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RESEARCH ARTICLE

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Deconstruction of a plant-arthropod community reveals influential plant traits with nonlinear effects on arthropod assemblages

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Abstract

1. Studies of herbivores and secondary consumer communities rarely incorporate a comprehensive characterization of primary producer trait variation, thus limiting our understanding of how plants mediate community assembly of consumers.
2. We took advantage of recent technological developments for efficient generation of phytochemical, microbial and genomic data to characterize individual alfalfa plants (*Medicago sativa*; Fabaceae) growing in an old-field, semi-naturalized state for 770 traits (including 753 chemical features). Using random forest modelling, we investigated the effect of variation in these traits on arthropod and fungal assemblages while accounting for plant genetic structure.
3. We found that traits indicative of plant vigour, including size, percentage of flowering stems and leaf area, were positively associated with arthropod richness and abundance. Most phytochemicals were, by comparison, poor predictors, although phytochemical diversity and several individual phenolic compounds were important. Plants with a higher proportion of flowering stems were hotspots of interotrophic interactions with higher species richness of secondary consumers. The effects of many traits on plant-associated assemblages were best modelled as nonlinear functions, often incorporating threshold effects. Foliar fungal richness was not well predicted by our models, suggesting we have much to learn regarding the role of plant traits on phyllosphere fungi at small spatial scales.
4. Our results support the need for characterization of multiple axes of plant phenotypes in studies of plant-arthropod-microbe communities and demonstrate the value of modern analytical techniques for understanding the nonlinear ways in which plant traits mediate the structure of associated biotic communities.

KEYWORDS

arthropod community ecology, intraspecific variation, nonlinear effects, plant-vigour hypothesis, random forest, threshold effects

1 | INTRODUCTION

In the last half century, the ecological consequences of interindividual variation in both producers and consumers have become more widely appreciated (Bolnick et al., 2003; Roughgarden, 1972; Van Valen, 1965; Violle et al., 2012). For example the rise of the community genetics literature has amply demonstrated the importance of intraspecific genetic variation for ecological interactions, such as those between plants and their associated biota (Bernhardsson et al., 2013; Busby et al., 2015; Robinson, Ingvarsson, Jansson, & Albrectsen, 2012; Whitham et al., 2003). However, in many cases the phenotypic variation that mediates interactions among taxa is poorly understood. For instance a substantial number of plant traits can affect arthropod herbivores, both directly through survival, reproduction or other aspects of performance (Denno & Mcclure, 2012; Strong, Lawton, & Southwood, 1984) or indirectly through mediation of predation or parasitism rates (Bukovinszky, van Veen, Jongema, & Dicke, 2008; Smilanich, Dyer, Chambers, & Bowers, 2009), but understanding the relative influence of these plant traits on arthropod community assembly remains a challenge. For logistical reasons, most studies linking plant traits to the richness or abundance of primary and secondary consumers focus on a subset of plant trait variation, such as plant architecture or the concentrations of a particular class of secondary metabolites. Because many plant traits covary and likely interact with one another to influence primary and secondary consumers (Agrawal, 2011; Johnson, Agrawal, Maron, & Salminen, 2009), long-standing hypotheses in the community ecology of plant–insect interactions will be most successfully tested by studies that take a comprehensive approach to measuring plant traits.

The plant vigour hypothesis, for example suggests that large, vigorous plants host richer and more abundant herbivorous arthropod assemblages (Carmona, Lajeunesse, & Johnson, 2011; Cornelissen, Wilson Fernandes, & Vasconcellos-Neto, 2008; Price, 1991). However, many traits covary with plant vigour, which necessitates a multitrait approach to uncover the underlying traits that most affect consumers. More generally, we still have much to learn about the relative importance of plant traits that potentially influence consumer assembly. For instance Barbour et al. (2015) linked variation in 40 traits of *Salix* clones to herbivorous arthropod assemblages. The authors found a significant marginal effect of genotype, despite the large number of traits surveyed, which points to the importance of unmeasured, genetically controlled plant traits and highlights the complexity of the task facing researchers attempting to dissect plant-arthropod communities. This task becomes even more complex when applied to microbial consumers, as very little is known regarding the effect of plant traits on these organisms (e.g. Kembel & Mueller, 2014; Kembel et al., 2014), and few studies simultaneously address the effect of plant traits on both microbes and arthropods (Friesen et al., 2011; Stout, Thaler, & Thomma, 2006; Tack, Gripenberg, & Roslin, 2012).

Alfalfa (*Medicago sativa)* has a number of features that make it a useful plant with which to investigate plant traits and consumer assemblages. Alfalfa is cultivated throughout Western North America and has a diverse suite of associated organisms—often more arthropod species are associated with alfalfa than nearby native plants (Forister, 2009; Pimentel & Wheeler, 1973). Alfalfa is a rich resource for arthropods in part because it associates with rhizosphere bacteria, which fix nitrogen that is subsequently incorporated into plant tissues. However, alfalfa is phytochemically diverse and well-defended by a variety of triterpene saponins, phenolics, flavanoids and other compounds that can affect insect herbivores (Dyer, Richards, Short, & Dodson, 2013; Harrison, Gompert et al., 2016; Oleszek, 1996; Sen, Makkar, & Becker, 1998). Alfalfa is also more genetically diverse than most crops as it is an obligate outcrosser and cultivars are multiparental in origin (Julier, Huyghe, & Ecalle, 2000), which results in more phenotypic variation within alfalfa fields than is typical for monocultures.

