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ARTICLE

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Predator dispersal influences predator distribution but not prey diversity in pitcher plant microbial metacommunities

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Abstract

The spatial distribution of predators can affect both the distribution and diversity of their prey. Therefore, differences in predator dispersal ability that affect their spatial distribution, could also affect prey communities. Here, we use the microbial communities within pitcher plant leaves as a model system to test the relationship between predator (protozoa) dispersal ability and distribution, and its consequences for prey (bacteria) diversity and composition. We hypothesized that limited predator dispersal results in clustered distributions and heterogeneous patches for prey species, whereas wide predator dispersal and distribution could homogenize prey metacommunities. We analyzed the distribution of two prominent bacterivore protozoans from a 2-year survey of an intact field of *Sarracenia purpurea* pitcher plants, and found a clustered distribution of *Tetrahymena* and homogeneous distribution of *Poterioochromonas*. We manipulated the sources of protozoan colonists and recorded protozoan recruitment and bacterial diversity in target leaves in a field experiment. We found the large ciliate, *Tetrahymena*, was dispersal limited and occupied few leaves, whereas the small flagellate *Poterioochromonas* was widely dispersed. However, the bacterial communities these protozoans feed on was unaffected by clustering of *Tetrahymena*, but likely influenced by *Poterioochromonas* and other bacterivores dispersing in the field. We propose that bacterial communities in this system are structured by a combination of well dispersed bacterivores, bacterial dispersal, and bottom-up mechanisms. Clustered predators could become strong drivers of prey communities if they were specialists or keystone predators, or if they exerted a dominant influence on other predators in top-down controlled systems. Linking dispersal ability within trophic levels and its consequences for trophic dynamics can lead to a more robust perspective on trophic metacommunities.

KEYWORDS
metacommunities, microbial communities, pitcher plants, predator–prey dynamics

INTRODUCTION

Predation can be an important determinant of prey abundance and community structure (Croll et al., 2005; Lawler & Morin, 1993; Paine, 1966). By consuming prey, predators can cause local extinctions or mediate coexistence by reducing competitive exclusion (Borrvall & Ebenman, 2006; Caswell, 2002; Crowley, 1979; Paine, 1966, 2003). However, dispersal can change predator–prey dynamics by altering the local abundance of species (Amarasekare, 2008a; Holt, 2002). If there is a net influx of prey, local predator–prey fluctuations dampen and the chance of local coexistence increases (Briggs & Hoopes, 2004; Maly, 1978; Rosenzweig & MacArthur, 1963). In contrast, if dispersal of predators increases local predation pressure, then the likelihood of prey extinctions increases and destabilizes predator–prey systems (Gravel et al., 2011; Holyoak, 2000; Huffaker, 1958; Pillai et al., 2011). Therefore, the outcome of predator–prey interactions in communities interconnected by dispersal ("metacommunities," see Leibold et al., 2004) depends on the scale at which predator and prey species move across space (Guzman et al., 2019; Holmes et al., 2017; Holyoak et al., 2005).

Dispersal can also vary among species in the same trophic level with potential consequences for other trophic levels (McCann et al., 2005). For example, large herbivores like ungulates may be able to access more plant patches than smaller herbivores such as small mammals or insects (Olff & Ritchie, 1998). The damage resulting from large mammal consumption will be more evenly distributed across the landscape than damage from insect or small mammal herbivory, which will appear more patchy. Therefore, from the perspective of the prey, clumped predators may cause a heterogeneous and patchy landscape, whereas well distributed predators represent a more homogeneous landscape (Abrams, 1993; Genkai-Kato & Yamamura, 2000; Kretzschmar et al., 1993; Leibold, 1989, 1996; Phillips, 1974). Whether the predator's distribution is detrimental for prey abundance or beneficial for prey diversity depends on the direct and indirect effects of each predator on the prey community.

When multiple predators co-occur in a region, differences in predator dispersal abilities could have the additional consequence of creating a heterogeneous landscape of multipredator patches, with highly connected patches hosting multiple predators, and isolated patches hosting only a few. This spatial heterogeneity in predator load can influence prey communities (Burkepile & Hay, 2008; Canter et al., 2018; Griffin et al., 2013). At the local scale, increased predator richness could suppress prey via feeding complementarity (Losey & Denno, 1998; Miyashita et al., 2016) or benefit prey when strong competition among predators reduces their combined effect (Canter et al., 2018; Nilsson et al., 2006). An alternative but important possibility is that prey communities may be unaffected by predator heterogeneity if bottom-up processes primarily drive prey diversity and abundance (Hunter & Price, 1992; Maron & Pearson, 2011).

Dispersal is a necessary component of many communities with impermanent habitats and may strongly influence the assembly of communities. For example, the microbial communities within the leaves of the purple pitcher plant (*Sarracenia purpurea*) undergo constant resetting as old leaves become damaged and new leaves must be colonized by resident species (Butler & Ellison, 2007). Bacteria are at the base of this food web and conduct critical degradation pathways to break down insects captured by the plant (Cochran-Stafira & Von Ende, 1998; Gallie & Chang, 1997; Luciano & Newell, 2017; Mouquet et al., 2008). Bacteria are then prey for protozoans, rotifers, and mites, which can be, in turn, consumed by mosquito larvae (*Wyeomyia smithii*) (e.g., Gotelli & Ellison, 2006; Kneitel & Miller, 2002; Peterson et al., 2008). Whereas the pitcher plant's inquiline community has been studied extensively as a model system in ecology (Miller et al., 2018; Miller & Kneitel, 2005; Srivastava et al., 2004), we know little of the dispersal abilities of the component species, or the role dispersal plays in driving trophic interactions.

Variation in predation and dispersal abilities among bacterivores in pitcher plants makes this a strong system for testing hypotheses linking dispersal and predation. For example, Kneitel (2012) found a wide range of colonization rates among protozoans, yet these were uncorrelated with competition and other ecological traits. In another study, Canter and collaborators (2018) used a controlled greenhouse experiment to show that protozoan diversity was positively correlated with microbial evenness and found some species-specific predatory effects. We propose that variation in dispersal abilities and effects of predation among bacterivores could affect bacterial prey communities in these metacommunities. In this study, we will focus on two bacterivores: the ciliate *Tetrahymena* sp. (TA) and the flagellate *Poterioochromonas* sp. (PS), two dominant competitors against other protozoa in the system (Miller et al., 2022). We hypothesize that their dispersal will depend on size, with the larger TA remaining clustered in space and the smaller PS being widely distributed. We further hypothesize that TA's clustered distribution may result in a heterogeneous landscape for bacteria due to either direct predation effects or indirect effects through competitive interactions with other bacterivores. Direct and indirect effects of PS would result in more homogeneous landscapes due to its hypothesized wide distribution. Additionally, we expect PS and TA to

co-occur when TA is present, and thus prey responses to TA's clumped distribution should be the most evident trophic effect. Although these effects may influence the regional (gamma) diversity of bacteria, our focus in this study will be on local (alpha) effects of predator dispersal to emphasize the potential for landscape heterogeneity.

