Trophic phylogenetics: evolutionary influences on body size, feeding, and species associations in grassland arthropods

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Abstract. Contemporary animal–plant interactions such as herbivory are widely understood to be shaped by evolutionary history. Yet questions remain about the role of plant phylogenetic diversity in generating and maintaining herbivore diversity, and whether evolutionary relatedness of producers might predict the composition of consumer communities. We tested for evidence of evolutionary associations among arthropods and the plants on which they were found, using phylogenetic analysis of naturally occurring arthropod assemblages sampled from a plant-diversity manipulation experiment. Considering phylogenetic relationships among more than 900 arthropod consumer taxa and 29 plant species in the experiment, we addressed several interrelated questions. First, our results support the hypothesis that arthropod functional traits such as body size and trophic role are phylogenetically conserved in community ecological samples. Second, herbivores tended to co-occur with closer phylogenetic relatives than would be expected at random, whereas predators and parasitoids did not show phylogenetic association patterns. Consumer specialization, as measured by association through time with monocultures of particular host plant species, showed significant phylogenetic signal, although the strength of this association varied among plant species. Polycultures of phylogenetically dissimilar plant species supported more phylogenetically dissimilar consumer communities than did phylogenetically similar poly-cultures. Finally, we separated the effects of plant species richness and relatedness in predicting the phylogenetic distribution of the arthropod assemblages in this experiment. The phylogenetic diversity of plant communities predicted the phylogenetic diversity of herbivore communities even after accounting for plant species richness. The phylogenetic diversity of secondary consumers differed by guild, with predator phylogenetic diversity responding to herbivore relatedness, while parasitoid phylogenetic diversity was driven by plant relatedness. Evolutionary associations between plants and their consumers are apparent in plots only meters apart in a single field, indicating a strong role for host-plant phylogenetic diversity in sustaining landscape consumer biodiversity.

Key words: arthropod phylogeny; Cedar Creek LTER, Minnesota, USA; community phylogenetics; diversity; grassland; herbivores; parasitoids; predators.

Introduction

Communities of primary producers have a fundamental influence on the structure and function of trophic webs. In terrestrial ecosystems, the richness of plant species serves as a reasonable first-order predictor of herbivore richness and perhaps other trophic groups as well (Basset et al. 2012). Patterns of host specialization in herbivores (Weiblen et al. 2006) and their parasitoids (Hrcek et al. 2011) raise the possibility that associations of consumer species, beginning with herbivores but including higher trophic levels, are generally explained by plant evolutionary relatedness. Consumer communities include many different trophic roles and lineages, sometimes varying depending on ecological context.

Here, we define primary consumers (referred to hereafter as herbivores) as those known or thought to consume mostly plant tissue, and secondary consumers as inclusive of predators (which consume animal tissue as adults) and parasitoids (which utilize living animal tissue for development of their offspring). The explanatory power of evolutionary relatedness in predicting associations among consumers and producers, and across consumer trophic levels, is largely unknown.

Previous experimental work has demonstrated the importance of plant species richness in determining the abundance, richness, and trophic structure of consumer communities (Siemann et al. 1998, Haddad et al. 2009, Borer et al. 2012, Dinnage et al. 2012, Rzanny and Voigt 2012). For instance, a long-term biodiversity experiment showed that increasing grassland plant species richness supports a predictable increase in herbivore richness (Siemann et al. 1998), with weaker effects on predatory arthropod richness but a strong increase in the

abundance of secondary consumers (Haddad et al. 2009). An analysis of consumer communities in a similar plant diversity experiment found increased diversity of trophic interactions among consumer functional groups (Rzanny and Voigt 2012), indicating not just effects on consumer species diversity, but also that the intensity of food-web relationships changes with plant diversity. Finally, structural equation modeling of whole communities of plants and consumers suggests producer biomass may be equally or even more important than plant diversity in promoting consumer diversity (Borer et al. 2012). Although these studies have documented the overall influence of primary producer diversity on consumers at the ecosystem level, mechanistic explanations of consumer–host species relationships, as mediated by trait interactions and evolutionary history, are also needed (Rafferty and Ives 2013).

Speciation and ecological specialization have long been hypothesized to explain the diversity of plant–insect associations, because colonization of new host plants by herbivores may involve adaptation to overcome particular plant defenses as well as the evolution of reproductive isolation (Ehrlich and Raven 1964, Farrell 1998, Tilmon 2008). Considering that many herbivores feed on a limited set of closely related plants, the phylogenetic diversity of a plant community should predict the diversity of the herbivore assemblage (Mitter et al. 1991, Novotny et al. 2006), sometimes called the herbivore niche hypothesis. The analogous hypothesis for higher-order consumers, such as predators and parasitoids, is that herbivore phylogenetic and trait diversity should predict "enemy" diversity (Bailey et al. 2009). Importantly, the strength of this prediction should be lesser for predators that have transient interactions with herbivores as a meal for adults, versus parasitoids whose offspring will be endophagous to an herbivore and thus more likely to experience selection for specialization against herbivore defenses. In any case, whether higher-order consumers of either guild show significant phylogenetic structure with respect to either primary producers or primary consumers, remains an open question.

Community phylogenetic tools have enabled ecologists to detect the influence of evolutionary history on contemporary ecological patterns and interactions (Webb et al. 2002, Cavender-Bares et al. 2009). The emerging literature on community phylogenetics has focused largely on primary producers (e.g., Cavender-Bares et al. 2004, Strauss et al. 2006) or individual monophyletic functional consumer groups (e.g., Helmus et al. 2010, Pellissier et al. 2013). Examinations of trophic interactions in phylogenetic context mainly have focused on the primary producer community rather than the evolutionary relationships of the consumers (e.g., Fine et al. 2006, Weiblen et al. 2006, Dinnage et al. 2012, Whitfeld et al. 2012b; but see Pellissier et al. 2013). An analysis of the ecological importance of phylogenetic relatedness in consumer communities, particularly one spanning multiple trophic levels and deeper branches in the animal tree of life, has yet to be attempted.