We deconstructed the plant-arthropod-microbe community of a fallow alfalfa field in Northern Nevada by thoroughly characterizing consumer assemblages and variation in 770 plant traits, including 285 mass spectrometry features from saponin compounds, 265 features from phenolic compounds, 203 features from unidentified metabolites, drought stress and additional morphological traits, while controlling for plant genotypic variation (Table S1). Using these data, we asked: which plant traits have the greatest influence on the richness and abundance of arthropod herbivores and the richness and diversity of foliar fungi. Previous studies linking herbivore richness and abundance to alfalfa traits report a negative effect of defensive traits (i.e. saponin concentration; Agrell, Oleszek, Stochmal, Olsen, & Anderson, 2003) and a positive effect of traits indicative of plant vigour (Dyer & Stireman, 2003; Pearson, Massad, & Dyer, 2008). It is less clear how drought stress may affect the associated arthropod community. Previous work has shown complex indirect effects of drought stress on arthropod interactions and taxon-specific population growth rates (Barton & Ives, 2014). However, we expect a generally negative response of consumers to plant stress (Huberty & Denno, 2004).

2 | MATERIALS AND METHODS

2.1 | Study location and sampling strategy

Fifty alfalfa plants were selected randomly within a 100 m diameter circle in a fallow alfalfa field in Fallon, NV (39°30'17"N 118°55'06"W). This site is located in the Great Basin Desert—an area characterized by cold winters and hot, dry summers. The field had not been irrigated since 2010 (5 years pre-sampling), and no longer resembled a cultivated field: surviving alfalfa plants were heterogeneously distributed, and both native and exotic plants had invaded the open spaces. Arthropods were sampled from all fifty focal plants on July 10, 20 and August 3, 2015. For the first two sampling events, we used a backpack style vacuum (*c*. 1 min per plant), and for the third sampling event (August 3) we used sweep netting (four sweeps per plant). Sweep netting was not used during earlier sampling to avoid damaging plants but was used for the final sampling event to

dislodge arthropods that were resistant to capture. Arthropods from each plant were pooled across sampling events, sorted to morphospecies and identified to the lowest possible taxon (at least to family) and assigned to an ecological guild. Evenness of the community was represented as Pielou's evenness, which was calculated as Shannon's diversity index divided by the natural logarithm of the estimated number of taxa in a sample as output by the function `specaccum` in `vegan` (Oksanen, Kindt, Legendre, O'Hara, & Stevens, 2016). We did not perform analyses with arthropod diversity equivalents as a response variable, preferring to examine the underlying components of diversity.

To account for spatial autocorrelation, we calculated Moran's eigenvector maps (MEMs) using the `dbmem` function of the `adespatial` package v0.0–7 (Dray et al., 2016). The first MEM was extracted and retained in all analyses (see Supplemental Methods for details).

2.2 | Structural and phenological traits

At the conclusion of arthropod sampling, plant volume was measured as the product of maximum height and width, and width perpendicular to the widest portion of the plant. The number of flowering, fruiting and vegetative stems was counted during the second sampling event. We counted the number of inflorescences and infructescences and the number of peduncles for three haphazardly selected stems per plant. Peduncle counts were averaged across stems for a plant to give an index of its floral output. Area (cm^2) of three leaflets from each stem (nine leaflets) was measured. Leaflets were weighed and specific leaf area (density) was calculated as leaf area divided by dry weight. Leaf toughness was determined for five haphazardly chosen leaflets from each plant in the field using a penetrometer (the youngest and oldest leaves were avoided). Seed viability was determined through a tetrazoliumchloride assay (Porter, Durrell, & Romm, 1947).

2.3 | Plant performance measurement

Plant drought stress was measured for three stems per plant during each sampling event, between 11 a.m. and 3.30 p.m., with a pressure chamber (Scholander, Hammel, Hemmingsen, & Bradstreet, 1964). Measurements were averaged within plants to estimate short-term drought stress. Long-term drought stress was measured separately using the $\delta^{13}C$ isotopic signature in 30 mg of leaf tissue (including leaflets from three stems) (Farquhar, Ehleringer, & Hubick, 1989). Foliar protein content in *c*. 30 mg dry tissue was assayed using the Bicinchoninic acid assay (Pierce Biotechnology, Waltham, MA). We used the percent nitrogen in alfalfa foliar tissue derived from fixation alone (NDFA) as a proxy for the amount of symbiotic dinitrogen fixation (Högberg, 1997). We were unable to obtain $^{13}C/^{12}C$ ratios for two focal plants, and nitrogen fixation activity for an individual plant. We used the `rfimpute` function in the `randomForest` package in R to impute values for these two missing data points to avoid omitting these plants from downstream analyses.

2.4 | Characterization of phytochemistry via LC-MS

Phytochemistry was assayed using an LC-MS approach (see Supporting Information Methods). Briefly, dried foliar tissue (*c*. 100 mg) was extracted in 70% aqueous ethanol and extracts were injected onto an Agilent 1,200 analytical high performance liquid chromatography instrument, coupled to an Agilent 6,230 Time-of-Flight mass spectrometer via an electrospray ionization source. Spectra were processed using `runLC` in `metaMS` v1.6.0 (Wehrens, Weingart, & Mattivi, 2014). Putative phenolics (200–400 ppm) and saponins (400–650 ppm) were identified using the relative mass defect characteristic of each phytochemical family (Ekanayaka, Celiz, & Jones, 2015). Intensities were summed after normalization for both phenolics, and saponins, to estimate the relative concentration of either class in a focal plant.

