish flowering in early August. We calculated the nested rank of each forb species in each of these weighted seasonal networks using nestedrank and method NODF in the R package bipartite 2.11. We tested the degree to which the nested rank of forb species in interaction networks was explained by the nested rank of their floral VOCs using a multiple regression and included peak floral abundance (log-transformed), duration of flowering (square-root transformed), date of peak flower and flower colour as covariates because they can influence the position of a species in the nested network and contribute to overall network structure (e.g. Kaiser-Bunbury, Vázquez, Stang, & Ghazoul, 2014; Koski et al., 2015; Watts, Dormann, Martín González, & Ollerton, 2016). Across species, there were no significant correlations between peak flower, duration of flowering phenology, floral abundance, floral colour or the nested rank of floral volatiles ($-.19 < r < .22$, $N = 40$ to 47, $p > .17$; Table S2). See Table S3 for a nestedness analysis conducted at the level of the entire season.

2.5.5 | Modularity

To investigate the degree to which floral VOCs influenced forb–bee interaction network modularity, we first assigned forbs to modules using metaComputeModules in bipartite (Dormann, Fründ, Blüthgen, & Gruber, 2009) using the Beckett algorithm (Beckett, 2016) based on the entire-season forb–bee interaction network. We used the entire-season interaction network to calculate modularity because some plant species that do not overlap with each other in phenology might attract similar suites of pollinator species (i.e. some bee species are active over much of the flowering season; see Figure 1). We then calculated Bray–Curtis dissimilarity in floral VOCs for each pairwise forb–forb combination. We tested whether floral VOCs of forbs within modules were more similar (arcsine-transformed for normality) than VOCs of forbs in different modules using a *t* test across modules following Carstensen et al. (2016). We further investigated which, if any, modules showed evidence of being structured by floral VOCs by testing whether floral VOC similarity differed among modules (including similarity values of forb pairs that spanned different modules as a control group) using an ANOVA followed by Tukey HSD test. If certain modules are structured, at least in part, by floral VOCs, then we would expect the dissimilarity of floral VOCs of forb pairs within a module to be lower (i.e. more similar) than those spanning different modules. Given that there was no phylogenetic signal detected in floral VOC composition (see Results), we did not include phylogenetic control in this analysis.

2.5.6 | Variation in floral VOC composition across forb species

We tested the degree to which timing of peak bloom, flowering duration (square-root transformed), floral colour and peak floral abundance (log-transformed) explained the variation in floral VOC composition across species ($N = 47$) using PERMANOVA (adonis) on the Bray–Curtis dissimilarity matrix. We also investigated whether there was a phylogenetic signal in floral VOC composition among species ($N = 47$) by calculating pairwise phylogenetic distances among species and testing the correlation between this distance matrix and the Bray–Curtis dissimilarity matrix using a Mantel test.

2.5.7 | Uniqueness, originality, dispersion and richness of floral VOCs

We calculated the uniqueness, originality and dispersion of each forb species relative to the rest of the community co-flowering at that time (i.e. within-season subnetworks, weighted by mean floral abundance of each species) in order to consider relevant community context. Uniqueness was calculated as the nearest neighbour using nndist in spatstat based on forb species centroids from betadisper in vegan.

Originality was calculated as distances of forb species centroids from the overall community centroid. Dispersion of each forb species was calculated as the average distance of individuals from the forb species centroid. We investigated correlations among these metrics, and patterns in these metrics across the growing season using linear regression with day of peak bloom of each forb species as the independent variable.

To investigate whether species with the most original and unique (i.e. >75 percentile) floral VOCs systematically differed from unoriginal and non-unique species in the composition of their floral VOCs, we used PERMANOVAs (adonis) on the Bray–Curtis dissimilarity matrix. Additionally, to determine which, if any, volatile compounds were associated with originality and uniqueness of floral VOCs across forb species, we used similarity percentage analysis (simper). Based on these latter results, we targeted (*Z*)-3-hexenyl acetate (cube-root transformed for normality), (*E*)-beta-ocimene (log-transformed) and benzyl acetate (log-transformed) for investigation of seasonal patterns in their emissions across forb species using linear regressions, with day of peak bloom of each forb species as the independent variable and the mean emissions of each compound across individuals of each forb species as the dependent variable.

To better understand how sensitive these metrics were to community context and temporal scale (i.e. species values relative to co-flowering species only vs. relative to the entire community across the season), we calculated originality and uniqueness of floral volatiles for each species ($N = 47$) based on within-season subnetworks (as described above) and based on the entire network involving all species across the season. We used separate correlations to investigate the relationships between the two values for each metric across species. We did not do this for dispersion, which is independent of community context.