The goal of this study was to identify variation in bacterivore dispersal ability and quantify its effect on bacterial diversity and structure. We used two complementary approaches: (1) a spatial analysis of temporal patterns of protozoan colonization and (2) a manipulative experiment to reveal the effects of differential predator dispersal on their bacterial prey communities. The spatial analysis entailed a reanalysis of data from Miller and terHorst (2012), a study that followed natural pitcher plant inquiline communities for more than 2 years in the field. We found that TA exhibited a clustered distribution and associated strongly with spatial factors, whereas PS is widely distributed. In the field experiment, we manipulated sources of TA and PS colonists and then quantified (1) their ability to recruit to nearby leaves and (2) their subsequent effects on bacterial diversity and composition. We expected to confirm the dispersal abilities found in the 2012 data, with TA exhibiting weaker dispersal ability than PS. If TA has a strong effect on its prey, we expect that the few TA colonized leaves will contain bacterial communities distinct from leaves where TA is absent. Alternatively, if PS has a stronger effect on the bacterial community, it may homogenize bacterial communities across the field. We also tracked the overall bacterivore community colonizing from the field (including TA and PS) to assess how intermediate consumers may impact lower trophic levels. By considering differing dispersal abilities in a consumer trophic level and their consequences for local prey communities, this study aims to advance our understanding of trophic metacommunity dynamics.

METHODS

Sarracenia purpurea is a carnivorous plant that occurs in the eastern North America (also called *S. rosae*, Ellison et al., 2012; Naczi et al., 1999). In North Florida, during the growing season (April–December), plants produce approximately one cup-shaped leaf per month and leaves senesce after 40 weeks, on average (Miller & terHorst, 2012). Leaves fill with rainwater and capture insects (mostly fire ants, *Solenopsis invicta*) that supply nitrogen for the plant and resources for a microscopic trophic web. Specifically, bacteria break down captured insects, releasing nutrients and building biomass, which is then available to other trophic levels. Archaea are typically negligible in this system, thus we focus our study on bacteria as protozoan prey (Canter et al., 2018).

The intermediate trophic level is composed of bacterivores that differ in body size and feeding mode, including protozoans, rotifers, and mites (Kneitel, 2012; Kneitel & Miller, 2002; Šimek et al., 1997). Here, we focused on the dispersal ability and predatory effects of two protozoans, *Poterioochromonas* sp. (PS) and *Tetrahymena* sp. (TA). We chose these two predators because of known differences in size and feeding strategies (Fenchel, 1980; Jezbera et al., 2005; Ma et al., 2018). PS is a small (2–13 μm length) flagellate (Chrzanowski & Šimek, 1990; Ma et al., 2018) with a mixotrophic diet (Sanders, 1991; Zhang & Watanabe, 2001) that selectively grazes on bacteria and algae with preference for particles ranging from 1 to 7 μm in size (Chrzanowski & Šimek, 1990; Zhang & Watanabe, 2001). TA is a large filter feeding ciliate (20–50 μm) that selects for small food particles, including bacteria, based on size, biochemistry, and motility (Montagnes et al., 2008; Thurman et al., 2010; Verni & Gualtieri, 1997). In addition, TA and PS are dominant competitors within the pitcher plant protozoans (Miller et al., 2022) and recurrent inhabitants of pitcher plants in the field (Miller & terHorst, 2012; note that TA was identified as *Colpidium* sp.). Importantly, all these inquiline organisms must be able to colonize new leaves to persist.

Field distribution analysis

To investigate whether dispersal limitation creates spatial patterns in unmanipulated pitcher plant communities, we used data from Miller and terHorst (2012). This study mapped and sampled pitcher plants within a 20 × 20 m area of pine savanna in the Apalachicola National Forest in northwestern Florida. A subset of new leaves from these plants was randomly selected monthly for one full year (2003), then censused biweekly until each leaf senesced, for a total of 94 individual leaves followed from 2003 to 2005. The original study tested hypotheses about succession regarding changes in community stability, similarity, and diversity over time, suggesting that ecological drivers may result in previously overlooked complex successional patterns. Importantly, the bacterial community in this study was only assessed via dilutions and plating (in LB medium) and only the broader diversity and similarity patterns were analyzed. The specific effect of TA or PS on their prey was not established.

For our analysis, we focused exclusively on leaves with community data (excluded leaves that were tagged but not sampled) and determined presence or absence of TA and PS within each leaf. We used two approaches to

evaluate the role of dispersal on pitcher plant community assembly. First, we used a generalized linear model (GLMM) with a binomial distribution to ask whether protozoa occupancy depends on the age of a leaf, with earlier occupancies assumed to be associated with greater dispersal abilities. We initially included fluid volume, leaf identity, and the date the leaf opened in the analysis but found no significant effects or changes in the qualitative findings. Because the simpler model with only leaf age outperformed others, we present this simpler model without the additional covariates.

Second, we used spatial data (Miller and terHorst, unpublished) in combination with successional patterns to assess the role of spatial factors in driving occupancy. We first performed a global test using permutations on Redundancy Analysis that included protozoan community and leaf location. Then, we decomposed the contribution of spatial location to community composition by calculating distance-based Moran's eigenvectors map (dbMEM, Dray et al., 2006) using the "quickMEM" function developed by Brocard 2016. dbMEMs use matrix algebra to maximize the spatial autocorrelation to provide spatially explicit multiscale variables (Dray et al., 2012). Specifically, dbMEMs with positive eigenvalues indicate positive autocorrelation with space and can be used as explanatory variables. We thus selected positive significant dbMEMs and then used GLMMs with a binomial distribution to determine whether protozoan occupancy was explained by the age of the leaf, the spatial factors, or both. We expected species with lower dispersal to exhibit more and stronger associations with these spatial factors. This can be interpreted as evidence for clustered distribution in space. In fact, which MEMs associate with species distribution is particularly indicative of a clumped distribution, with the first MEMs indicating broader distributions and later MEMs suggesting small-scale clumping. We included leaf identity and opening date as random factors in this model. We progressively removed dbMEMs and compared model fit based on Akaike information criteria (AIC). We generated distribution maps to illustrate these patterns (Figure 1c,d).

Field experiment

The objective of our manipulative experiment was to establish a link between protozoan ability to recruit to nearby leaves and their subsequent effects on bacterial diversity and composition. We present here the methods outlining our (1) experimental design, (2) protozoan and other bacterivore quantification, and (3) bacterial community profiling.

Experimental design

We manipulated initial local spatial patterns of bacterivores in the Pleaphase savanna located north of Sumatra, FL in the Apalachicola National Forest in June, 2017. This field is near and very similar in vegetation and exposure to the pine savanna used in Miller and terHorst (2012). We haphazardly selected 28 purple pitcher plants (*Sarracenia purpurea*) from across the field, with each plant a minimum of 2 m from any other treatment plant. We selected plants that had one new, central leaf (hereafter target leaf) surrounded by at least four older leaves (hereafter neighbor leaves). In plants with more than five leaves, any additional leaves were removed. Prior to experimentation, neighbor and target leaves were emptied and treated with 3% hydrogen peroxide for 20 min, followed by three washes with sterile deionized water. This cleaning method eliminates all or most of the prior leaf occupants with minimum damage to the leaf (Miller, personal observation). We then experimentally manipulated the composition of the inquiline community within the four neighbor leaves and tracked the colonization in the target leaves. The target leaves were filled with 10 ml from a standard bacterial mixed culture (obtained from pitcher plants as explained below), initially devoid of any protozoans.

Plants were assigned to one of four treatments: TA+, PS+, Empty, or Natural. The first two treatments assessed the influence of short-distance dispersal of TA and PS within a plant by adding a 10 ml culture of *Tetrahymena* sp. (TA+) or *Poterioochromonas* sp. (PS+) to the neighbor leaves, and then quantifying colonization of the target leaf. The other two treatments assessed the influence of long-distance dispersal by PS and TA and other bacterivores among plants within the field. In the Empty treatment, we intended to decrease local dispersal, as we left the neighbor leaves empty of fluid; thus the target leaf had to be colonized by dispersal from other plants or other habitats in the field. In the Natural treatment we did not manipulate the neighbor leaves (were not emptied or treated with hydrogen peroxide), thus allowing for natural colonization of the target leaf. Each treatment was replicated eight times in a randomized block design. All leaves were left uncovered in the field and untouched other than our regular sampling.