Phytochemicals can interact additively or non-additively to influence plant-associated biota (Richards et al., 2016). Representing phytochemical variation as diversity allows for an exploration of the possible influence of chemical interactions on biotic communities (Marion, Fordyce, & Fitzpatrick, 2015). Accordingly, for each sample, we calculated the numbers equivalent of Shannon's diversity index individually for saponins, phenolics and unidentified compounds.

2.5 | Genotyping of focal plants

A restriction endonuclease digestion approach for reduced representation library generation was used to characterize plant genetic variation (also known as genotyping by sequencing, or GBS; Gompert et al., 2012; Parchman et al., 2012). Sequencing was performed on a HiSeq 2500 (one lane; 1 × 100 bp) by the Genome Sequencing and Analysis Facility (GSAF) at the University of Texas. Sequences were aligned (231,973,765 reads) to a previously generated draft genome of *M. sativa* (Harrison, Gompert et al. 2016) using BWA (Li & Durbin, 2009). Variable positions within aligned contigs and genotype likelihoods at those positions were determined using the UNIFIED GENOTYPER in `GATK` (DePristo et al., 2011). This process generated a total of 43,920 single nucleotide variants. The resulting genetic covariance matrix was decomposed into two principal components, which, respectively, explained 21% and 5% of variation in the data (meeting expectations for data from a single population).

2.6 | Description of phyllosphere fungi

Fungi occurring on three haphazardly chosen leaflets per plant were described using a culture-independent approach (see Supporting Information Methods for details). Leaflets were removed from pressed specimens that were collected during late July before the final arthropod sampling event and stored at room temperature. Sequencing of the ITS1 locus was performed on the Illumina MiSeq (2 × 250 bp) platform by GSAF. Sequences were processed using USEARCH v8.1.1831 (Edgar, 2010; Edgar & Flyvbjerg, 2015). Reads were clustered into operational taxonomic units (OTUs) using a 97% similarity threshold. OTUs were assigned a taxonomic status using the `UTAX` software

and the Warcup training set (Deshpande et al., 2016). The numbers equivalent of Simpson's diversity was calculated using read counts for each OTU that were normalized using the TMM method of the `edgeR` package (Robinson, McCarthy, & Smyth, 2010; Robinson & Oshlack, 2010). Fungal richness was obtained by rarifying reads from each plant to 100 reads using the function `rrarefy` in `vegan`. This very stringent rarefaction was necessitated by the recovery of few fungal reads from some samples. Fungal evenness was represented using the Pielou index. OTUs were assigned a putative trophic status, whether pathotrophic, symbiotrophic or saprotrophic, using the FUNGuild database (accessed March 2017; Nguyen et al., 2016).

2.7 | Analysis of associations between plant traits and biota

We used the random forest algorithm (Breiman, 2001) as implemented in the `randomforest` R package v4.6–12 (Liaw & Wiener, 2002) to predict variation in arthropod and fungal assemblages among plants and identify traits that influenced plant-associated biota (full details in Supporting Information Methods). This algorithm can capture nonlinear relationships among predictor variables, and implicitly accounts for interactions (Wright, Ziegler, & König, 2016). The algorithm also allows for visualizations that facilitate biological insight, unlike some other machine learning techniques used for function approximation (e.g. neural nets). Briefly, the algorithm works by first growing a regression tree using a subset of the data, while also considering only a subset of the predictor variables. The tree is grown by recursively splitting the data into groups based on similarity of the response variable. The possible ways to split the data are the values of the predictor variables (for instance different levels for a categorical predictor, or greater or less than a certain value for a continuous predictor). Choice of splitting variable is robust to multicollinearity because each variable is considered independently. Splitting continues until some predetermined limit, for instance there are fewer than the desired number of observations in the terminal node. Many such regression trees are grown and combined into a predictive ensemble (the forest). The performance of each tree is its predictive ability when using data withheld during tree growth, which is called "out of bag" data (OOB). The performance of the ensemble is the average predictive ability of all trees. Variable importance is determined by calculating the average increased prediction error to OOB when permuting only the variable of interest and reanalysing. This method facilitates accurate ranking of covarying predictors but may possibly downweight the influence of covarying predictors compared to other variables. This is because if a variable is permuted and the model rerun, a covarying predictor that was not permuted would explain some of the variance in the ensemble that was previously explained by the permuted variable. However, the method is robust to this issue because many trees in the ensemble will likely only have one of a cadre of highly correlated predictors (see Supplemental Methods), thus allowing for accurate ranking of the relative influence of correlated predictor variables. The most correlated variables in our dataset include arthropod richness and abundance, plant size, the percentage of flowering stems and phytochemical diversity. In many cases, these variables were still ranked as some of the most influential predictors, consequently we suggest that the conservative nature of the variable ranking algorithm we used has not unduly influenced our inferences. Moreover, to determine if a variable was influential beyond null expectations, we generated null predictor variables by permuting actual predictor variables using the `Boruta` package v5.2.0 (Kursa & Rudnicki, 2010) and compared the performance of these null variables to actual predictors after accounting for multiple comparisons.

We built random forest models to predict richness and abundance of arthropod functional groups and fungal richness and diversity using all aforementioned z-standardized predictor variables. Variables that were influential beyond null expectations as determined through `Boruta` simulations were used to construct a final model for each response variable (see Supporting Information Methods). The strength and directionality of association between the response and a particular predictor variable was investigated using partial dependence plots output by the `plotmo` package, v 3.3.2 (Milborrow, 2016) and feature contribution plots output by the `forestFloor` package, v 1.11.1 (Welling, Refsgaard, Brockhoff, & Clemmensen, 2016).