2.5.8 | Linking floral VOC metrics to pollinator visitation

To investigate links between forb floral VOC compound richness, uniqueness, originality and dispersion to pollinator visitation and plant–pollinator networks, we calculated the specialization of each forb species in within-season (i.e. four 3-week periods) plant–pollinator subnetworks. Specifically, we calculated (a) *degree* (i.e. bee visitor richness, or the number of links per forb species) and (b) *normalized degree* (i.e. links per forb species, standardized by subnetwork size—which varies strongly over the growing season, see Results; normalized degree ranges from 0 to 1). While both of these metrics are descriptors of species-level connectedness and typically correlate with other aspects of network topology, they provide complementary information on the absolute and relative levels of specialization. We tested the relationships between richness of compounds, uniqueness, originality and dispersion of floral VOCs (explanatory variables) with degree (log-transformed) and normalized degree (ln-transformed) (response variables) across forb species using multiple regression.

3 | RESULTS

3.1 | Overview

Of the 47 forb species sampled for floral volatiles, 40 forb species were visited by 76 species or morphospecies of bee pollinators, totalling 232 forb–bee species links. A total of 166 volatile compounds were detected across the 47 forb species, with an average of 51.2 compounds per species. The most abundant VOCs included terpenoids (72 compounds: 46 monoterpenoids, 23 sesquiterpenoids and 3 irregular terpenes), aliphatics (51 compounds), benzenoids (31 compounds), 3 nitrogen-containing compounds, 3 miscellaneous cyclic compounds, 2 C5-branched chain compounds, and 4 unknowns (Figure 2). Over the season, the richness of forb species blooming (Figure 3a) and the richness of active bee species (Figure 3b) increased, peaking in early July. Additionally, the number of links (i.e. interactions with bee species) per forb species increased over the season (Figure 3c; regression: $F_{1,38} = 4.71$, $r^2 = .26$, $p = .0005$).

FIGURE 2 Matrix illustrating presence of floral volatile organic compounds (VOCs) (columns) across forb species (rows). Forbs are ordered according to their peak flowering date with early-blooming species closer to the top, as in Figure 1. Floral VOCs are colour-coded by compound class: aliphatic (blue), benzenoid (green), C5 branched chain compounds (yellow), miscellaneous cyclic compounds (purple), nitrogen-containing compounds (pink) and terpenes (shades of tan). Irregular terpenes in light tan, monoterpenoids in medium tan and sesquiterpenoids in dark tan. Unknown compounds that could not be confidently assigned to a class are in grey

3.2 | Total floral VOC emissions

There was no relationship between total floral VOC emission rate (ng/hr flower^{-1}) and peak flowering of species over the growing season (r^2 = .035, $F_{1,45}$ = 1.64, p = .21). Emission rate of aliphatics (regression: r^2 = .12, $F_{1,45}$ = 6.30, p = .016; Figure S1) and benzenoids (regression: r^2 = .13, $F_{1,45}$ = 6.53, p = .014; Figure S1) declined with date of peak flowering of species, but there was no relationship between terpene emission rate and peak flowering (regression: r^2 = .0005, $F_{1,45}$ = 0.020, p = .89, Figure S3).