Assembling current phylogenetic knowledge into hypotheses of relatedness for community samples is a major challenge for ecologists (Beaulieu et al. 2012). Here, we present a phylogeny estimate derived from an intensively sampled grassland arthropod community including >900 taxa, the largest of its kind to date. We use this community phylogeny to examine the influence of evolutionary relatedness on arthropod traits, feeding associations, and co-occurrences. We collected these arthropods within a plant biodiversity manipulation experiment, thus allowing us to examine the phylogenetic distribution of the arthropod community responses to plant species richness and plant phylogenetic relatedness. Specifically, we set out to answer the following questions: (1) Is there phylogenetic signal in two ecologically important arthropod traits, body size and trophic role, in a multitrophic grassland arthropod consumer community? (2) Is there phylogenetic structure in the co-occurrences of arthropod taxa at scales relevant to ecological interactions (e.g., sampled plots)? (3) How do plant species identity, richness, and phylogenetic diversity influence the phylogenetic diversity of the consumer community? Do the relationships between consumers and plants differ by trophic role? (4) Do secondary consumer communities differ by mode of attack (predator or parasitoid)? Are these higher trophic levels more influenced by the phylogenetic relatedness of the herbivore community, or the plant community? (5) Does increasing evolutionary distance among plant assemblages (phylogenetic beta diversity) drive increasing evolutionary distance among consumer assemblages?

METHODS

Arthropod sampling, identification, and traits

The arthropods from this study were collected within a plant diversity experiment at the Cedar Creek LTER (Minnesota, USA; 45.401° N , 93.201° W), established by plowing and disking a former agricultural field in 1993, then seeding with prairie plants in 1994. Each of the 168 experimental plots was 13 × 13 m, and was seeded with 1, 2, 4, 8, or 16 locally occurring plant species drawn randomly from a pool of 36 species (a total of 29 unique plant species were present in the plots analyzed here). Plots were annually weeded to retain the assigned plant species composition treatment. Plants were chosen to represent five functional groups (C_3 and C_4 grasses, forbs, legumes, and woody species). Plant species abundances were measured annually in these plots, as percent cover (1996–2000). Further experimental details are provided in Tilman (1996).

Arthropods were collected annually in late summer (August) in the plant diversity plots from 1996 to 2006, and additional collections were made in June from 1997 to 2002. Arthropod sampling was performed using 25 net sweeps per plot; all individuals were examined,

identified to species or morphospecies within a known genus or, in some cases, family, and counted. The combined data set included 905 taxa from 15 orders, represented by 65 534 individuals. Each taxon was assigned to a trophic role (herbivore, detritivore, parasitoid, or predator) following Siemann et al. (1997, 1998). Body sizes, estimated as a volume for individual taxa as length × width × depth (mm³), were assigned for 91% of the individuals, following Siemann et al. (1998) and Borer et al. (2012).

Community phylogeny estimation

Due to a lack of available genetic information and other challenges (detailed in Appendix) we followed a grafting approach (Beaulieu et al. 2012) to assemble a phylogenetic hypothesis for the 905 arthropod taxa from Cedar Creek. Initially, taxa named in the Tree of Life web project were assumed to be monophyletic at each rank in the Linnean hierarchy (e.g., order, family, subfamily, genus) unless contradicted by recent evidence from the systematics literature; in this case, an unresolved polytomy was retained at the rank immediately above. The backbone topology of relationships among major clades and orders followed Regier et al. (2010) for arthropods and Trautwein et al. (2012) for the class Insecta. Relationships within orders were based on recently published molecular phylogenetic hypotheses (see Appendix for references). Particular taxa not sampled in the recent literature were placed in the tree as polytomies of higher taxa on the assumption of monophyly of families, subfamilies, and genera, etc. Incompletely identified taxa (e.g., "geometrid larva") were also assigned as polytomies of the nearest identifiable clade (e.g., Geometridae). Polytomies were retained in all analyses. Example source tables and R code used to create the phylogeny are available in a Supplement.

We estimated relative divergence times among community members by assigning minimum ages in millions of years ago (Ma) to 120 of 392 (31%) of ancestral nodes based on fossil evidence as summarized in Grimaldi and Engel (2006). We then used the bladj algorithm in the program phylocom (Webb et al. 2008) to obtain ages for all nodes by distributing the ages of remaining nodes evenly between dated nodes and tips. Although the bladj algorithm makes the unrealistic assumption of constant evolutionary rates among lineages, it seems to perform as well as more sophisticated molecular dating techniques (Whitfeld et al. 2012a).

Analysis

Trait conservatism in community phylogeny.—We tested for evidence of phylogenetic influence in the distribution of two key traits, body size and trophic role, using the geiger package (Harmon et al. 2008) in R (R Development Core Team 2011). For both traits, we estimated Pagel's λ (Pagel 1999), which varies from 0 (trait random with respect to phylogeny) to 1 (trait

evolved according to Brownian motion on the phylogeny). We additionally calculated Blomberg's K (Blomberg et al. 2003) for body size (K is not meaningful for categorical states like trophic role).

Calculating phylogenetic structure of co-occurrence.— We estimated the phylogenetic structure of species occurrences in a given sample using the D statistic introduced by Fritz and Purvis (2010). Originally, D was developed to analyze phylogenetic structure in extinction risk, which, like occurrence of a consumer in a given plant community, is not an evolved trait per se, but is likely to be highly correlated with evolved species traits. We calculated D for each observed sample of arthropods using 1000 replicate simulations in the phylo.D function of the caper package (Orme et al. 2012) in R. We first calculated D for the arthropod tree as a whole, and second for each of the three most abundant trophic groups, herbivores, predators, and parasitoids, on phylogenetic trees that had been pruned to match these groups. We hypothesized that herbivores would be more likely to be phylogenetically structured than the higher-order consumers, due to their stronger evolutionary associations with the manipulated host-plant diversity. We further hypothesized that parasitoids (in lineages Hymenoptera and Diptera) would be more phylogenetically structured than predators (including members of Araneae, Heteroptera, Coleoptera, etc.) due to the close association of parasitoids with their hosts.