To create the initial bacterial communities, a bulk collection of the bacteria from pitcher plant fluid was obtained from the field as described by Canter and collaborators (2018) and cryopreserved (Kerckhof et al., 2014) with 2% DMSO at −80°C. When needed, these samples were thawed, added to a solution of one part dry ground ants and five parts deionized sterile water (1:5 dilution), and incubated overnight at 27°C, prior to

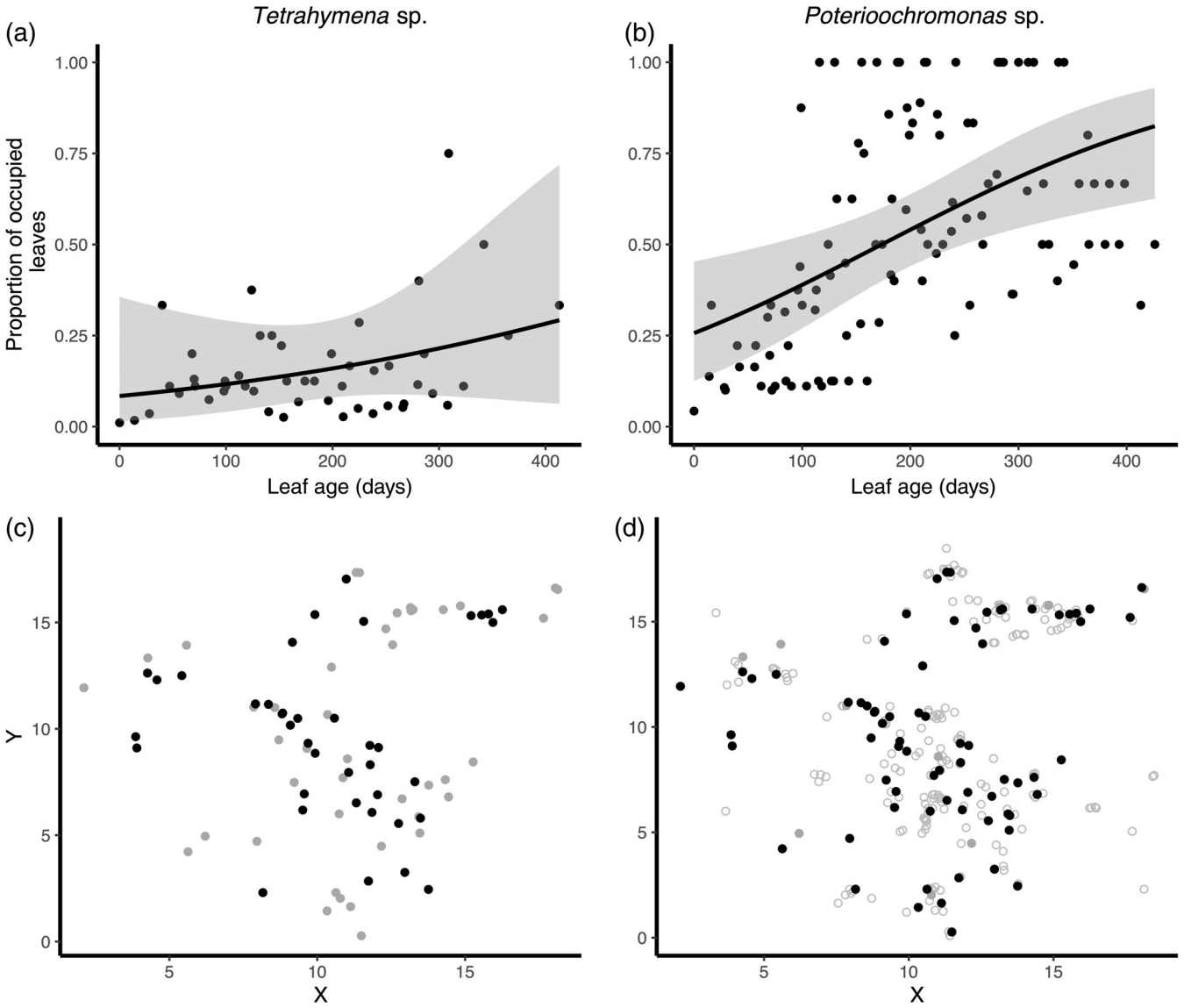

FIGURE 1 TA and PS occupancy (a, b) and distribution maps (c, d) obtained from Miller and terHorst (2012) data. Temporal changes in occupancy for TA (a) and PS (b) were measured from 2004 to 2006 for 267 leaves. Spatial distributions for TA (c) and PS (d) were established at the end of the study period to assess their association with space (see text). *X* and *Y* axes in (c) and (d) were measured in meters. Black circles denote occupied leaves, dark gray circles indicate unoccupied leaves, and empty gray circles are leaves that were tagged but not sampled.

the start of the experiment. We preserved (at −80°C) three replicate samples from this standard bacterial mixed culture ("original broth" hereafter) to establish a baseline of composition and diversity for the experiments. The original broth was also sampled in triplicate to assess for protozoan contamination using phase contrast microscopy. No contamination was found. Protozoan cultures for the experiments were obtained from stock lines maintained by the Miller laboratory at Florida State University. Individual 50 ml Falcon tubes with 10 ml of original broth were inoculated with 50 cells of PS or TA and incubated for 3 days in a 12/12 light and 23/27°C cycle. Cultures from each tube were added to one leaf in the field according to the treatments described below. Other than nutrients from the 1:5 ant:water dilution in the original broth, no further additions were made to the leaves over the course of this experiment.

Protozoan and other bacterivore quantification

We sampled the target leaves for protozoa every 4 days. Sterile pipettes were used to mix the fluid and extract a 0.5 ml sample from each leaf into a sterile microcentrifuge tube. Protozoans, rotifers, and mites were directly counted in the laboratory by adding 0.1 ml of the sample to a Palmer cell and counting moving cells at ×100 magnification using a phase contrast microscope. Count data are

publicly available at DOI 10.5281/zenodo.712135. Presence or absence of mosquito larvae was recorded by direct observations of the fluid within the leaf and the pipette. Leaves from all treatments in our experiment had between three and seven mosquito larvae. Because mosquito abundance was not correlated with protozoan abundance (Kruskal–Wallis: $\chi^2 = 0.109$, $df = 3$, $p = 0.990$), we did not include this factor in the final analyses. At each sampling date, we also haphazardly sampled one neighbor leaf per plant for TA+ and PS+ treatments to confirm the persistence of those populations. We found they persisted for the duration of the experiment, and that neighbor leaves were also colonized by other bacterivores. We confirmed that TA+ and PS+ plants had at least two neighbor leaves with the focal protozoa (TA or PS) for the duration of the experiment. Because of the sparsity of these data, we did not analyze further, and used it exclusively to confirm the potential colonization from neighboring leaves in these treatments. After 28 days, all leaves were sampled as described above and the remaining fluid collected to obtain bacterial community profiles, with sterile pipettes in 15 ml sterile Falcon tubes placed on ice for transport, and frozen and stored at −80°C before further processing.

Bacterial community responses to predator occupancy

DNA extraction, sample processing, and sequencing details are provided in the Supplementary materials. The resulting sequences are available in the National Center for Biotechnology Information (NCBI) sequence read archive under PRJNA885239. The bioinformatics pipeline used to process the raw sequences can be found in the Supplementary materials (Appendix S1: Section S1).