3 | RESULTS

3.1 | Plant-associated biota

We collected 18,306 arthropods from 157 morphospecies across the three collection events (Figure 1). Of these, 42 morphotaxa were primary consumers (herbivores) and 91 were secondary consumers (predators and parasitoids); we were unable to assign a trophic status to the remaining morphospecies because of insufficient natural history information. Secondary consumer richness was dominated by hymenopterans (31 taxa) and spiders (Araneae, 31 taxa), whereas Hemiptera dominated herbivore richness. The most abundant arthropods were aphids (*Aphis* spp.), thrips (Thysanoptera) and other sucking herbivores.

Sequencing of phyllosphere fungi generated 14,457 fungal reads and 78 OTUs. Comparison of taxa to the FUNGuild database suggested that assemblages were split between pathotrophs and saprotrophs (Figure 1c). We observed a significant pairwise correlation between fungal richness and plant genetic variation, and a positive association between fungal and arthropod richness (Figure 2). Fungal richness was also generally greater on larger plants with larger leaves.

3.2 | Medicago sativa phenotypic and genotypic variation

Variation was observed among focal plants for all traits considered. We did not observe spatial autocorrelation for any focal trait (no significant correlation between traits and MEM; see "Spatial autocorrelation" in Figure 2). Several traits were associated with our metrics of genetic structure, including nitrogen fixation rate

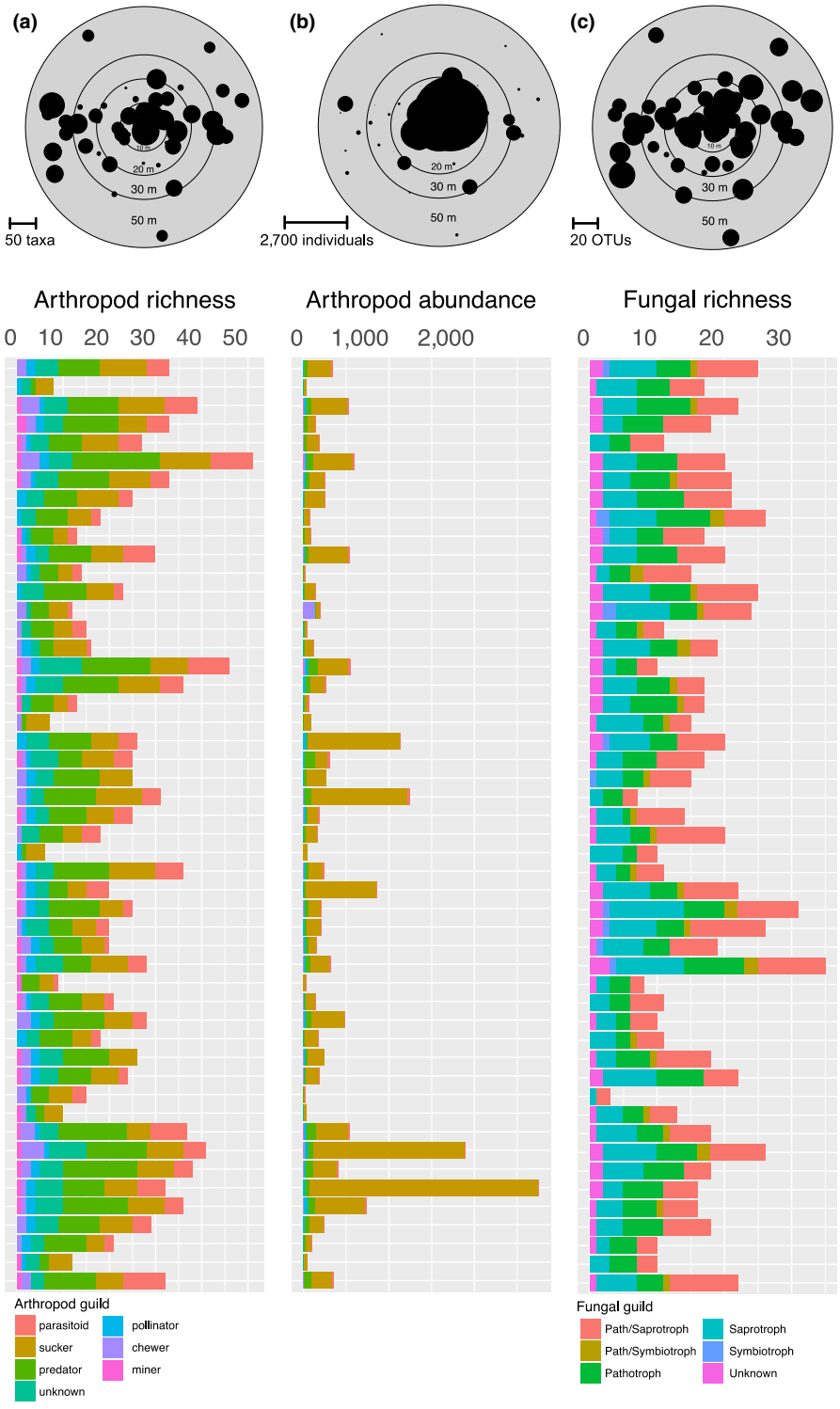

FIGURE 1 Location of focal plants and the abundance, richness and functional composition of biotic assemblages on each plant. Points in bullseye plots are scaled proportionally to magnitude of richness/abundance. Colour-coded bar plots denote proportion of total biota comprised of members of a particular guild. (a) arthropod richness; (b) arthropod abundance; (c) fungal richness (rarified)

(Spearman's rank correlation with PC1; $\rho = 0.34$, $p = .02$), leaf toughness (PC1; $\rho = 0.31$, $p = .03$) and short-term drought stress (PC2; $\rho = 0.29$, $p = .04$). Short-term drought stress was negatively correlated with plant size, leaf density, percentage flowering stems and floral density (Figure 2), and positively correlated with leaf area. More vigorous, less stressed plants had higher concentrations of phenolic and saponin compounds and elevated phytochemical diversity (Figure 2).