Calculating arthropod consumer and plant community phylogenetic diversity.—We calculated phylogenetic diversity of arthropods sampled in a given plot using two measures. One was Faith's PD, the summed distance from each observed taxon to the root of the tree (Faith 1992). Here, we take advantage of the fact that PD increases monotonically with species richness, as it represents a composite phylogenetic diversity response variable. We also calculated the mean phylogenetic distance (MPD) among taxa in a sample, weighted by the abundance of taxa in a plot in a given year (Webb et al. 2002). We separately calculated plot-level PD and MPD within each sampling year for herbivores, predators, and parasitoids. To relate the phylogenetic diversity of the primary producer community to the phylogenetic diversity of the consumer community, we used the plant phylogeny from Cadotte et al. (2009). Similar to the methods of Dinnage et al. (2012), we calculated abundance-weighted, standardized MPD, as well as PD for the plant community in each year. All phylogenetic diversity metrics were calculated using the picante package in R (Kembel et al. 2010).

We used mixed-effects multiple regression analysis to evaluate the power of plant phylogenetic diversity (PD_p and standardized MPD, not intentionally manipulated in the original experiment) to explain phylogenetic diversity of herbivores alone (with both PD_{herb} and MPD_{herb} as response variables), and predators (PD_{pred} and MPD_{pred}) and parasitoids (PD_{para} and MPD_{para}). Models were constructed for the five years in which data

from all three trophic levels were available (1996–2000). In the model predicting diversity of higher consumers, we also included the MPD_{herb} and PD_{herb} data from each plot, to test whether the phylogenetic diversity of the secondary consumers was influenced by taxonomic or phylogenetic diversity of herbivorous arthropods. Because PD is known to covary strongly with species richness, we used plant species richness as a grouping or random factor, and allowed slopes of all relationships to vary by plant species richness level in each model, and by herbivore species richness in secondary consumer models. Thus, predictor effect size estimates and significance tests in the models are evaluated after accounting for variance due to species richness. In all models, we used sample year as a random intercept term. We used the method of Nakagawa and Schielzeth (2013) to calculate marginal R^2 values for each model, which indicates the amount of explanatory power of the predictor variables, once variation due to random effects is accounted for.

Phylogenetic influence of plant community on herbivore community.—We used two further procedures to estimate the influence of evolutionary relatedness on herbivore co-occurrence with respect to plant community phylogenetic structure. First, we took advantage of the fact that the biodiversity experiment contained monoculture plots to test whether individual plant species supported phylogenetically structured herbivore communities. Put another way, does herbivore affinity for a given plant monoculture appear to be phylogenetically conserved? To test this, we used the arthropod phylogeny pruned to only contain herbivores to model both random and Brownian evolution in abundance in each monoculture plot, summed across all sample years. We used the FitContinuous function in the geiger package (Harmon et al. 2008) in R to compare the likelihood of the following models: Brownian motion ($\lambda = 1$), no phylogenetic influence (or random, $\lambda = 0$), and the best-fit λ value (between 0 and 1). We then compared AIC of models for each plant species to determine the strength of phylogenetic influence on the herbivore community found feeding on that host-plant species.

Our second approach was to examine the strength of correlation between the abundance-weighted differences in community phylogenetic distance among all pairs of plant plots (phylogenetic beta diversity, hereafter phylobeta) and the community phylogenetic distance among their associated herbivore communities. We used the comdist function of the picante package to create two pairwise distance matrices between all plots; one for MPD of the plant communities and the other for the MPD of herbivores. These matrices thus depict the standardized expected phylogenetic distance between an individual randomly drawn from each community, from both producers and consumers, weighted by the abundance of the members of the respective communities. We then used Mantel tests to evaluate the strength of correlation between the phylobeta matrices. Under

the herbivore niche hypothesis, an increase in the phylogenetic distance between plant communities should result in a corresponding increase in herbivore phylogenetic distance. We performed these tests for the experiment as a whole, and separately for each of the plant diversity levels.

Phylogenetic influence of herbivore community on parasitoid and predator communities.—Extending the logic of the herbivore niche hypothesis, specialized secondary consumers such as parasitoids should have phylogenetic structure in association with their hosts (herbivores), while more typically generalist predators may not. We tested these two hypotheses as for herbivore–plant associations, in this case using the phylobeta matrix of herbivore communities to predict predator and parasitoid phylobeta matrices. We expected to see a positive correlation in phylogenetic distance between communities of herbivores and parasitoids, but little or no correlation with predators.

RESULTS

We produced a dated phylogeny including 905 taxa sampled from a single grassland arthropod community (Fig. 1). We were able to resolve 392 of 904 ancestral nodes (43%), spanning 15 arthropod orders containing 184 families. Many of these polytomies were due to incomplete identification; of the 905 unique taxa, 225 were identified only to family (including many larval samples and parasitoid taxa). The remaining unresolved nodes were due to lack of information in the phylogenetic systematics literature. Dominant (diverse and abundant) herbivore clades included leaf beetles (Coleoptera: Chrysomelidae), grass flies (Diptera: Chloropidae), and leafhoppers (Hemiptera: Auchenorrhyncha). Dominant predators included spiders (Araneae), wasps (Hymenoptera: Vespoidea), and ants (Hymenoptera: Formicidae). Parasitoids were dominated by wasps (Hymenoptera: Ichneumonidae and Hymenoptera: Pteromalidae). Complete information on clade diversity, resolution and age estimates can be found in Appendix: Table A2.