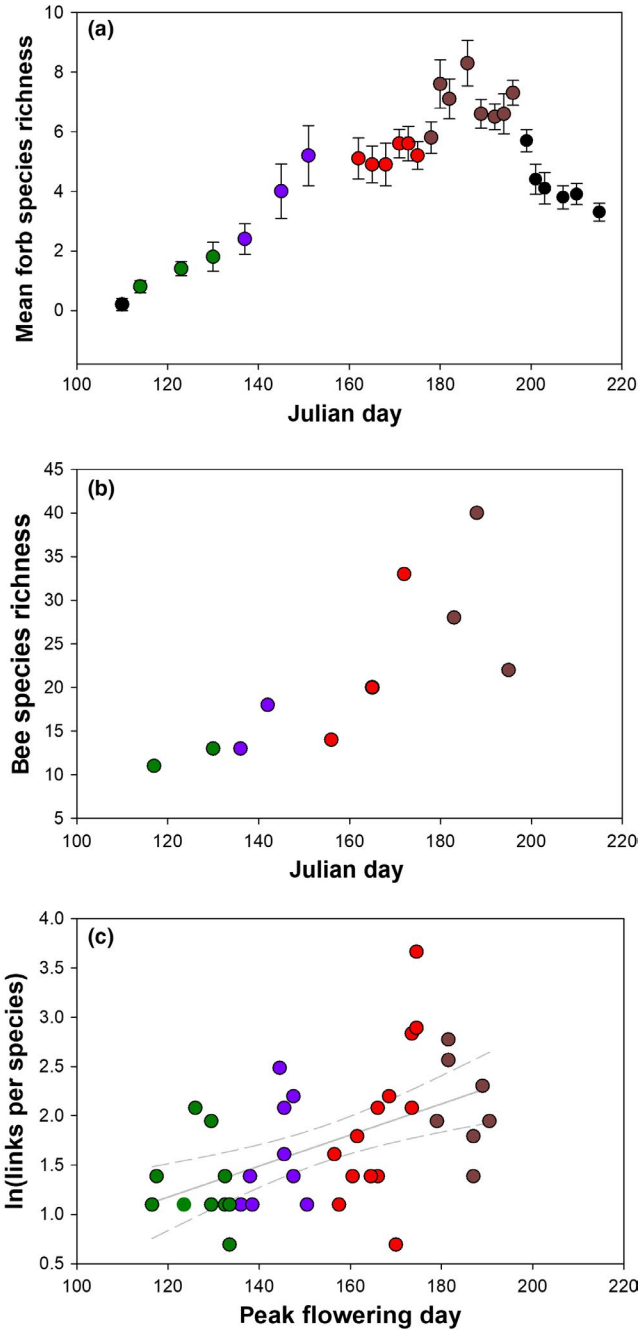

FIGURE 3 Forb (a) and bee species richness (b) increased over the growing season, peaking in early July. Dots reflect sampling days. (c) The richness of bee species visiting a forb species (i.e. links per species) increased with peak flowering date of the forb species (dots) over the season. Colours as in Figure 1; black points in (a) represent samples outside of peak sampling period when very few bees were present

3.3 | Nestedness

The forb–bee interaction networks and the forb-VOC emission networks from each within-season period were significantly nested (p < .05 in all cases), and the nested structures of the forb-VOC emission subnetworks contributed to the nested structures of the forb–bee interaction subnetworks. Specifically, the nested rank of forb species in terms of their VOCs was the strongest contributor to the nested rank of forb species in the forb–bee interaction subnetworks (Table 1; Figure S4). Forb species with low rank in the forb-VOC emissions subnetworks also had a low rank in the forb–bee interaction subnetworks, meaning that forb species emitting core compounds present in the bouquets of many other forb species were also core generalist players in the plant–pollinator subnetworks. Of similar importance to the nested rank of forb species in the interaction networks was floral density (Table 1; Figure S4)—florally dominant forb species had low ranks in the interaction subnetworks, as has been shown previously (i.e. core generalists) (reviewed in Vazquez, Bluthgen, et al., 2009). Flowering duration of forb species was weakly related to the nested rank of forb species in the interaction subnetwork (Table 1), with forb species with longer flowering phenophases tending to have lower ranks. Date of peak flower and floral colour were not significantly related to the nested rank of forb species in the interaction subnetwork (Table 1).

3.4 | Modularity

There was little evidence that floral VOCs contributed to the modular structure of forb–bee interactions. First, the degree of similarity of floral VOCs between forb species pairs was unrelated to whether that pair included forb species from within the same interaction network module or from different modules (t test: t = 0.32, df = 778, p = .75). Second, there was only one interaction network module (of 9) for which the floral VOCs of the forbs within that module were more similar to each other than the similarity between forb pairs from different modules (ANOVA: $F_{9,770}$ = 1.90, p = .049, Figure S5).

TABLE 1 Effects of nested rank of forb species in their floral volatile organic compounds (VOCs), floral density, flowering duration, date of peak flower and floral colour on the nested rank of forb species in within-season forb–bee interaction subnetworks

Source	*df*	*F*	*p*
Nested rank (VOCs)	1,34	4.35	**.045**
Floral density	1,34	4.15	**.049**
Flowering duration	1,34	2.80	.10
Peak flower	1,34	0.23	.63
Floral colour	1,34	0.16	.70

Note: p-values at α < 0.05 are bolded.

In this case, the mean dissimilarity of the floral VOCs in the module involving *Fritillaria pudica*, *Lomatium cous*, *Ranunculus glaberrimus* and *Viola nuttallii* was 37% lower compared to pairs spanning different modules (Tukey: $p = .047$).