3.3 | Results from random forest analysis

The random forest model of secondary consumer richness explained 57.6% of the variation in out of bag validation data (OOB; 95% confidence intervals of this and the following estimates are omitted because of high precision), whereas our model of secondary consumer abundance explained 47.2% of OOB (Figure 3). Herbivore richness and abundance were more challenging to predict; the best model of

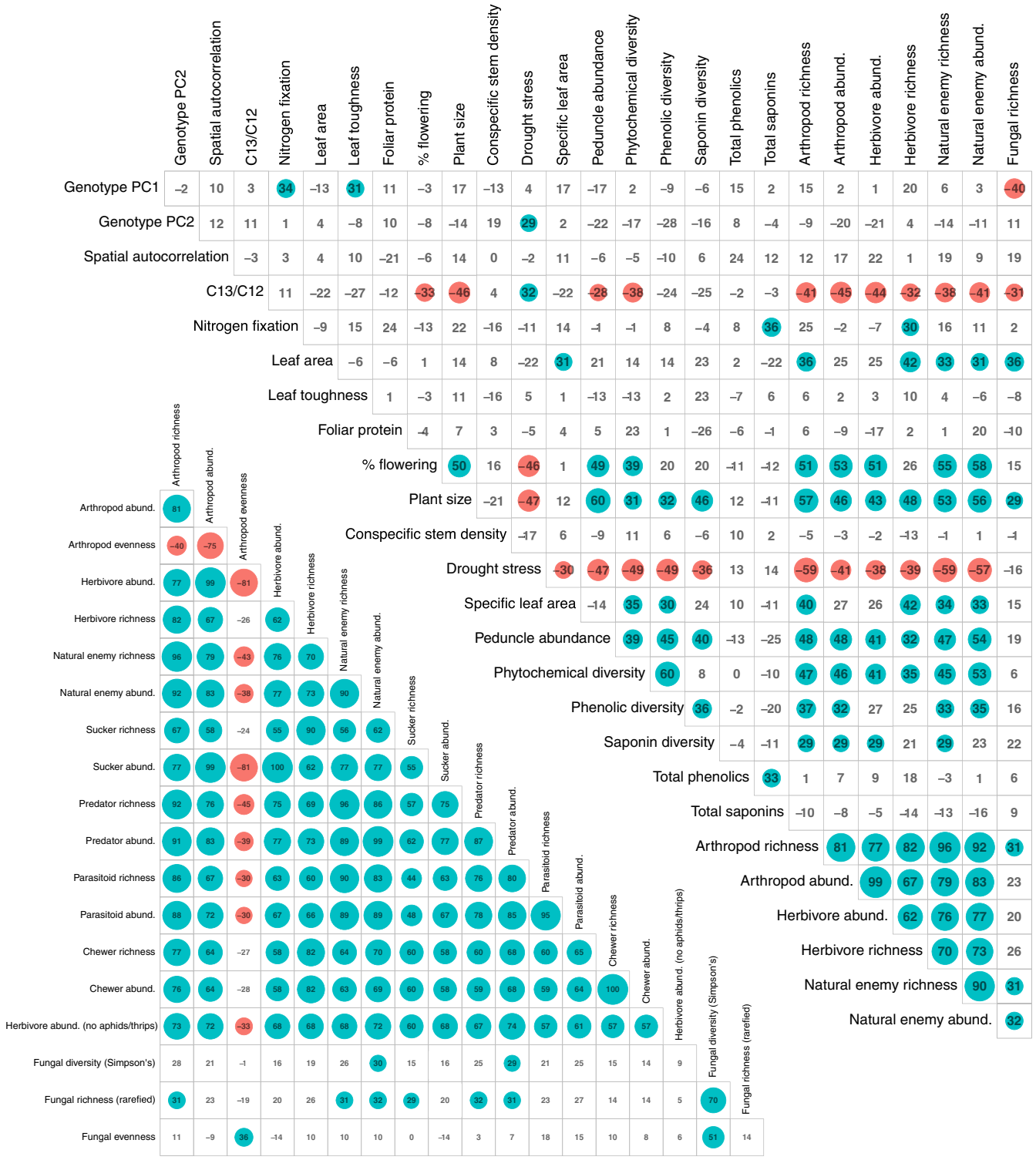

FIGURE 2 Correlation matrices of plant traits and plant-associated biota (upper right), and among biotic guilds (lower left). Integers in each cell are Spearman's rank correlation coefficients multiplied by 100 for visualization. Significant negative correlations are shaded red and positive correlations are blue. Unsupported correlations are not shaded. Genotype PC1 and PC2 refer to components output from a principal component analysis of genotype estimates at 43,016 SNVs. Diversity of phytochemistry, including saponins and phenolics, is represented as the numbers equivalent for Shannon's diversity. Phytochemical diversity refers to diversity of unidentified compounds only. See main text for details regarding other traits

richness only explained 18.3% of OOB, and we were unable to generate a supported model of abundance while including the two most abundant herbivorous taxa: aphids and thrips. When excluding these taxa, we were able to explain 9.7% of OOB data. Predicting fungal community variation was similarly challenging, and we were not able to generate a supported model of either richness, or diversity (Figure S10).