Experiment data analysis

To establish protozoan recruitment to target leaves and their subsequent effects on bacterial diversity and composition, we used a combination of general linear model (GLM), GLMM, and multivariate analyses. We divide our analyses into four parts: (1) temporal changes in TA and PS occupancy and abundance, (2) final day patterns in TA and PS occupancy and abundance, (3) other bacterivore community profiling, and (4) bacterial community profiling.

Temporal changes in TA and PS recruitment

To assess whether treatments influenced temporal changes in occupancy (presence/absence) of focal species within target leaves, we used a GLMM with a binomial distribution and a logit link function, using the function *glmer* from the "lme4" package in R (version 1.1–27.1, Bates et al., 2015). The model included sampling day, treatment, and protozoa species as fixed effects, and leaf identity as a random effect. We only included interactions between the treatment and the protozoa species because including interactions with day decreased the model fit (higher AIC values). We used likelihood ratio tests to determine significance of each factor in the model using the function *Anova* from the "car" package in R (version 3.0–10; Fox et al., 2019). We determined the appropriate error distribution using the function *qqp* from the "car" package (this method was used for all models below).

To assess the changes in abundances of the focal species (PS and TA) within target leaves over time, we used a linear mixed model on the log-transformed abundance (log of abundance +1) for PS and TA and included day, treatment, and species as fixed effects and leaf identity as a random effect. We used the *glmer* function from the "lme4" package in R. The combination of occupancy and abundance data provides a broader picture of dispersal and colonization dynamics; whereas occupancy is a more direct measure of colonization success, abundance data incorporate both dispersal and local persistence. Given their size differences, we were interested in whether abundance data were informative of biomass for TA and PS, and we used the average abundance at time of stabilization. We multiplied this average abundance by each species estimated volume obtained by Canter and collaborators (2018) using microscopy: $3.1 \times 10^5\ \mu m^3$ for TA and $2.1 \times 10^3\ \mu m^3$ for PS.

Final day TA and PS occupancy and abundance

In addition, we analyzed the abundance and occupancy (presence/absence) data from the final day separately. This allowed us to compare patterns of occupancy and abundance in the protozoa with the bacterial data we collected at the end of the experiment (day 28). We used a GLM fit with a binomial distribution on logit transformed occupancy (presence/absence) data for protozoa, with treatment and protozoa species as fixed effects. We then tested the abundance patterns on day 28 using a two-way ANOVA. Departures from normality were tested with a Shapiro–Wilks test, whereas heteroscedasticity was tested using a Bartlett's test of homogeneity. We calculated estimated biomass for abundances at the end of the experiment, as explained in the previous section.

Bacterivore community profile

Leaves were colonized by protozoa species other than PS and TA, thus we calculated overall protozoan richness and evenness for each target leaf (Pielou's evenness; Pielou, 1959) on day 28, and assessed the effects of the treatments by using a two-way ANOVA (parametric assumptions tested as above). The effects of the treatments on protozoan assemblage composition were visualized with Non-Metric Multidimensional Scaling (NMDS) on relative abundance data. Two axes were employed unless a solution was not reached or if stress was above 0.2; in that case, three axes were used. We also assessed the effect of treatments on community similarity by analyzing the multivariate homogeneity of group dispersions (Anderson et al., 2006). To assess significant differences between treatments, we used a PERMANOVA with 999 permutations on a Bray–Curtis dissimilarities distance matrix using the *adonis* function in the "vegan" package in R (version 2.6–2, Oksanen et al., 2017). We repeated this analysis by including only samples from TA+ and PS+ that contained the respective taxa to better determine whether their presence influenced the bacterial community. Because we found bacterivore richness, evenness, and composition were unaffected by the experimental treatments, we did not include these data in further statistical models.

Bacterial community profile

Similarly, we tested whether bacterial diversity and composition responded to treatments. We assessed significant differences in richness (number of ASVs) and evenness (Pielou's evenness; Pielou, 1959) across treatments using one-way ANOVAs after first log-transforming the diversity metrics to meet parametric assumptions. We visualized the effects of treatments on bacterial community composition using NMDS ordination with Cumulative Sum Scaling (CSS) normalized ASV data (Paulson et al., 2013). Significance was again assessed using a PERMANOVA on a Bray–Curtis dissimilarity distance matrix. We first included the original broth samples in this analysis to investigate how bacterial communities changed in our experiment. Then, we excluded the original broth samples to highlight differences between treatments. We aimed to investigate how the treatments, and consequent bacterivore community would influence the bacterial composition. Last, we assessed the effect of our treatments on individual bacterial taxa to establish if individual ASVs responded to the differential dispersal of our focal predator species, TA and PS. We used Kruskal–Wallis tests on CSS normalized ASV data, with a Bonferroni correction on resulting *p*-values. We used Wilcoxon-sum tests for pairwise differences in taxa where treatments resulted in significantly different abundances.

Unless otherwise indicated, analyses described in this section were conducted using the R environment (R core Team, 2020) with functions described in the packages "vegan" (version 2.6–2, Oksanen et al., 2017), "phyloseq" (version 1.30.0, McMurdie & Holmes, 2013), and "MASS" (version 7.3.51.4, Venables & Ripley, 2002).

RESULTS

Field distribution analysis

Using census data from Miller and terHorst (2012), we found that the natural proportion of leaves occupied by TA and PS increased significantly with leaf age (Figure 1a,b, TA: $df = 1$, $\chi^2 = 18.6$, $p < 0.001$, PS: $df = 1$, $\chi^2 = 54.0$, $p < 0.001$). TA occupancy was low in young leaves and increased slowly, with the youngest leaves having less than 1% occupancy, and reaching just less than 32% occupancy in 1-year-old leaves. In contrast, PS colonized young leaves quickly, with 25% of young leaves being occupied in the first week, and occupying 59% of surviving 1-year-old leaves.

We found TA was strongly associated with space at small scales, indicative of clumping, whereas PS was not ($F_{2,1525} = 7.382$, $p = 0.001$). We found nine dbMEMs with positive eigenvalues which indicate positive autocorrelation in space at different spatial scales, with the first ones representing broader scales and the later ones progressively smaller scales. TA was significantly correlated to four dbMEMs and marginally to one dbMEM (Appendix S1: Table S1). These significant dbMEMs were indicative of finer scale spatial patterns (clumped distributions at small spatial scales). PS was only associated significantly with one MEM, but the significance was lost in the reduced model (Appendix S1: Table S1) indicating no significant clumping in the field.

Field experiment

We found 12 bacterivore taxa in our experimental leaves. PS was the most abundant bacterivore within and among leaves, whereas TA ranked sixth (Figure S1). Nine of these taxa were protozoans (*Bodo saltans*, two *Colpoda* spp., *Colpidium* sp., and five unidentified protozoan taxa), whereas the other three were rotifers (*Habrotrocha rosa*), mites (*Sarraceniopus gibsonii*), and unidentified nematodes. Mosquito larvae (*Wyeomya smithii*) were present in 0% of leaves at day 4, 63% of the leaves at

day 8, and 100% thereafter, mostly as first or second instars. We found no evidence of further insect capture within target leaves in this experiment, yet it is important to note that we would have been unable to tell between debris resulting from crushed ants added to the original broth and fresh ants captured by the plant. Our sampling over time did not reveal any new prey, which suggests few to no new prey were captured.