3.5 | Variation in floral VOC composition across species

Although statistically significant or marginally significant, timing of peak bloom, flowering duration, floral colour and floral density each explained little of the variation in floral VOC composition across species (Table 2). Phylogenetic distance between forb species was not significantly correlated to their similarity in floral VOCs (Mantel: $r = .03$, $N = 47$, $p = .38$).

3.6 | Uniqueness, originality, dispersion and richness of floral VOCs

We found that forb species varied in their uniqueness, originality and dispersion of floral volatiles. Across all 47 forb species, originality and dispersion were positively correlated with one another ($r = .40$, $N = 47$, $p = .0056$), and originality and uniqueness were positively correlated ($r = .37$, $N = 47$, $p = .0094$), but uniqueness and dispersion were not correlated ($r = -.0061$, $N = 47$, $p = .97$). VOC richness was not correlated to any of these metrics ($-.19 < r < .15$, $N = 47$, $.20 < p < .42$).

Originality (regression: $r^2 = .36$, $N = 47$, $p < .0001$; Figure 4a) and, to a lesser degree, uniqueness (regression: $r^2 = .11$, $N = 47$, $p = .026$; Figure 4b) and dispersion (regression: $r^2 = .087$, $N = 47$, $p = .044$; Figure 4c) of forb species' floral VOCs increased across the growing season. There was no pattern in VOC richness of forb species across the season (regression: $r^2 = .009$, $N = 47$, $p = .52$).

Original species differed from unoriginal species in the composition of their floral VOCs (PERMANOVA: $F_{1,129} = 8.36$, $r^2 = .061$, $p = .001$). Interestingly, it was less the presence of certain compounds that contributed to originality but the *absence* of compounds. That is, across species, the most original species were lacking or had low levels of (*Z*)-3-hexenyl acetate, (*E*)-beta-ocimene and benzyl acetate, among others. Across forb species, emissions of (*Z*)-3-hexenyl acetate (regression: $F_{1,45} = 21.63$, $r^2 = .32$, $p < .0001$) and benzyl acetate (regression: $F_{1,45} = 52.92$, $r^2 = 0.54$, $p < .0001$) declined over the growing season (Figure S6). In fact, 21 of the 25 species that bloomed in the second half of the summer did not emit any benzyl acetate, while this was the case for only 1 of the 22 species that bloomed in the first half of the summer. There were no clear seasonal patterns in (*E*)-beta-ocimene across species (regression: $F_{1,45} = 0.35$, $r^2 = .008$, $p = .55$).

Additionally, each original species emitted a rare compound or suite of compounds that separated the species from the community mean. For example, phenylethyl alcohol and p-cymen-2-ol were relatively uncommon compounds more likely to be emitted by original species compared to unoriginal species. In fact, p-cymen-2-ol was only emitted by *M. fistulosa*, and in large amounts. There were no clear seasonal patterns in phenylethyl alcohol emissions across species; there was a weak tendency for species blooming later in the season to emit this compound (chi-squared test: $N = 47$, $\chi^2 = 2.54$, $p = .11$).

TABLE 2 Effects of date of peak bloom, flowering duration, floral colour and floral density on floral volatile organic compounds (VOCs) composition across species

Source	*df*	*F*	r^2	*p*
Peak flower	1,42	4.01	.083	**.001**
Flowering duration	1,42	1.48	.017	**.047**
Floral colour	1,42	1.47	.013	.061
Floral density	1,42	1.35	.017	.092

Note: *p*-values at $\alpha < 0.05$ are bolded.