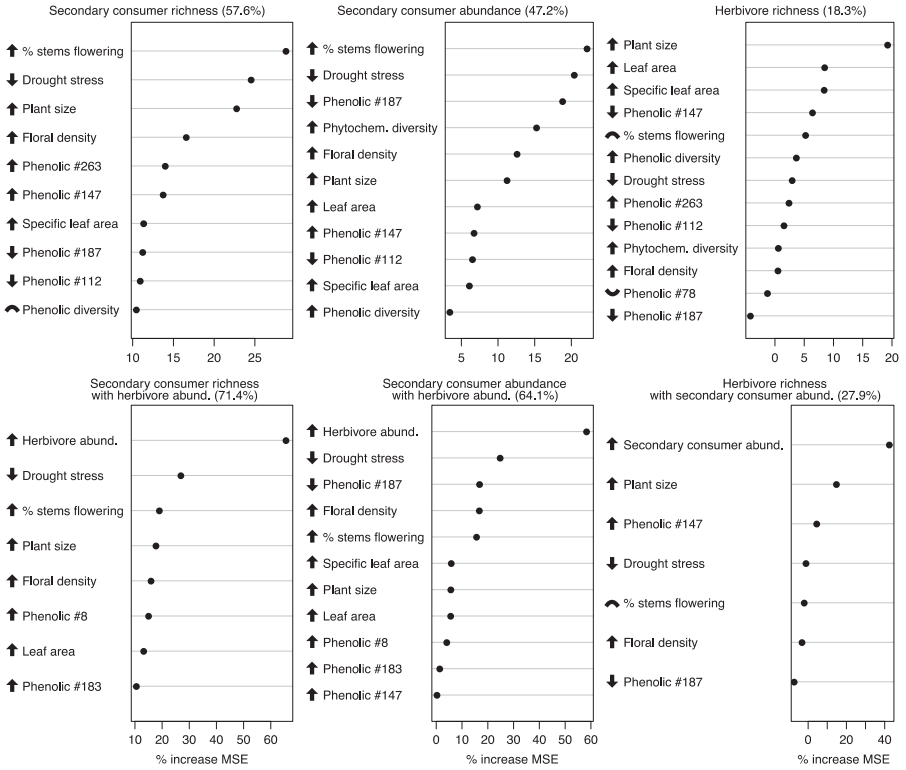

FIGURE 3 Variable importance plots from random forest analysis of plant traits on secondary consumer and herbivore richness and abundance (top row). The bottom row depicts results obtained when including biotic interactions into the model (herbivore abundance in models of natural enemies; secondary consumer abundance in models of herbivore richness). Variables are listed in descending order of importance. Percentages shown for each model are the proportion of variation explained in "out of bag" data and is a metric of model performance (see main text for details). The *x*-axis of each plot describes the decrease in model performance when omitting a particular variable (increase in mean squared error, MSE); larger values denote more influential variables. Arrows, or curved arcs, denote direction of the relationship between the predictor and response variables with arcs denoting a hump-shaped effect. Models of herbivore abundance were unsupported and are not shown

Neither were we able to successfully model the proportion of viable seeds as a function of arthropod communities and other plant traits.

Many of the same plant traits influenced the richness and abundance of both secondary consumers and herbivores, but the relative influence of these traits shifted depending on the group of organisms considered. For instance drought stress and the number of flowering stems were more strongly associated with secondary consumer richness and abundance than they were with herbivore richness (Figure 3). While some phenolic compounds, and phenolic diversity, were important predictors in our analyses, putative defensive traits were typically less influential than structural and phenological traits. Indeed, when all LC-MS features were removed and models rerun, performance as measured by explained variance in OOB data declined by <10% for all models (and in most cases the decrease was <5%). For those phenolic compounds that were influential, the directionality of the effect varied with some compounds negatively associated with arthropod richness or abundance and others positively associated.

When including either abundance, or richness (not shown) of an adjacent trophic level in models, variation explained typically increased by *c*. 10–15% (Figure 3). Moreover, for all models, the adjacent trophic level was selected as the most influential variable. For instance herbivore abundance was the most influential variable in our model of secondary consumer richness, and secondary consumer abundance was the most influential variable in the model of herbivore richness.

The feature contribution (partial dependence) plots output by random forest analyses show the effect of a predictor on the response across values of the predictor (Figures S1–S9). This visualization technique revealed that the effects of many predictors were modelled as nonlinear, including sharp thresholds demarcating variation in the effect of the predictor over its range (Figure 4). This was particularly notable for the influence of short-term drought stress on secondary consumer richness and abundance (Figures 4, S1–S2), which were both greater on plants with higher water potential. For instance our model estimated that enemy abundance increased by approximately 20–30 individuals, and 3–4 taxa on less stressed plants (Figure 4).

3.4 | Guild-specific results

Model performance was high for predator abundance (46.5% OOB) and richness (52.4% OOB), and parasite abundance (25.9%) and richness (41.4%) (Figure S10). A richer and more abundant assemblage of predators was observed on larger plants with more flowering stems. Drought stress was a more influential predictor variable in models of parasite assemblages than those of predator assemblages. The only herbivore guild for which we had sufficient data to construct a model of richness was suckers. Sucker assemblages were richest on plants with denser leaves that were larger and had higher phytochemical diversity (Figure S10). Drought stress was not significantly associated with fungal richness, but arthropod and fungal richness were associated (Figure 2). Guild-specific models of fungal richness (e.g. saprotrophs) were unsupported.