Phylogenetic conservatism in trophic role and body size

We found that trophic role and body size had different associations with the phylogenetic history of our naturally occurring community samples (Fig. 1). Trophic role was strongly phylogenetically conserved as indicated by an estimated $\lambda = 1.0$, an identical likelihood to a model of Brownian motion evolution along the tree. Body size also showed significant phylogenetic conservatism, with an estimated $K = 1.18$ ($P = 0.001$ in randomization tests; all effects throughout this study significant at $P = 0.05$), indicating slightly greater clustering on the phylogeny than would be expected under Brownian evolution.

Phylogenetic structure of arthropod communities

Overall, the co-occurrence of arthropod taxa across the phylogenetic tree exhibited little evidence for

evolutionary signal, as $D = 0.899 \pm 0.005$ (mean $\pm$ standard error of the mean) for the community as a whole (in this analysis $D = 1$ indicates perfect randomness of data with respect to the tree). Taking advantage of the experimental replication to analyze each plot sample as a community reveals more dynamic patterns. On a plot basis, where there was more variation, in 53% of assemblages (165 out of 313 plots), D was significantly <1. However, no plots were found with the strong phylogenetic conservatism expected if occurrence was controlled strictly by the influence of traits undergoing strict Brownian evolution ($D \approx 0$).

This overall result hid important differences among trophic groups, with more closely related herbivores but less closely related parasitoids in plots than would be expected at random (Fig. 2). In particular, 79% of herbivore plot-scale assemblages showed significant phylogenetic clustering within plots (as revealed by D significantly <1). Of predator assemblages within plots, 25% were significantly clustered (D significantly <1) with respect to arthropod phylogeny, most exhibiting strong phylogenetic clustering (D not significantly different from 0). Still, the majority of predator assemblages (72%) showed random co-occurrence patterns. Likewise, although parasitoids as a whole appeared to be overdispersed on the phylogeny (Fig. 2), 92% of the parasitoid assemblages were not distinguishable from those expected at random.

Influence of plant phylogenetic diversity on the phylogenetic diversity of arthropods

The phylogenetic diversity of the herbivore community was significantly explained by the plot-scale phylogenetic diversity of the plant community (Fig. 3, Table 1). Both PD_p and MPD_p contributed significantly to the model, which had an overall marginal $R^2 = 0.13$. When each plant community predictor including species richness (SR) was used alone in single-parameter models, all had a significant positive influence on PD_{herb}; but PD_p alone had better explanatory power than either of the other two variables (marginal R^2 values $PD_p = 0.11$; $SR_p = 0.07$, $MPD_p = 0.06$). Notably, PD_{herb} increased with increasing PD_p within each plant richness class (Fig. 3). When MPD_{herb} was used as the response variable, weighting the phylogenetic diversity of herbivores by abundance of taxa, PD_p remained the strongest predictor in combined models (Table 1), although the overall explanatory power of the model was much less (marginal $R^2 = 0.03$). On average, more phylogenetically diverse plant communities supported more phylogenetically diverse herbivore communities.

The best predictors of secondary consumer phylogenetic diversity differed by trophic guild (Fig. 4, Table 2). Predator phylogenetic diversity (PD_{pred}) responded strongly to PD_{herb}, across and within herbivore richness levels (Fig. 4). In contrast, parasitoid phylogenetic diversity (PD_{para}) was explained by MPD_p, such that increasing standardized MPD in plant communities

resulted in lower PD_{para}. This result held across and within plant richness levels (Fig. 4), when MPD_{para} was used as a response variable (Table 2). In sum, predator phylogenetic diversity increased with increasing herbivore phylogenetic diversity, while parasitoid phylogenetic diversity declined with increasing plant phylogenetic diversity.

Phylogenetic clustering of consumers on plant monocultures

The majority of plots maintained as plant species monocultures were occupied by herbivore communities that were significantly phylogenetically clustered, with λ_{est} between 0.5 and 1.0 (Table 3). There were extremes in the degree of clustering; in particular herbivores on the oaks (Quercus sp.) showed almost perfect Brownian distribution ($\lambda_{est} = 0.99$), while the forb Monarda and legume Lespedeza supported communities that did not differ from a random sample from the complete arthropod community.

Phylogenetic beta diversity of arthropods relative to plot-scale plant composition

We found weak but significant correlations in plot–plot phylobeta diversity of consumers relative to that of plant hosts, despite high variance in plot–plot MPD for the consumer samples (Fig. 5). The phylobeta diversity among arthropod assemblages was more strongly correlated with plant phylobeta diversity (Mantel $r = 0.27$, $P < 0.001$) than was herbivore phylobeta diversity (Mantel $r = 0.13$, $P = 0.003$). Thus, when phylogenetic distances between plant communities were low, arthropod phylogenetic distances were also low. As plant phylogenetic distances increased, phylogenetic distances in arthropods also increased, until a point at which evolutionary distances among plants no longer influenced phylogenetic turnover of arthropods. This saturation effect coincided with paired comparisons of plots having constructed plant communities dominated by monocots with those dominated by eudicots. Consumer phylobeta remained high but did not increase with increasing difference above this threshold, resulting in relatively weak linear associations overall. Similarly, herbivore phylobeta diversity was not an especially good predictor of predator (Mantel $r = 0.05$, $P = 0.001$) or parasitoid (Mantel $r = 0.04$, $P = 0.095$) phylobeta diversity.