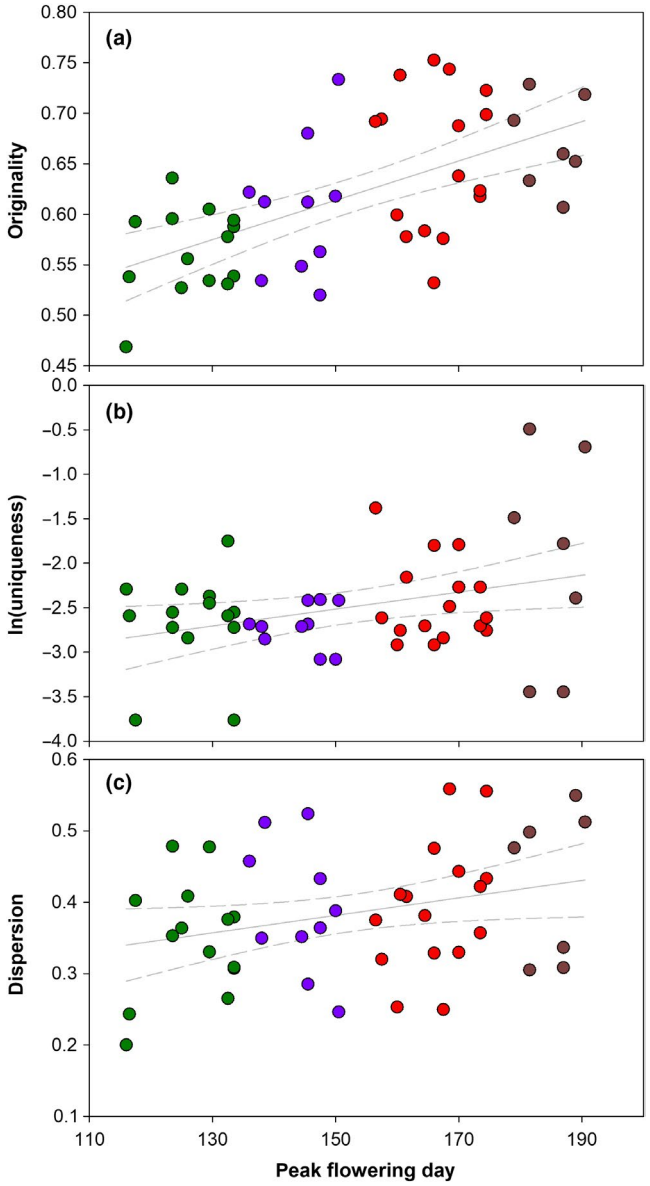

FIGURE 4 Patterns in the originality (a), uniqueness (b) and dispersion (c) of floral volatiles of forb species (dots) across the growing season. Colours as in Figure 1

Unique species differed from non-unique species in the composition of their floral VOCs (PERMANOVA: $F_{1,129} = 2.98$, $r^2 = .023$, $p = .001$). It was both the presence of some compounds and the absence of others that were associated with uniqueness. For example, (*Z*)-3-hexenyl acetate, (*E*)-beta-ocimene and benzyl acetate were higher in non-unique species than unique species, while phenylethyl alcohol and p-cymen-2-ol (see above) were much higher (by 400%–800%) in unique species.

Within-season and entire-season values of originality (correlation: $r = .91$, $N = 47$, $p < .0001$) were highly, positively correlated across forb species. By contrast, there was no relationship between within-season and entire-season values of uniqueness across forb species (correlation: $r = -.08$, $N = 47$, $p = .62$).

3.7 | Linking floral VOC metrics with pollinator visitation

Across forb species, normalized degree (i.e. bee visitor species richness, standardized by subnetwork size) increased with floral VOC compound richness (Table 3, Figure 5a) and declined with originality of floral VOCs (Table 3; Figure 5b). Degree (i.e. bee visitor species richness) increased with dispersion of floral VOCs (Table 3; Figure 5c).

TABLE 3 The influence of floral volatile organic compounds (VOCs) richness, originality, dispersion (i.e. intraspecific variation), and uniqueness on normalized degree and degree across forb species

		ln (normalized degree)		log (degree)	
Source	*df*	*F*	*p*	*F*	*p*
Volatile compound richness	1,35	4.74	**.036**	0.91	.35
Originality	1,35	4.99	**.032**	0.0001	.99
Dispersion	1,35	4.05	.052	5.60	**.023**
Uniqueness	1,35	0.69	.41	0.59	.45

Note: *p*-values at $\alpha < 0.05$ are bolded.

There were no relationships between normalized degree and dispersion or uniqueness across forb species (Table 1). Additionally, there were no relationships between bee visitor species richness and floral VOC compound richness, originality or uniqueness across forb species (Table 3).

4 | DISCUSSION

In this study, we investigated patterns in floral VOCs across the growing season in a species-rich community. We found that forb species varied in the originality, uniqueness and dispersion of their floral VOCs, and these metrics increased across the growing season. Forbs with more original floral VOCs were less connected, while forbs with higher dispersion of floral VOCs were more connected to pollinators. Overall, floral VOCs influenced forb interactions with pollinators, and the role of floral VOCs was evident in the nested structure, but not modular structure, at the community level. In fact, floral VOCs were equally important, or more important, than other factors (like floral abundance) known to contribute to the nestedness of plant–pollinator interactions. Phenological shifts in flowering time may alter floral VOC originality or dispersion with implications for interactions with pollinators, representing yet another indirect pathway by which climate change may influence pollination services, potentially in predictable ways. Indeed, given the potential for climate change to influence flowering phenology, understanding seasonal patterns in floral VOCs may be particularly important as shifts occur in the suites of co-flowering species.