4 | DISCUSSION

We report that much of the variation in plant-associated biotic assemblages, particularly of secondary consumers, could be explained

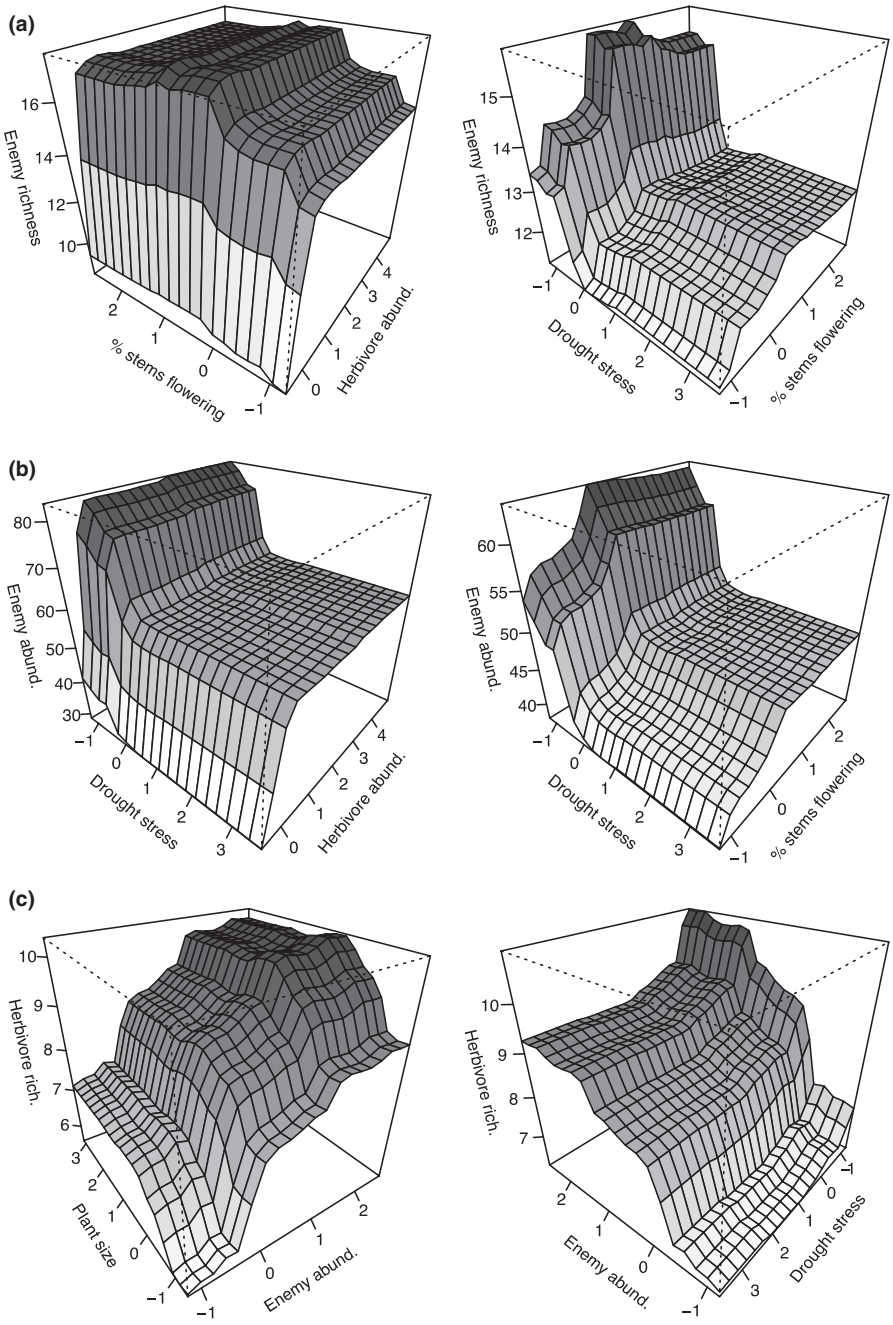

FIGURE 4 Selected interactions between predictor variables that influenced secondary consumer (abbreviated as enemy) richness (a) and abundance (b) and herbivore richness (c) as determined from a random forest analysis of variable influence. The response variable is not z-standardized to aid interpretation, but the predictor variables are standardized

by models incorporating nonlinear effects of plant trait variation and either prey availability (for secondary consumers) or predator abundance (for herbivores; Figure 3). Most notably, the influence of drought on the richness and abundance of secondary consumers was modelled as a threshold effect, which suggests that an ecologically relevant tipping-point exists between stressed and unstressed plants. We also uncovered nonlinear effects of herbivore abundance on enemy richness and abundance, and, conversely, of enemy abundance on herbivore richness and abundance (Figures 4 and S1–S4). Nonlinear effects of many additional plant traits were also observed—for instance in the effect of certain phenolics, or in plant size (Figures S1–S9). These results suggest that nonlinear relationships between plant traits and species richness and abundance at multiple trophic levels may be a widespread, but understudied, aspect of community assembly.

The most influential plant traits that we observed were indicative of plant condition, structure and phenology: the percentage of stems that were flowering, floral density, drought stress, leaf area and density and plant size (Figure 3). Although several phenolic features were important determinants of arthropod richness and abundance, the majority of LC-MS features used to characterize phytochemical variation were not influential predictor variables. These results are in accordance with a meta-analysis by (Carmona et al., 2011) which suggests that herbivore communities respond most strongly to life-history traits of their host plants, such as size and phenology, as opposed to, for example defensive traits.