DISCUSSION

By assembling a dated phylogeny estimate for a taxonomically broad sample of arthropod consumers within experimentally controlled primary producer communities, we have demonstrated how evolutionary relatedness influences plot-level ecological interactions among multiple trophic levels. First, consumer phylogenetic relatedness effectively described two commonly measured and ecologically important arthropod traits, body size and trophic role. Second, multiple lines of

Fig. 1. Assembled phylogenetic tree of 905 arthropod taxa sampled from a grassland biodiversity experiment at the Cedar Creek LTER in central Minnesota, USA. Dates (in millions of years ago, Ma) of nodes were assigned from fossil evidence where available, and otherwise modeled using assumption of constant evolutionary rates between dated nodes and tips. Right side shows body size (originally measured in mm^3) of an individual of the given taxa as measured or extracted from the literature. Taxa have been color-coded by trophic role. Major clades of interest are labeled by name and indicated by a circle at the root of the clade.

evidence demonstrate the phylogenetic conservatism (evolutionary specialization) of herbivore–host plant affinity in sampled communities. Most importantly, the phylogenetic diversity of herbivore assemblages was driven by the phylogenetic diversity of the plant community, showing the predictive ability proffered by the evolutionary histories of plant assemblages for their herbivores.
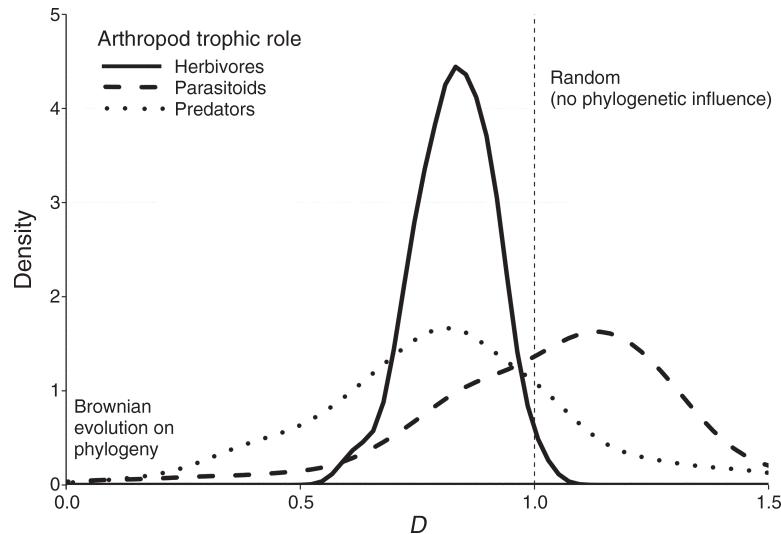
FIG. 2. Density plot of *D* statistics (Fritz and Purvis 2010) depicting phylogenetic structure of co-occurring arthropod assemblages by trophic role for the three most abundant trophic groups. Plots of all plant diversity levels were included in the analysis. For herbivores ($N = 537$ taxa), predators ($N = 101$ taxa), and parasitoids ($N = 82$ taxa), the occurrence of taxa in a given plot was modeled as a binary variable. The *D* statistic is the observed number of state changes throughout the tree, scaled by 1000 replicate expectations of the states due to random ($D = 1.0$) and Brownian ($D = 0.0$) models.

We present three lines of evidence consistent with the herbivore niche hypothesis (Novotny et al. 2006), which predicts that herbivore diversity is driven by evolutionary association with host plants, implicitly assuming herbivore dietary specialization. First, herbivores of most plant monocultures were more closely related than expected by chance. We interpret this as evidence of phylogenetic conservatism in feeding preferences among closely related specialist herbivores. Second, more phylogenetically diverse assemblages of arthropod herbivores were found in plots containing more phyloge-

netically diverse plant communities. Plant phylogenetic diversity also had more power to predict the phylogenetic diversity of herbivores than plant species richness, and relationships were consistent within plant species richness levels. Finally, plot–plot comparisons showed that phylogenetic turnover among arthropod communities (phylogenetic beta diversity) was positively correlated with phylogenetic distances among plant communities, as has been found in more phylogenetically limited analyses (Pellissier et al. 2013). However, we found that turnover was saturating when evolution-
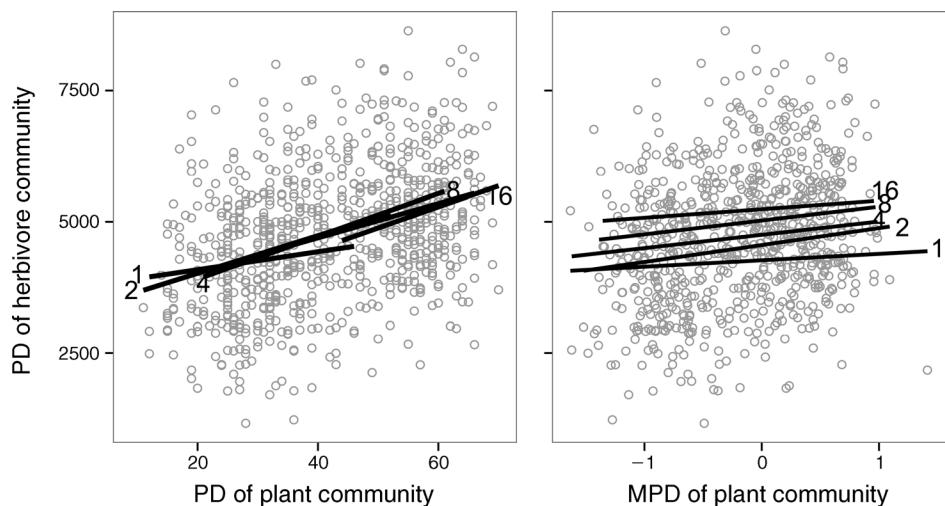

FIG. 3. Herbivore community phylogenetic diversity (PD) increases with increasing plant PD and standardized mean phylogenetic distance (MPD). Relationships were analyzed in a mixed-effects model with year as a random intercept, and slopes were allowed to vary by plant species richness. Regression lines indicate relationships within plant species richness classes, and are labeled by the richness class; manipulated plant species richness in plots: 1, 2, 4, 8, or 16 species of plants.

TABLE 1. Results of the mixed-effects model predicting herbivore phylogenetic diversity (PD_{herb}) and abundance-weighted mean phylogenetic distance (MPD) by plant PD (PD_p) and abundance-weighted standardized plant MPD (MPD_p).