4.1 | Total floral VOC emissions

Given that there was no pattern in the per-flower total floral volatiles emitted by species across the growing season, we did not observe early-blooming species investing more in floral scent when pollinator abundance is low, as was found by Filella et al. (2013) in a Mediterranean shrubland. This disparity may be due to the extreme seasonality in Mediterranean regions in which flowering is concentrated in early

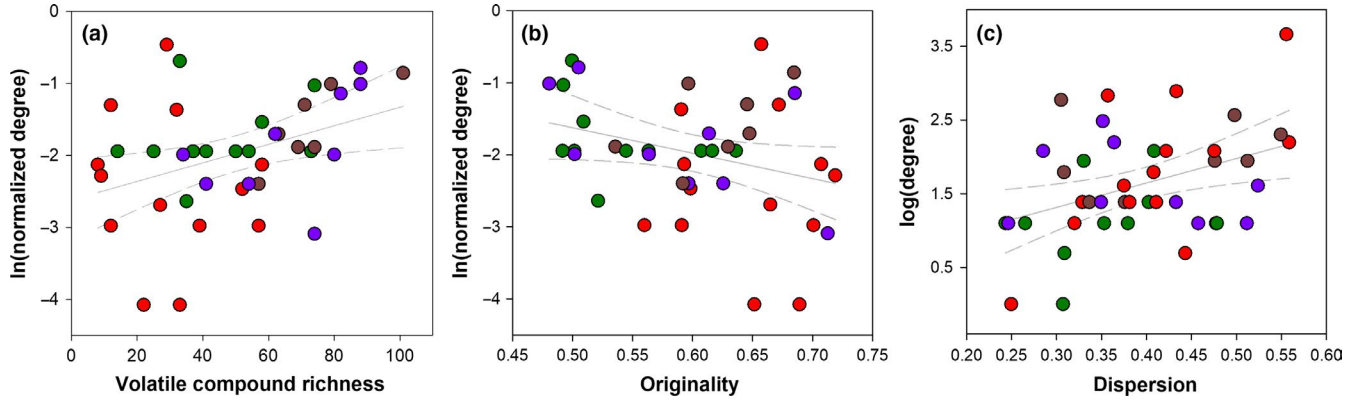

FIGURE 5 Across forb species (dots), normalized degree increased with volatile compound richness (a) and declined with increasing originality of floral volatile organic compounds (VOCs) (b). Degree (i.e. links per species, or bee species richness visiting a forb species) increased with intraspecific dispersion of floral VOCs (c). Colours as in Figure 1

spring, resulting in a narrow window of strong competition for limited pollinators (Filella et al., 2013; Petanidou, Kallimanis, Tzanopoulos, Sgardelis, & Pantis, 2008). In the Northern Rocky Mountains, where the present study was conducted, seasonality is not so extreme and flowering is spread out more evenly over 2–3 months. However, we did observe early-blooming forbs investing relatively more in common floral VOCs that are likely generalist attractants (e.g. some aliphatics and benzenoids), resulting in similar floral VOC blends, while later-blooming forbs emitted more complex (i.e. with more uncommon compounds) and variable VOC blends (Figure S7).

4.2 | Contribution of floral VOCs to the structure of forb–bee interaction networks

Previous studies have illustrated the importance of floral VOCs in community-level plant–pollinator interactions, mainly in Mediterranean systems with disparate groups of pollinator taxa (Kantsa et al., 2018; Kantsa et al., 2019). Here, in a mesic montane meadow, we show that floral volatiles contributed to the nested structure but not the modular structure of forb–bee interactions. While several factors have been shown to contribute to nestedness in plant–pollinator networks, including abundances and trait matching (e.g. Santamaria & Rodriguez-Girones, 2007; Stang et al., 2006; Stang, Klinkhamer, & van der Meijden, 2007; Vazquez, Chacoff, et al., 2009), this study is the first to demonstrate that floral VOCs also contribute to nested structure, with similar, if not greater, importance to that of floral abundance. These results indicate that forb species that serve generalist, core roles in pollination networks (i.e. those that are highly connected and visited by many bee species) also tended to emit common compounds like beta-myrcene, limonene, (*Z*)-3-hexenol and (*Z*)-3-hexenyl acetate. These 'generalist' floral compounds could function as signals that attract a broad suite of pollinators. The degree to which these patterns hold across divergent systems has yet to be tested.