Temporal changes in TA and PS recruitment

Leaf occupancy patterns (presence/absence) for the focal species (PS and TA) within target leaves were affected by the neighbor treatments ($df = 3$, $\chi^2 = 21.6$, $p < 0.001$), changed over time ($df = 1$, $\chi^2 = 44.1$, $p < 0.001$), and depended on the protozoan species identity (PS or TA: $df = 1$, $\chi^2 = 38.5$, $p < 0.001$), yet the interaction between neighbor treatment and protozoan species was marginally nonsignificant ($df = 3$, $\chi^2 = 7.26$, $p = 0.064$) in the final model (Appendix S1: Table S2). When neighbor leaves were inoculated with PS (PS+), we found PS within their target leaves by day 8, occupying six out of eight leaves by day 12 (Figure 2a, Appendix S1: Table S2a). PS also colonized leaves in other treatments starting on day 12. Although we cannot distinguish dispersal from our experimental cultures or from elsewhere in the field, colonization of empty leaves indicates that PS can disperse beyond neighbor leaves at relatively long distances. In contrast, TA seldom occupied leaves through long-distance dispersal. By day 20, TA occupied only 25% of the target leaves in leaves with TA neighbors (TA+) and half the target leaves in that treatment by the end of the experiment (Figure 2b). TA's maximum occupancy of non-TA+ leaves was 37% in leaves allowed to be colonized by natural communities from neighboring leaves (natural treatment), by day 20 and declined thereafter (Figure 2b).

The total abundance of focal species within the target leaves was significantly affected by the neighbor treatments

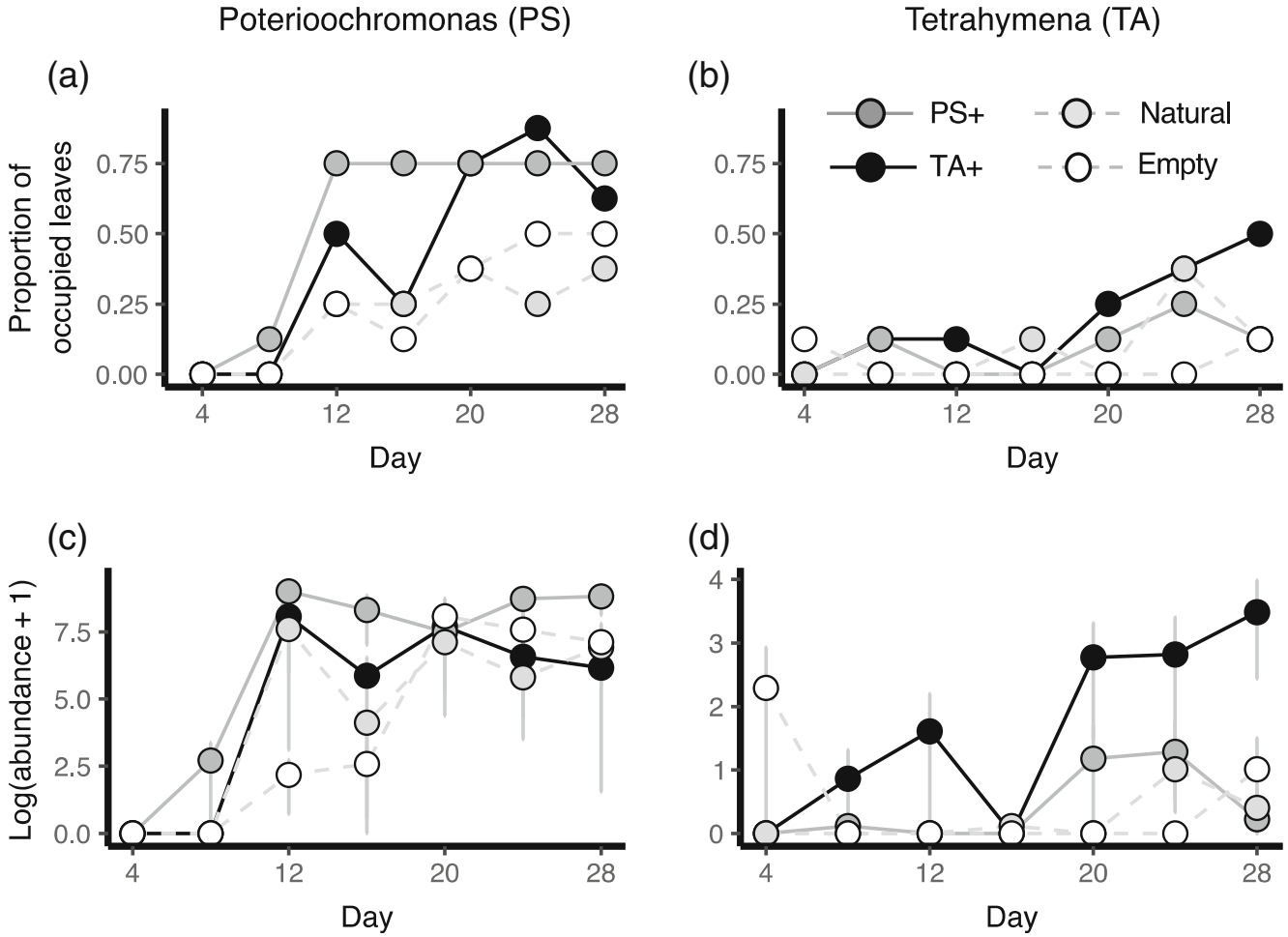

FIGURE 2 Temporal patterns in occupancy (a, b), abundance (c, d) for PS (a, c), and TA (b, d). Arrival time is categorized as early (2–8 days), intermediate (12–16 days), late (20–28 days), or never. Treatments are represented by colors as indicated in panel (b). Bars indicate standard error of the mean in (c, d).

(df = 3, $\chi^2 = 33.6$, $p < 0.001$), time (df = 1, $\chi^2 = 55.0$, $p < 0.001$), and protozoan species (df = 1, $\chi^2 = 105.4$, $p < 0.001$, Appendix S1: Table S2b). Interactions were significant between protozoan species and treatment (df = 3, $\chi^2 = 28.7$, $p < 0.001$), and protozoan species and day (df = 1, $\chi^2 = 33.2$, $p < 0.001$), mostly due to the different trajectories of abundance between PS and TA in target leaves. PS abundance stabilized early at an average of more than 6500 cells per ml in all treatments (Figure 2c). In contrast, TA's abundance increased with time, but only in the TA+ treatment, reaching 31 cells per ml by the end of the experiment (Figure 2d). Based on estimated cell volume the overall biomass for our focal species is 9.61×10^6 μm^3 for TA and 13.61×10^6 μm^3 for PS at the time of abundance stabilization. This rough biomass estimation suggests TA and PS have equivalent biomass values, with TA exhibiting a slightly lower value. Because cell counts are more direct metrics of ecological interactions, population growth, and evolution, we will continue to focus on abundance but believe the biomass comparison is a useful complement to our study.

Final day TA and PS occupancy and abundance

At the end of the experiment (day 28), species differed strongly in occupancy and abundance patterns across treatments (Figure 3a,b; Appendix S1: Tables S3, S4). We note this timepoint to emphasize the long-term effects of predator dispersal abilities and because it is also the time at which we sampled bacterial communities (see below). PS occupied 75% of target leaves in the PS+ treatment, and between 37% and 62% of the leaves in other treatments. In contrast, TA only occupied 50% of the leaves within the TA+ treatment and 12% of the leaves in other treatments. PS and TA abundances were different (df = 3, $\chi^2 = 21.6$, $p < 0.001$), but they were not significantly affected by the treatments (df = 3, $\chi^2 = 1.74$, $p = 0.169$), likely because of high variance within treatments (Figure 3b; Appendix S1: Table S4). The abundance of PS (averaging 6716.6 cells per ml) was consistently higher than TA (averaging 31.6 cells per ml) throughout all treatments. Based on the above, we calculated estimated biomass for each focal species and found equivalent magnitudes between species with 9.79×10^6 μm^3 for TA and 14.1×10^6 μm^3 for PS at the end of the experiment.