We report that secondary consumer assemblages in particular were influenced by plant phenology. These assemblages were dominated by predatory hemipterans, spiders and hymenoptera, which were likely parasitic. Root (1973) suggested that parasitoids can increase in abundance when floral nectar is available as a resource—a hypothesis that has since received support from studies in a number of systems (Wäckers, 2004). Another possibility is that phytochemical changes characteristic of flowering plants attracted enemies. For instance plant volatile profiles are known to shift over ontogeny (Barton & Boege, 2017), and floral volatiles have been shown to attract some parasitoids and predators (Price et al., 1980; Shahjahan, 1974; Vinson, 1976). Our chemical analyses were based on LC-MS and therefore were not suited to describing volatile organic compound variation among plants. It is also possible that many of the spiders and other predators we collected prefer to hunt on flowering plants because of the availability of floral visitors as possible prey (Nelson, Pratt, Cheseto, Torto, & Jackson, 2012). More generally, the effect of plant traits on secondary consumer foraging behaviour could explain the stronger predictive relationship between plant traits and the richness and abundance of secondary consumers compared to herbivores (Figures 2, 3 and S10). Regardless of underlying mechanisms, our results suggest that when variation in phenology exists within an alfalfa population, the most vigorously flowering plants are hotspots of intertrophic interactions. Maintaining flowering plants in alfalfa fields could thus facilitate the attraction of a diverse predator and parasitoid assemblage desired for successful integrated pest management (Gurr, Wratten, Landis, & You, 2017; Landis, Wratten, & Gurr, 2000).

Putatively defensive traits were relatively poor predictors of variation in arthropod richness and abundance, with the exception of several individual phenolic features, phenolic diversity and phytochemical diversity, the latter of which was generally positively related to arthropod richness (Figure 3). Richards et al. (2015) report a similar positive influence of phytochemical diversity on arthropod richness in a study of tropical *Piper* plants, which was apparently due to specialization of arthropods on *Piper* taxa with different suites of phytochemicals. Our results suggest that phytochemical diversity may facilitate arthropod richness at even smaller scales, namely within an individual plant. Indeed, from the vantage point of an arthropod, a single plant is a mosaic of habitat differing in suitability. Phytochemistry can vary within individual alfalfa plants (Agrell et al., 2003), and we hypothesize that such interindividual heterogeneity is a possible driver of the phytochemical diversity we observed because we pooled leaves from several different stems for our LC-MS-based analyses. If phytochemical diversity does indeed reflect within-plant variation, then this should cause an increase in the niche space associated with an individual plant, thus facilitating richness of associated arthropods. Alternatively, perhaps plants with higher phytochemical diversity were simply more vigorous and, consequently, a better resource for arthropods despite the high phytochemical diversity (Figure 2). In contrast to the effect of phytochemical diversity, neither summed concentrations of saponins, nor phenolics were influential predictors in any analysis. However, individual features from phenolic compounds were both negatively, and positively associated with arthropod richness and abundance (Figure 3), which suggests that detailed analytical chemistry that facilitates parsing of compounds within a class is required to accurately determine the effects of secondary metabolites on arthropod assemblages (Poelman, Dam, Loon, Vet, & Dicke, 2009).

Even in very thorough studies, a large portion of the variation in herbivore community structure often remains unexplained by plant trait and genetic variation (Barbour et al., 2015; Whitfeld et al., 2012). Similarly, our model of herbivore richness only explained 18.7% of the variation in herbivore richness, whereas our model of herbivore abundance was unsupported. When secondary consumer abundance was included as a predictor variable in our model of herbivore richness, model performance increased by approximately 10% (Figures 3 and S10), which suggests an importance of top down pressures in our system (Vidal & Murphy, 2018). However, the addition of secondary consumer abundance to our model of herbivore abundance did not lead to a supported model (Figure S10). Given this poor performance, and despite the large number of traits we measured, we hypothesize that neutral forces, such as ecological drift or stochasticity in host plant colonization, may determine much of the variation in herbivore abundance among plants at small spatial scales (Barber & Marquis, 2011).

We were not able to link variation in plant traits or arthropod assemblages to variation in fungal richness or diversity using the random forest algorithm (Figure S10), which suggests we have much to learn regarding how plant-associated microbial communities assemble (Andrews & Harris, 2000; Harrison, Forister, Parchman, & Koch, 2016). It is possible that the fungal community was partly homogenized during air drying and storage, thus leading to the poor performance of our models. However, we did observe a significant positive pairwise correlation between fungal richness and the richness and abundance of arthropods, particularly secondary consumers and sucking herbivores (Figure 2). It remains unclear if this correlation is because of direct interactions between fungi and arthropods (e.g. insects as vectors; Malloch & Blackwell, 1992) or is due to indirect interactions with the plant (e.g. influence of either insects, fungi, or both, on the plant immune response; Pieterse & Dicke, 2007). These possibilities will remain as hypotheses to be tested with further investigations into fungal-arthropod interactions.

5 | CONCLUSIONS

Our results confirm the value of combining a comprehensive characterization of plant traits with machine learning techniques to shed light on classic ecological questions. This approach let us observe the complex, nonlinear ways in which plant traits influence consumer assemblages. We found that traits indicative of plant vigour were better predictors of consumer richness and abundance compared to plant defensive traits. Despite decades of interest, there is still much to learn regarding the assembly of organisms into plant-associated communities, particularly for microbes. Our results suggest that a possible way forward is an expansion of focus from characterizing

how a particular plant phenotypic axis (e.g. defence, vigour) affects community structure to an examination of the consequences of interactions between organisms and multiple axes of the plant phenotype.

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AUTHOR'S CONTRIBUTIONS

J.H. and M.F. conceived the experiment. J.H., Z.G., B.S., C.P. conducted analyses. All authors were involved in data collection and manuscript preparation.

DATA ACCESSIBILITY

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.vg089 (Harrison et al. 2018).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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