Response and predictor	R^2	95% CI of effect	Estimated effect on response	χ^2	P
PD_{herb}	0.13				
PD_p		19.6, 31.5	25.6	71.9	<0.001
MPD_p		157.5, 416.5	287.0	18.9	<0.001
MPD_{herb}	0.03				
PD_p		0.05, 0.96	0.50	4.67	0.031
MPD_p		−0.68, 3.19	6.81	3.19	0.074

Notes: R^2 is model marginal R^2, sensu Nakagawa and Schielzeth (2013), the explanatory power of the predictor variables having removed variance due to the conditional grouping class (in this case, year and plant species richness). Estimated effect and 95% confidence intervals (lower and upper; CI) are given for each plant community predictor. P values were estimated using Type II analysis of deviance (marginal effects), using a chi-square test with df = 1. Slopes of predictors were allowed to vary within plant SR classes, and sampling year was treated as a random intercept.

ary distances among host plant communities were high, especially across the monocot–eudicot split. These results are concordant with work demonstrating that herbivore diversity increases, but the diet breadth of herbivores does not, among plant communities of increasing phylogenetic diversity (Novotny et al. 2006), thus supporting a growing understanding of the role of plant phylogenetic diversity in determining herbivore diversity (Novotny et al. 2006, Ness et al. 2011, Dinnage et al. 2012, Pellissier et al. 2013, Castagneyrol et al. 2014).

The interpretation of our results includes some caveats. Among the most important is that it was not feasible to document feeding behavior among 905 arthropod taxa to confirm actual herbivory or predation in a given plot. Strictly speaking, our observations examine the occurrence of arthropods with a given plant species or community, rather than feeding associations. Nonetheless, feeding relationships are the simplest explanation for patterns of herbivore occurrence as a function of plant relatedness at such a fine spatial scale, with plots located only meters apart in a single field. Likewise, we did not measure specific traits mediating herbivory or secondary consumer interactions, such as phytochemistry, diet breadth, or parasitoid life history. Plants vary in attractiveness and palatability to herbivores in relation to various traits, especially nitrogen content and defensive chemistry (Loranger et al. 2012), which can result in predictable changes in herbivore composition and consumption rates (Whitfeld et al. 2012b). Deterrents to herbivory may be phylogenetically conserved, for instance, ubiquitous chemical defense in particular plant lineages adapted to resource-limited conditions (Fine et al. 2006). Such adaptive traits, on the
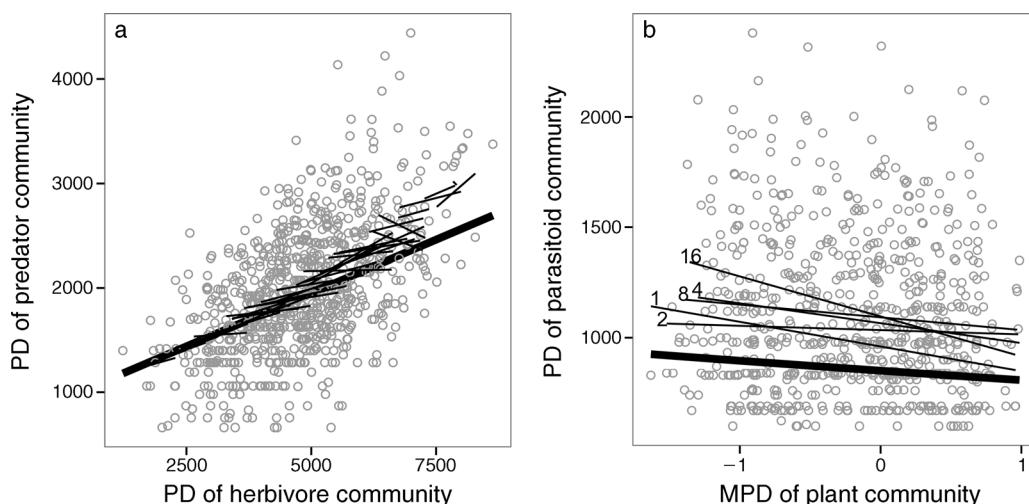

FIG. 4. Response of higher trophic groups to plant and herbivore phylogenetic diversity. Predator and parasitoid PD were analyzed separately using mixed-effects models with year as a random intercept, and slopes allowed to vary by plant species richness and herbivore species richness. (a) Predator PD increases most strongly with herbivore PD. (b) Parasitoid PD is more strongly influenced by plant diversity and declines with increasing plant MPD. Thick lines are the regression of the main effect of predictor variable; thin lines, within-group slopes for each level of herbivore species richness (a) or plant species richness (b).

TABLE 2. Results of the mixed-effects multiple regression model predicting secondary consumer (predator and parasitoid) phylogenetic diversity (PD_{pred}, PD_{para}, MPD_{pred} and MPD_{para}, respectively) by herbivore and plant species richness (SR), herbivore and plant PD, and herbivore and plant abundance-weighted standardized MPD.