Bacterivore community profile

Bacterivore richness, evenness, and composition were unaffected by the neighbor treatments (Figure 3c–e). Bacterivore richness was between 0 and 5 species across all treatments and there were no significant effects of treatments ($F_{3,28} = 0.255$, $p = 0.857$). Bacterivore evenness was between 0 and 0.34 and there was a marginal effect of treatments ($F_{3,28} = 2.962$, $p = 0.051$). Treatments had a marginally nonsignificant effect on bacterivore composition (Figure 3e; perMANOVA, $F = 1.634$, $R^2 = 0.164$, $p = 0.051$). We performed this analysis again but removed those TA+ replicates that lacked TA to determine whether bacterivore diversity would respond to TA presence specifically. Although the richness of the TA+ treatment was higher in this analysis, there were still no significant differences among treatments (Figure S2a, $F_{3,28} = 1.213$, $p = 0.326$). Evenness patterns were significantly different among treatments (Figure S2b, $F_{3,28} = 3.598$, $p = 0.029$) and, although Tukey honestly significant difference (HSD) tests revealed no significant pairwise differences, the overall effect appears to be driven by differences between the Empty, Natural, and PS+ treatments. Because bacterivore diversity and composition at the end of the experiment were not clearly affected by the neighbor treatments, we focused the results on patterns for the protozoans PS and TA.

Bacterial community profile

Out of the 28 target leaf samples, bacterial community analysis was carried out on 25 samples, and we obtained a total of 844,419 reads with a mean of 30,905 reads per sample (Appendix S1: Section S2.3). Bacterial richness, evenness, and composition in our field samples differed from the original broth but we found no effect of our neighbor manipulation treatments. Bacteria had significantly higher richness and lower evenness than the original broth (Figure 4; Richness: $F_{4,23} = 9.514$, $p < 0.001$, Evenness: $F_{4,23} = 9.961$, $p < 0.001$). These diversity patterns were retained when we repeated our analysis by removing leaves from TA+ and PS+ treatments where TA or PS were absent, respectively (Appendix S1: Figure S3, Table S6), suggesting our treatment results are robust.

Similarly, bacterial communities from the field experiment were similar in composition across treatments but differed from the original broth (Figure 4c, perMANOVA: $F_{4,23} = 1.630$, $R^2 = 0.221$, $p = 0.001$). We removed samples from the original broth and repeated this analysis, confirming that there were no significant differences in composition among treatments ($F_{3,21} = 0.873$, $R^2 = 0.111$, $p = 0.817$; Figure S2). Lack of compositional effects was maintained when we conducted this analysis for a third time, now removing leaves from TA+ where TA was absent (Appendix S1: Figure S3). Likewise, there were no

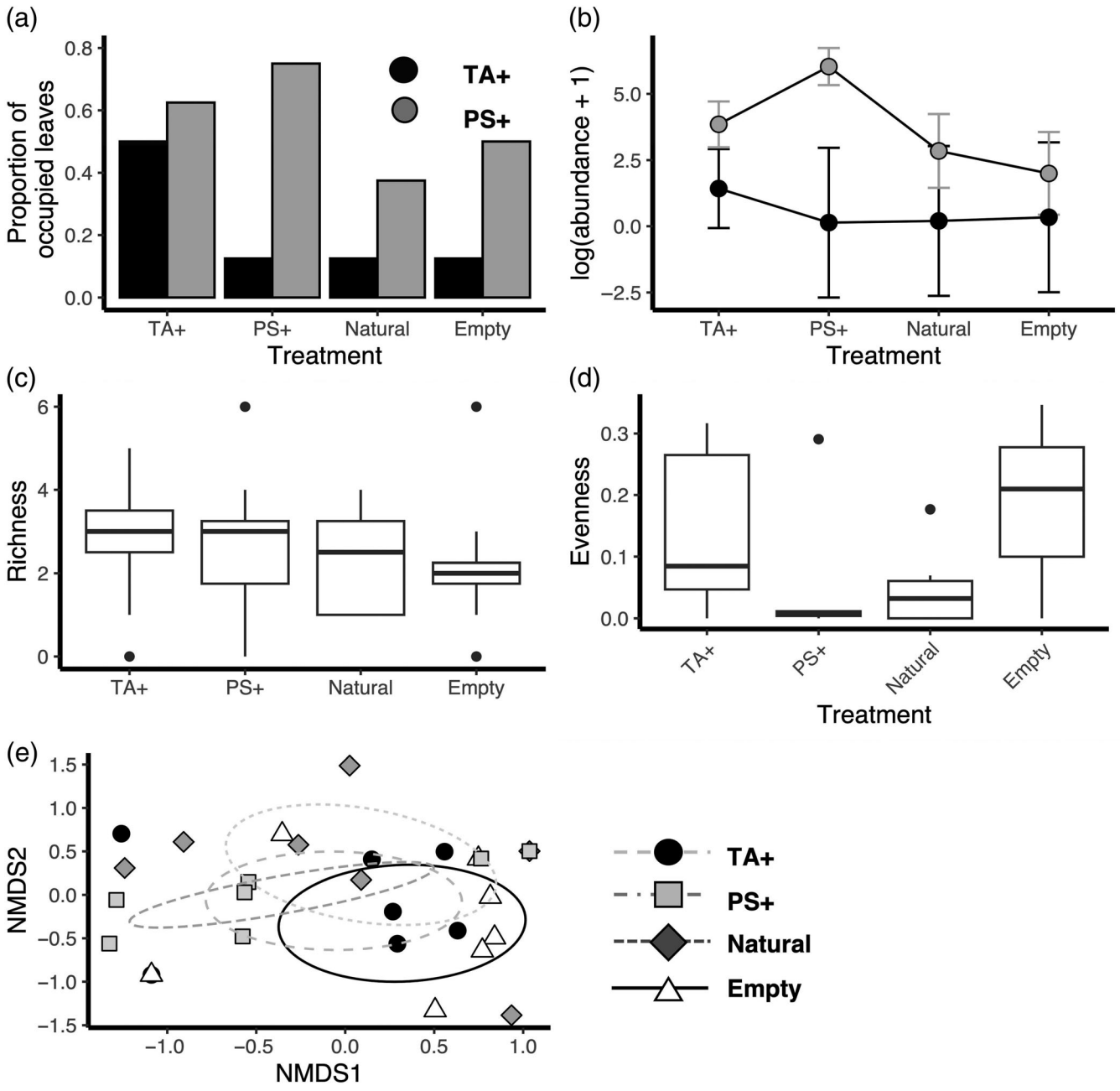

FIGURE 3 Effects of treatments on bacterivore distribution (a), abundance (b), diversity (c, d), and composition (e). Error bars in (b) indicate standard error. Ellipses in (e) indicate 95% confidence intervals. Non-Metric Multidimensional Scaling (NMDS) using two axes had a stress value of 0.149.