It is interesting that—at the temporal scale of consideration (i.e. the entire season)—there was little evidence that floral VOCs contributed to modularity in this forb–bee network. That is, forb species with similar floral bouquets did not attract similar suites of bees to a strong enough degree to form distinct modules. For the one module that contained forb species with similar floral bouquets and that attracted similar suites of bees, these forbs were also all spring-blooming species with yellow flowers, so we cannot rule out the possibility that other traits and bee sensory biases were at play. However, at a broader spatial or temporal scale that would encompass several pollination syndromes and greater phylogenetic diversity, we might expect a stronger signal of floral VOCs to the modules that these broad taxonomic pairings could create. For example, although Kantsa et al. (2018) did not explicitly evaluate network-level metrics of plant–pollinator interaction structure (e.g. modularity or nestedness) with respect to floral VOCs, they found that one group of floral VOCs—sesquiterpenes—was related to the distribution of plant–pollinator interactions (i.e. links) for all pollinators as well as bees alone, suggesting that floral VOCs may influence the modularity of flower–bee interactions in other systems.

4.3 | Originality, uniqueness and dispersion of floral VOCs across the growing season

Originality, uniqueness and dispersion of floral volatiles increased across the growing season. In this system, we generally observe more species diversity of both forbs and bees as the season progresses, indicating that perhaps floral volatiles become relatively more important in mediating forb competition for pollinators later in the season. If so, this increase in competition did not result in greater investment in total per-flower emissions of floral VOCs, but rather in selection for species to emit more distinct floral VOC bouquets, given intraspecific variation in (reviewed in Delle-Vedove, Schatz, & Dufay, 2017) and heritability of (Cai, Zu, & Schiestl, 2016; Zu, Blanckenhorn, & Schiestl, 2016) floral VOCs. Alternatively, environmental conditions in this system change over the growing season—from cool and moist to hot and dry—which could influence plant physiology and biochemical pathways across species. For example, dry conditions have been shown to increase the intraspecific variation (i.e. dispersion) in floral VOCs in some species (Burkle & Runyon, 2016). If plant competition for pollinators is indeed a driving factor of these seasonal patterns in floral VOCs in other systems, then we would expect originality and uniqueness to generally follow system-specific phenologies, increasing during the peak flowering period and when competition for pollinators is greatest.

Across forb species in our community, the originality and dispersion of floral VOCs were positively correlated. Thus, species with highly original floral VOCs also tended to have high intraspecific variation in floral VOCs (high dispersion), whereas species whose floral VOCs were close to the community mean (low originality) were more consistent among individuals (low dispersion). The pressure to emit a consistent floral bouquet might be relaxed in species with highly original VOCs because they already stand out in the community (i.e. high 'apparency', sensu Feeny, 1976), and increased intraspecific variation in scent advertisement may not significantly affect pollinator attraction. Alternatively, species with highly original VOCs might have stronger selection for increased intraspecific variation in floral scent to 'hedge their bets' and attract a broader suite of pollinators. A similar strategy has been suggested for some specialized plant species which vary the timing of nectar production of flowers within an individual to attract generalist pollinators and improve the likelihood of pollination (Willmer, 2011). We note that these observed patterns in intraspecific variation in floral VOCs are based on few individuals ($N = 3$ for each species) and therefore will require bolstered replication to confirm their ecological significance. It is interesting that this relationship between intraspecific variation and originality—and subsequent consequences for pollinator visitation—does not appear to have been explored for visual floral traits of flowering plant species within communities. Given the importance of morphological trait matching for plant reproductive success and for pollinator acquisition of nectar and pollen, we might expect some aspects of flower size to exhibit less intraspecific variation than floral VOCs, though their relative variation as well as the spatial scales at which visual versus chemical floral traits are important cues for

pollinator attraction or signal 'originality' is poorly understood. More examination is needed to determine the ecological and physiological mechanisms driving these community-wide patterns in scent production.

Originality was mainly defined by the absence of certain compounds, including (*Z*)-3-hexenyl acetate, (*E*)-beta-ocimene and benzyl acetate. For (*Z*)-3-hexenyl acetate and benzyl acetate, forb species blooming towards the end of the flowering season were less likely to produce these compounds and were less likely to be visited by many of the pollinators available at that time (i.e. originality appears to discourage pollinators—see below).