Response and predictor	R^2	95% CI of effect	Estimated effect on response	χ^2	P
PD_{pred}	0.24				
PD_p		−2.3, 3.7	0.7	0.2	0.635
MPD_p		−48.7, 82.0	16.7	0.3	0.617
PD_{herb}		0.2, 0.3	0.2	73.1	<0.001
MPD_{herb}		−391.0, 71.6	−159.7	1.8	0.175
MPD_{pred}	0.00				
PD_p		0.00, 0.00	0.00	0.02	0.891
MPD_p		−0.08, 0.04	−0.02	0.52	0.473
PD_{herb}		0.00, 0.00	0.00	0.02	0.884
MPD_{herb}		−0.27, 0.13	−0.07	0.44	0.507
PD_{para}	0.10				
PD_p		0.00, 0.00	0.00	1.91	0.167
MPD_p		−0.09, −0.02	−0.05	8.97	0.003
PD_{herb}		0.00, 0.00	0.00	0.91	0.340
MPD_{herb}		−0.10, 0.14	0.02	0.09	0.760
MPD_{para}	0.03				
PD_p		0.37, 1.99	1.18	8.13	0.004
MPD_p		−37.96, −13.94	−25.95	17.99	<0.001
PD_{herb}		−0.02, 0.00	−0.01	1.84	0.175
MPD_{herb}		−43.65, 42.34	−0.66	0.00	0.976

Notes: See Table 1 for details on calculating R^2, P values, 95% CI, and slope. In this table, year, plant species richness, and herbivore species richness were set as the conditional grouping classes.

other hand, may not necessarily be phylogenetically conserved but instead may be strongly convergent, especially if traits are ecologically important (Whitfeld et al. 2012b). However, our observation of phylogenetic signal in herbivore associations suggests that suites of conserved traits could be important in this grassland plant community.

Although herbivore diversity and herbivory rates can be determined by the phylogenetic diversity of plants (Novotny et al. 2006, Ness et al. 2011, Dinnage et al. 2012, Pellissier et al. 2013, Castagneyrol et al. 2014), plants vary in the predictability of consumers, as revealed by the communities sampled from plant species in monoculture in the experiment. Some plants, like the

TABLE 3. Strength of phylogenetic structuring of herbivores sampled from host-plant monocultures.

Plant species	λ_{est}	$AIC_{\lambda est}$	$\Delta AIC_{\lambda=1}$	$\Delta AIC_{\lambda=0}$
Achillea millefolium	0.03	4077.26	427.17	4.51
Agropyron smithii	0.90	3731.70	118.55	150.03
Amorpha canescens	0.95	4320.45	46.20	308.00
Andropogon gerardii	0.88	2540.60	181.78	137.98
Asclepias tuberosa	0.71	3681.56	178.72	26.87
Elymus canadensis	0.74	3604.05	228.28	43.58
Koeleria cristata	0.57	3929.60	320.42	**3.65**
Lespedeza capitata	0.03	3975.72	298.76	**0.00**
Liatris aspera	0.61	3507.51	273.76	12.60
Lupinus perennis	0.85	3976.74	148.56	113.84
Monarda fisculosa	0.07	4062.22	164.18	**3.42**
Panicum virgatum	0.06	2850.78	259.13	**2.99**
Petalostemum purpurea	0.79	4188.84	143.04	78.68
Poa pratensis	0.88	3448.79	193.68	122.74
Quercus ellipsoidalis	0.99	3845.83	**1.27**	408.69
Q. macrocarpa	0.99	3434.71	**2.74**	359.76
Schizachyrium scoparium	0.46	3032.78	507.93	5.14
Sorghastrum nutans	0.71	3153.21	389.20	40.01

Notes: For the cumulative herbivore assemblage on each plant species, estimated Pagel's λ (λ_{est}), the Akaike information criterion (AIC) for the estimated λ value, and the difference between the AIC of the λ_{est} model and that of Brownian evolution ($\lambda = 1$) and no phylogenetic influence ($\lambda = 0$). In all cases, the best-fit λ had the lowest (best) AIC values. We judged models within 2–4 AIC units to be equivalent. Values in bold indicate either no significant difference between λ_{est} and $\lambda = 1$ (strong phylogenetic signal) or none between λ_{est} and $\lambda = 0$ (no phylogenetic signal).

cool-season grass *Koeleria cristata*, supported an apparently random selection of arthropods from the broader metacommunity, while others like the oak species *Quercus ellipsoidalis* and *Q. macrocarpa*, had a much more phylogenetically clustered arthropod fauna. This suggests arthropod presence in a *Quercus* monoculture is mediated by strongly phylogentically conserved traits. This result is notable given that the oak lineage, in contrast to many of the other plant species included in the experiment, has evolved combinations of condensed tannins that herbivores must be able to overcome, implying strong selection for feeding specialization and causing strong phylogenetic signal (Feeny 1975, Forkner et al. 2004). A converse association that supports this interpretation is that the tissues of the nitrogen-fixing legume *Lespedeza cuneata* have relatively high nitrogen content, a nutritional requirement of all herbivores which could lead to the phylogenetically non-clustered consumer communities we found on this species. These results extend recent work on plant monoculture traits and herbivory (Loranger et al. 2012), suggesting that correlated traits associated with palatability may provide an effective means for predicting the phylogenetic diversity of herbivores, and greater diversity of plant palatability traits will support a greater phylogenetic diversity of herbivores.

Our results also suggest that the phylogenetic association between herbivores and plants is likely able to capture the conservatism of unmeasured traits, which mediate trophic interactions (Rafferty and Ives 2013). We found that trophic level and body size are strongly phylogenetically conserved, but one important unmeasured arthropod trait is likely to be the diet breadth of herbivores (Bernays 2001, Castagneyrol et al. 2014). Many groups of arthropod herbivores are thought to be specialists, in that they feed on a restricted group of related plants (Novotny et al. 2006). However, Dyer et al. (2007) argued specialization differed between the tropics, where plant defensive chemistry was highly diverse and promoted specialization, and the temperate zone, where less diverse phytochemical profiles in host plants allow herbivore diet generalization. This debate has largely centered around arthropod herbivores from long-lived, woody plant species; the role of plant traits in promoting specialization (and thus diversity) among grassland arthropods is an area ripe for exploration.