differences in community similarity across treatments ($F_{3,21} = 1.643$, $p = 0.213$). We did find significant effects of treatments on the abundance of eight taxa across ASV in this study, yet these differences were lost when calculating pairwise differences (Appendix S1: Figure S4, Table S7, available on the online repository: https://doi.org/10.5281/zenodo.7121355). Even though not significant, some trends did emerge with the ASV level data. For example, a *Sphingomonas* ASV was higher in the TA+ leaves. Second, ASVs identified as *Rhodopseudomonas*, *Paludibacterium*, and *Mesorhizobium* were higher in leaves under the Empty treatment. Last, ASV from Chitinophagaceae, *Paenarthrobacter*, and another *Sphingomonas* were particularly high in the broth samples. Although these responses of these taxa to predator colonization could have functional consequences for the pitcher plant (e.g., *Sphingomonas* as diverse carbon use and strong bacterial competitor, Chitinophagaceae as chitin degrader; Balkwill et al. 2003; Rosenberg, 2014), we will refrain from discussing this further in the context of this study given the weakness of these trends in our study. Overall, microbial communities and individual ASVs in the field did not exhibit patterns

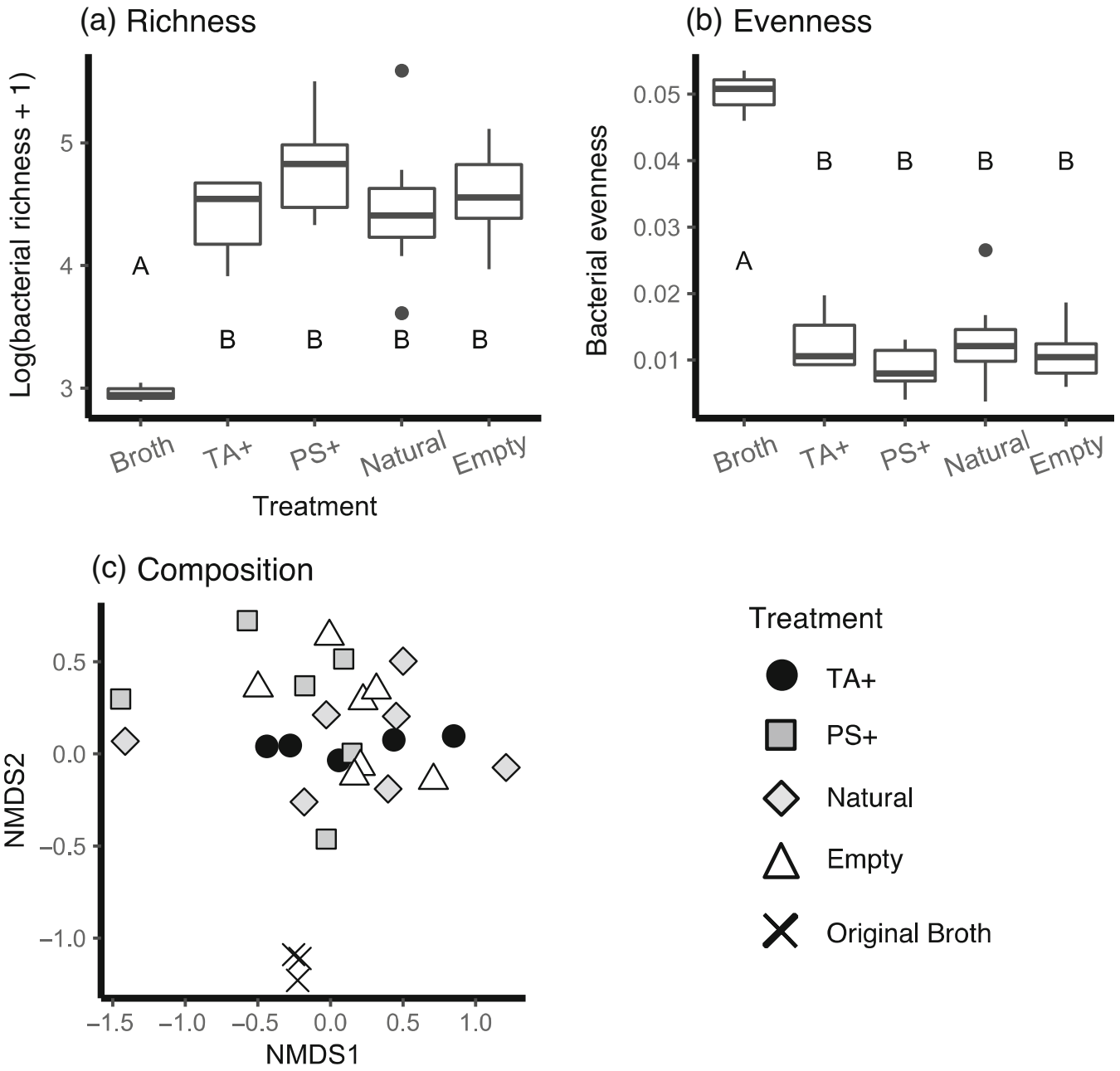

FIGURE 4 Effects of treatments on bacterial richness (a), evenness (b), and composition (c). Letters in (a) and (b) correspond to significant differences between groups as established with a Tukey honestly significant difference (HSD) test. Colors in (c) corresponds to labeling. Non-Metric Multidimensional Scaling (NMDS) with three axes in panel (c) had a stress value of 0.152.

related to our treatments, suggesting community structuring mechanisms other than predator distribution and dispersal limitation are at play.

DISCUSSION

The effects of predators in metacommunities depend on both their ability to disperse among and colonize local communities and their local effects on prey. We used a natural metacommunity to ask if two protozoan predators had different dispersal abilities and distinct effects on local prey communities. The larger ciliate *Tetrahymena* sp. (TA) was dispersal limited, resulting in a clumped distribution in natural populations of its host, *Sarracenia purpurea*. In contrast, the smaller flagellate *Poterioochromonas* sp. (PS) dispersed relatively quickly, both within leaves on the same plant and among plants, occupying most leaves in the field experiment and survey. Bacterial communities within pitcher plant leaves were unaffected by TA's clumped distribution, and potentially homogenized by PS selective feeding as it

successfully colonized most experimental leaves. However, because of its wide distribution, the effects of PS were indistinguishable from local and regional ecological processes that similarly affected all leaves. Therefore, whereas we detected differences in predator distribution resulting from differences in dispersal ability, we found no evidence of direct consequences for prey community diversity or composition. To our knowledge, this is the first study to test whether the variation in dispersal limitation among species of predators can have consequences for their prey in a metacommunity.

By incorporating space into Miller and terHorst (2012)'s analysis of succession in pitcher plants, we found patterns consistent with species-specific dispersal and colonization abilities (Figure 1; Appendix S1: Tables S1, S2). Moreover, our field experiment confirmed that PS was faster and more successful at colonizing leaves than TA (Figure 2; Appendix S1: Table S2). TA may be dispersal limited because it lacks a life history stage that facilitates dispersal, or its larger size may make it more difficult to take advantage of dispersal vectors, such as wind, water, or insects. In addition, TA may be excluded from newly opened leaves because of either (1) high abundance of mosquito larvae that preferentially prey on larger protozoa (Kneitel, 2012), (2) strong competitive interactions within a leaf (Cochran-Stafira & Von Ende, 1998; Kneitel & Miller, 2002), or (3) reduced growth rates due to the bacterial species present in the community (Khadempour et al., 2022). Hence, the distribution of a predator in space results from a combination of regional processes of dispersal and local processes that influence successful establishment (Mouquet & Loreau, 2003). Multiple predators may be able to co-exist regionally due to trade-offs between these regional and local scale traits such as tolerance to top-down drivers, dispersal ability, and competitive ability.