We found that, across species, originality was consistent regardless of community context (i.e. whether considering within-season subnetworks or the entire-season network) because the community mean floral bouquet was not variable across the season. Nevertheless, minor changes in the VOC blends (e.g. ratios of compounds) of individuals and species that may result from environmental changes and influence pollinator visitation (Burkle & Runyon, 2016; Glenny, Runyon, & Burkle, 2018). By contrast, the degree of uniqueness of the floral scent of a species (i.e. 'nearest neighbour') was much more dependent on the identity of co-flowering species. Thus, if these patterns are consistent across systems—and will require additional in-depth sampling to determine whether this is true—uniqueness of floral scent will be particularly sensitive to phenological shifts due to climate change. However, of the three metrics that we calculated to try to capture the potential functional roles of floral volatiles of forb species, uniqueness was the one for which we found no relationship with pollinator visitation (i.e. normalized degree or bee visitor richness). Thus, the implications, if any, of shifts in uniqueness due to climate change for pollinator visitation are not straightforward, given our results.

4.4 | Linking floral voc metrics with pollinator visitation

Species-level metrics describing aspects of the functional roles of floral VOCs were related to patterns of pollinator visitation, thereby joining other floral traits whose originality or intraspecific variation is important for plant–pollinator interactions (e.g. Coux et al., 2016; Elle & Carney, 2003; Galen & Kevan, 1980; Vieira, Cianciaruso, & Almeida-Neto, 2013). Across forb species, normalized degree (i.e. visiting bee species richness, relative to the species richness present at that time) increased with floral VOC richness and declined with originality of floral volatiles. Together, these results suggest that forb species that emitted fewer and more original floral volatiles were less connected to and had fewer interactions with pollinators, after accounting for differences in available pollinator diversity over the growing season. By contrast, Coux et al. (2016) found that plants with original traits (e.g. plant type, flowers per inflorescence, flower symmetry) were not visited by a narrowed suite of interaction partners. This discrepancy between studies may be due to differences among traits in the taxonomic level at which variation is housed, that is, among individuals, species, families, etc.

Bee visitor species richness (i.e. forb degree) increased with dispersion of floral volatiles, indicating that forb species with more variable floral volatiles were more connected to and had more interactions with pollinators. Given that this relationship may reflect seasonal patterns in bee diversity *and* intraspecific variation in floral VOCs, both of which increase over the summer, we further explored their joint influence on bee visitor richness to forb species. Bee visitor species richness still increased with dispersion across forb species ($F_{1,39}$ = 7.70, p = .044) even after accounting for these seasonal patterns (i.e. including date of peak flower, $F_{1,39}$ = 4.33, p = .0084), indicating that the intraspecific variation in floral VOCs seems to result in increased diversity of bee visitors, and forb species that bloom towards the end of the season might be especially prone to such effects. The consequences of potential shifts in floral VOC dispersion—due, for example, to changes in environmental conditions (e.g. Burkle & Runyon, 2016)—on bee visitor richness and plant reproductive success warrant further investigation.

5 | CONCLUSIONS

We have shown that floral VOCs mediate seasonal patterns in forb–bee interactions in a diverse community, influencing the breadth of bee visitors to individual forbs and the overall nested structure. Floral VOCs join other plant traits important for understanding how complex networks of interactions build over the growing season, though the relevance of floral VOCs at other temporal or spatial scales has yet to be tested. These findings also have implications for plant–pollinator interactions as floral VOCs (e.g. Fuentes, Chamecki, Roulston, Chen, & Pratt, 2016; Glenny et al., 2018) and phenologies (Cleland, Chuine, Menzel, Mooney, & Schwartz, 2007), and thus co-occurring species, shift due to climate change. Given that the influence of floral scents on pollinator attraction can range from the individual-level (e.g. Byers, Bradshaw, & Riffell, 2014) to the community-level and beyond (e.g. Junker et al., 2010), future work may consider further exploring the situations in which community context strongly (or weakly) impacts pollinator attraction. For instance, we might expect the community context of floral VOCs to be more important and to more strongly influence fitness outcomes in generalized plant–pollinator interactions, relative to specialized interactions, where floral scents may be more likely to act individually (e.g. via 'private channels', Chen et al., 2009), independent of community context.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

L.A.B. and J.B.R. designed the study and collected the data. L.A.B. analysed data and wrote the first draft. Both authors contributed critically to drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data are available in the Dryad Digital Respository: https://doi.org/10.5061/dryad.1m3tj32 (Burkle & Runyon 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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