This analysis of an extensive consumer community phylogeny pushes into new territory, thus uncertainty associated with our estimate of arthropod phylogeny deserves consideration. We assembled a community phylogeny from the published literature of systematics, in part, because comparable DNA sequence data were unavailable for our community sample. The assumption that named taxa (e.g., genera, families, order, etc.) are monophyletic unless proven otherwise by recent phylogenetic study is a source of uncertainty in our tree topology. Questions also remain about the impact of uncertainty due to incomplete phylogenetic resolution or
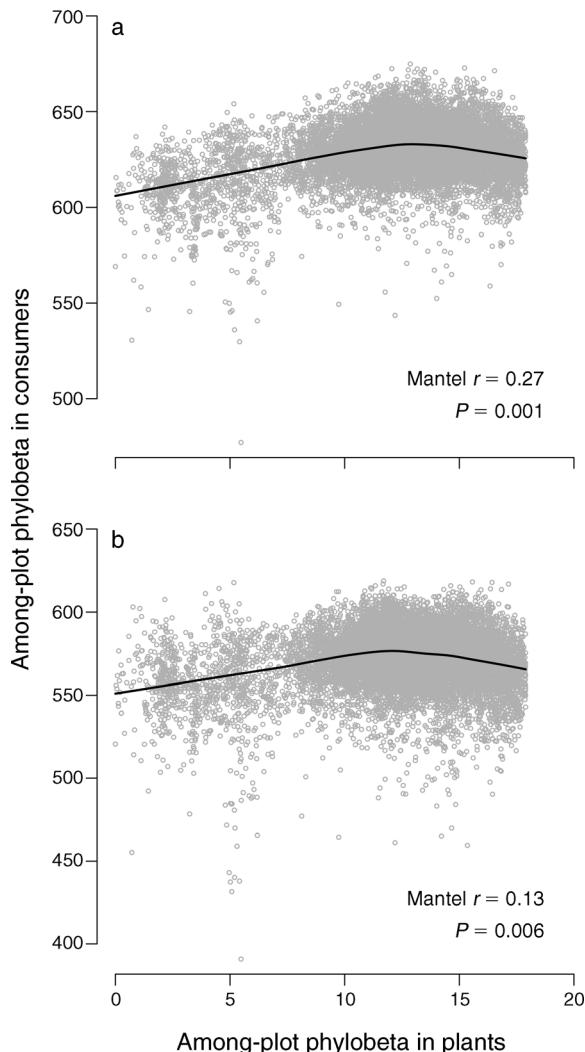

Fig. 5. Pairwise correlations among evolutionary distances between plant communities (*x*-axis), and consumer communities (*y*-axis) for (a) all arthropods and (b) herbivores only. Points depict MPD between plant and consumer communities, or for each trophic level, the expected evolutionary distance between a member picked at random from each community weighted by local abundance. Mantel tests between the distance matrices give overall correlation; a running mean (loess spline) is shown as a trend line depicting the saturating relationship. At some point, pairwise evolutionary distances are high enough that any signal from the plants is eroded. As long as phylogenetic beta diversity (phylobeta) of plants is high enough, phylobeta of insects is also very high.

species identification. For example, many genera in our community sample have yet to be included in a formal, dated molecular phylogenetic analysis, and some taxa were not identified to named species. However, even phylogeny estimates for completely diagnosed species with comparable DNA data will have error associated with incomplete taxon sampling and the stochasticity of molecular evolutionary processes (Zwickl and Hillis 2002). Assumptions about arthropod divergence times, including the accuracy of fossil-calibrated dates for

particular lineages and otherwise uniform evolutionary rates among the remainder, is yet another potential source of error. Exploring each source of error and potential effects on community phylogenetic analyses is an important area for future work. In the meantime, and until a comprehensive tree of life is available (Stoltzfus et al. 2013), we suggest that our approach, a literature-based estimate of arthropod phylogeny, represents a reasonably accurate, pragmatic alternative to inferring community phylogeny from DNA sequences (Beaulieu et al. 2012).

The phylogenetic approach we employed revealed that the probability of herbivore co-occurrence in a given plot increased with increasing shared evolutionary history of plant hosts, and herbivores are more closely related than would be expected at random, indicating a shared inheritance of feeding association. This lends a final leg of support to the role of phylogenetic history in explaining plant–herbivore trophic dynamics (Bernays 2001, Novotny et al. 2006). Likewise, the evolutionary distance among different plant assemblages predicted the evolutionary distance among arthropod consumers as a whole. However, this was a saturating relationship, such that at some evolutionary distances among host plants (corresponding roughly to the eudicot–monocot split), producer relatedness had no further influence on that of consumers.

In contrast, a more variable set of patterns was observed for predators and parasitoids, with some communities defined by highly conserved co-occurrence patterns but most samples being little different from random samples of the guild metacommunity. It was especially surprising that parasitoid assemblages were not more influenced by phylogeny or correlated with herbivore phylogenetic diversity, given their intimate life history with herbivores (Stireman et al. 2006, Bailey et al. 2009). Instead, the parasitoid assemblage phylogenetic diversity was negatively influenced by plant relatedness, such that on average, higher parasitoid phylogenetic diversity occurred on the most closely related plant communities. Predators, on the other hand, were more phylogenetically diverse with increasing herbivore phylogenetic diversity, a pattern holding within each herbivore diversity level. One contributing explanation to these contrasting patterns is the lower resolution of the parasitoid phylogenetic tree we used, which had higher numbers of polytomies than the corresponding herbivore and predator trees. However, because predators and parasitoid plot–plot phylobeta had little correspondence with herbivore phylobeta, it appears that, at local scales, phylogenetically structured trophic relationships may be most important for grassland herbivores.

By synthesizing disparate phylogenetic hypotheses and fossil evidence into a coherent, dated tree, we were able to analyze an entire arthropod consumer community as well as its trophic components, spanning deep branches of animal evolution. Overall, arthropod plant–herbivore interactions are largely reflective of evolutionary associations, while higher trophic level associations within experimental diversity plots differed by guild in surprising ways. Our results demonstrate that the evolutionary history of both plants and their consumers mediates species interactions to generate and maintain consumer diversity, even at local scales.

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Supplemental Material

Ecological Archives

The Appendix and Supplement are available online: http://dx.doi.org/10.1890/14-0784.1.sm