In our field experiment, other bacterivore species such as the rotifer, *Habrotrocha rosa*, and the protozoans *Colpoda* sp. (a ciliate) and *Bodo* sp. (a small flagellate) colonized the leaves, but their diversity and composition did not vary consistently across treatments (Figure 3). This result suggests that dispersal differences and occurrence patterns in the focal species (PS and TA) did not influence colonization dynamics or interactions with other bacterivores. This unexpected result contrasts with TA's strong competitive abilities in laboratory microcosms (Miller et al., 2022), yet confirms previous work showing no trade-offs between colonization and competitive abilities (Kneitel, 2012). These results also echo trends in plant communities, suggesting that dispersal limitation can play a minor role in species regional coexistence in diverse assemblages (Brewer et al., 1998; Coomes et al., 2002). Lack of variation in bacterivore diversity in our experiment also indicates sufficient equivalency in local conditions among target leaves in our field experiment, as well as homogeneous colonization from nonfocal species across the field (Figure 3c,d). Therefore, the major difference between our target leaves is the presence or absence of TA driven by our treatments.

Bacterial community diversity and composition within our target leaves at day 28 were not explained by bacterivore diversity. More importantly, bacterial richness and evenness were unaffected by the presence of TA (Figure 4, Appendix S1: Figure S2, Table S6). This result coincides with the weak predatory effects found by Canter and collaborators (2018) in microcosm experiments with TA. One simple explanation is that this focal species has feeding behaviors that are similar to co-occurring bacterivores and thus have redundant ecological roles. An alternative explanation is that TA is a generalist feeder, reducing the abundance, yet not changing the composition of its bacterial prey. Furthermore, TA's abundance in the field was lower than five other bacterivore species (Figure S1) and lower than greenhouse experiments focusing on predatory effects (Canter et al., 2018), suggesting that, even when present, TA's effect may be weak due to low abundance. Therefore, TA's dispersal limitation resulted in its clustered occurrence but was inconsequential for other members of the community, including those within TA's trophic level and their prey.

This finding, suggesting no effects of predator dispersal on prey communities, contrasts with the few studies that correlate predator dispersal with prey abundance and distributions. For example, Wieters et al. (2008) demonstrated that predators with pelagic larvae were uncorrelated with prey abundance or recruitment whereas those lacking broadcast larvae correlated with prey recruitment. Perhaps predator dispersal limitation plays important roles in communities where predators are locally abundant and have stronger effects in structuring community assembly across trophic levels, often termed keystone effects (Paine, 1969). There is ample evidence of keystone predators (Davic, 2003; Paine, 1969) but little consideration of their dispersal abilities (Amarasekare, 2008b), suggesting an open question remains regarding a relationship between the effect of a species on other community members and traits related to dispersal and colonization.

PS exhibited high dispersal abilities, colonizing the majority of our target leaves (Figures 1,2), reaching high abundances compared with other members of the bacterivore guild (Figures 1,2, S1), and potentially generating a homogenizing effect on the bacterial communities. In fact, in laboratory experiments, PS predation had significant effects on bacterial community composition

acting as a keystone predator (Canter et al., 2018), thus possibly representing a predator with strong dispersal abilities and predatory effects. However, in this study, the homogenizing effects of PS predation are indistinguishable from local and regional ecological processes that similarly affect all leaves. Specifically, there are three potential homogenizing mechanisms. First, all leaves were equally colonized by other bacterivores that may exert top-down control on bacteria. We showed that our treatments had no effect on the overall bacterivore diversity or composition (Figure 3), indicating that members of this trophic level can disperse well, even if TA cannot. Second, similar resource levels across leaves can result in an equivalent bottom-up control. In our experiment, target leaves began with the same original broth and did not capture any further insects for the duration of the experiment, suggesting low nutrient levels may be an important driver for the bacterial community. Third, equivalent influx of bacterial colonists can result in strong regional influences on bacterial communities within leaves. All our leaves were open to immigration of bacteria from the nearby habitats, resulting in a general increase in diversity and decrease in evenness when comparing the original broth to the field samples after 28 days (Figure 4). To fully identify the effects of a predator with broad dispersal, studies require an experimental design that includes sites that exclude such predator. Although predator exclusion experiments are used often in ecology (Gurevitch et al., 2000), to our knowledge, it has not been implemented in the study of predators with different dispersal abilities and their effects on prey communities.

Whether bacterial communities in our experiment are homogenized via colonization of non-TA bacterivores or bacteria (regional influence), common predators (top-down), or equivalent resources (bottom-up) is difficult to ascertain here, yet our findings can shed light on the influence of dispersal on pitcher plant bacteria and other ephemerous communities. Regardless of the main driver of bacterial community composition in our field experiment, we showed that the differential dispersal by major bacterivore protozoans (TA and PS) had no consequences for bacterial communities. In natural conditions, the bacterial community likely follows a successional shift from bottom-up drivers in early leaves to top-down drivers in older leaves (Miller & terHorst, 2012), even if some protozoans take longer to arrive to new leaves. Therefore, dispersal differences between protozoan species may instead influence the successional increase in protozoan diversity (Miller & terHorst, 2012) as poor disperser species, such as TA, take time to arrive and accumulate over time. In *S. purpurea* pitcher plants, bacterivore species richness increases over time, decreasing bacterial richness (Cuellar-Gempeler et al., in preparation) but potentially contributing to bacterial evenness (Canter et al., 2018). The role of dispersal limitation in driving successional processes is rarely considered when studying ephemerous habitats like pitcher plants and could have stabilizing effects on trophic dynamics (Anderson & Fahimipour, 2021). Although our understanding of these stabilizing effects has advanced via theoretical models (Gross et al., 2020), field and laboratory experiments such as ours are critical to fully integrate trophic dynamics in the metacommunity literature.

In this study, we aimed to link variation in dispersal abilities to community dynamics across trophic levels. Our findings suggest that variation in predator dispersal can create heterogeneity in predation intensity across a landscape, yet prey communities were unresponsive to this heterogeneity. Well dispersed bacterivores and equivalent local conditions had stronger homogenizing effects on the bacterial community. Although other trait trade-offs in pitcher plant protozoans have been previously shown (Kneitel, 2012), trophic interactions have seldom been associated with dispersal abilities or competitive effects, and we argue that a thorough understanding of species coexistence and resource use across space may further explain these pitcher plant inquiline community dynamics.

Beyond pitcher plant microbes, clustered predators could become strong drivers of prey community heterogeneity if they were specialists or keystone predators, or if they exerted a dominant influence on other predators. Thus, outcomes of trophic dynamics in metacommunities can differ based on the relationship between dispersal ability and each predator's effect on their prey. Importantly, a large portion of the metacommunity literature relies on artificial dispersal treatments that assume equal dispersal abilities across species (i.e., Logue et al., 2011), thus obscuring the potential effects of differential dispersal. In those studies where differential dispersal is considered, the role of dispersal ability of the prey is typically the focus (Amarasekare, 2008b; Howeth & Leibold, 2010). To overcome these limitations, future work should explicitly address multipredator dispersal abilities and its consequences for prey communities. Incorporating the variation of dispersal ability onto our understanding of trophic dynamics in spatially explicit systems may improve our ability to predict regional coexistence and identify scenarios with stable trophic dynamics.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The resulting sequences are available in the NCBI Sequence Read Archive (SRA) under accession no. PRJNA885239 at https://www.ncbi.nlm.nih.gov/bioproject/PRJNA885239/. Count data (Cuellar-Gempeler, 2022) are available in Zenodo at https://doi.org/10.5281/zenodo.7121355.

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SUPPORTING INFORMATION

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

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