COMMUNITY ECOLOGY - ORIGINAL RESEARCH

Testing successional hypotheses of stability, heterogeneity, and diversity in pitcher-plant inquiline communities

Thomas E. Miller · Casey P. terHorst

Abstract Succession is a foundation concept in ecology that describes changes in species composition through time, yet many successional patterns have not been thoroughly investigated. We highlight three hypotheses about succession that are often not clearly stated or tested: (1) individual communities become more stable over time, (2) replicate communities become more similar over time, and (3) diversity peaks at mid-succession. Testing general patterns of succession requires estimates of variation in trajectories within and among replicate communities. We followed replicate aquatic communities found within leaves of purple pitcher plants (*Sarracenia purpurea*) to test these three hypotheses. We found that stability of individual communities initially decreased, but then increased in older communities. Predation was highest in younger leaves but then declined, while competition was likely strongest in older leaves, as resources declined through time. Higher levels of predation and competition corresponded with periods of higher stability. As predicted, heterogeneity among communities decreased with age, suggesting that communities became more similar over time. Changes in diversity depended on trophic level. The diversity of bacteria slightly declined over time, but the diversity of consumers of bacteria increased linearly and strongly throughout succession. We suggest that studies need to focus on the variety of environmental drivers of succession, which are likely to vary through time and across habitats.

Keywords Climax · Community assembly · Protozoa · Resources · Seres

Communicated by Jonathan Shurin.

T. E. Miller (✉) · C. P. terHorst
Department of Biological Science, Florida State University, Tallahassee, FL 32306-4295, USA
e-mail: miller@bio.fsu.edu

Present Address:
C. P. terHorst
Kellogg Biological Station, Michigan State University,
3700 E. Gull Lake Drive, Hickory Corners, MI 49060, USA

Introduction

Ecological succession, the progressive change in species composition in a community through time, is a foundation concept in ecology, illustrating the interplay among disturbance, colonization, competition, and facilitation. Early work by Cowles (1899), Gleason (1926), and Clements (1936) initiated a century of research which viewed succession as a common phenomenon in which a community changes through a predictable series of successional states toward a stable climax community. Despite its inclusion in most basic ecology textbooks, succession remains a frustrating concept for many ecologists. Some argue that succession depends on context and therefore follows no consistent patterns and no general theory (e.g., McIntosh 1999; Walker and del Moral 2003). Others argue that consistent and identifiable mechanisms operate during succession (e.g., Connell and Slatyer 1977) producing predictable community-level patterns (e.g., Pickett et al. 1987). One explanation for this incongruity is that successional hypotheses are seldom clearly stated and tested.

We argue for three general expectations for succession that can be stated as hypotheses. The first is common to most successional work: communities progress toward

some climax state that is defined by stability, although multiple stable states may be possible (Lewontin 1969). Mechanistically, stability may result from an increase in community complexity through successional time (Neutel et al. 2007). Within-community stability should therefore increase as a community progresses through a series of successional states, although disturbance may reset succession to an earlier state and prevent communities from ever reaching a climax state (Connell 1978). Here, we define more stable communities as those with lower variances in the composition and abundances of species between time periods, and we predict that stability should increase through succession.

Second, if all communities approach the same climax state, then we hypothesize that heterogeneity (i.e., beta-diversity) among communities should decrease over successional time. Stochastic colonization is hypothesized to initially drive community structure in early successional states, resulting in initially heterogeneous communities (Margalef 1968). If each community progresses towards the same climax state, heterogeneity should decline over time (Margalef 1963, 1968). Alternatively, priority effects or local conditions may be important and might promote continuing heterogeneity among communities (Egler 1954). Empirical studies of heterogeneity through successional time have produced equivocal results; some have revealed a decrease in heterogeneity through time (e.g., Wassenaar et al. 2005; del Moral 2009), whereas others have demonstrated an increase in heterogeneity or lack of convergence through time (Facelli and D'Angela 1990; Myster and Walker 1997; Blatt et al. 2005). Nonlinear patterns in heterogeneity are also possible: Christensen and Peet (1984) found a decrease in heterogeneity from early to intermediate successional stages, followed by an increase in older communities.

Third, species diversity is hypothesized to increase initially as species accumulate in new areas (Margalef 1963; Odum 1969). This hypothesis relies on an assumption of a trade-off in species traits, such as colonization and competitive ability, although other trade-offs can support the same hypothesis. For example, when primary space opens, it is likely to be colonized by an assortment of species but should be dominated by species that are good colonizers, but poor competitors. Diversity is hypothesized to increase as more species accumulate through migration but then decrease through successional time as less successful competitors are eliminated (Odum 1969). Diversity may feedback on succession, as an increase in diversity may push communities towards a climax by preventing further colonization by weedy species (Van der Putten et al. 2000). As species consume available resources, the early colonizing species should gradually give way to species that are stronger competitors, such that late successional communities are dominated by strong competitors. A balance between good colonizers and good competitors is predicted to result in a mid-successional peak in diversity (Eggeling 1947; Connell 1978; Tilman 1985).

Replicated examples of successional sequences are needed to test these three predictions about community structure during succession. As succession progresses, (1) stability within a community increases, (2) heterogeneity among communities decreases, and (3) diversity peaks during intermediate stages. The ability to detect such patterns requires examining significant numbers of complete successional sequences, but because of the temporal scales required to track successional sequences in most communities, few data meet these criteria.

Most data on successional patterns come from one of three sources. Many examples of succession use species-abundance data from different locations that presumably represent different successional states, or chronosequences (e.g., shifting sand dunes, Cowles 1899; intertidal boulder fields, Sousa 1979; abandoned agricultural fields, Kardol et al. 2006). Chronosequences are based on the assumption that changes in space reflect changes in time, but this assumption is only valid with unchanging biotic and abiotic conditions (Johnson and Miyanishi 2008; but see Foster and Tilman 2000). Second, microcosm studies of protists or zooplankton (e.g., Drake 1991; Warren et al. 2003; Cadotte and Fukami 2005) have provided important insights into patterns of community assembly, but these studies have been limited to controlled laboratory settings without disturbance or natural dispersal and cannot mimic natural conditions. Finally, studies following primary or secondary succession directly through recolonization of disturbed areas (e.g., del Moral 2009; Kuiters et al. 2009) provide the best examples of succession in natural communities. Although these studies have provided important insights into successional processes, they usually suffer from insufficient duration and low replication and rarely, if ever, follow succession in more than a guild of species. Although many of the studies using the methods described above are useful for describing some aspect of succession within systems in which complete successional sequences are impossible to attain, they fall short of being able to reliably test the three predictions above.

Thus, despite its seminal role in ecology, ecologists have little documentation of the mean or, perhaps more importantly, the variance in patterns of succession, even within single systems. In the work reported here, we studied succession within natural microcosms—the communities found within the water-filled leaves of the carnivorous pitcher plant *Sarracenia purpurea*. This system allows us to study replicated seres of natural communities, following species at all trophic levels to test the three predictions described above.

Materials and methods

Species interactions in the inquiline community found in the water-filled leaves of the purple pitcher plant (*S. purpurea*) have been well described (e.g., by Addicott 1974; Miller and Kneitel 2005), but little is known about succession in this community (but see Fish and Hall 1978). The host plant is widely distributed, extending from northern Florida in the United States to the Northwest Territories in Canada, and the community is representative of a variety of other natural microcosm communities (Srivastava et al. 2004). Plants generally have 4–12 cup-shaped leaves that fill with rainwater and use nectar to attract insect prey, primarily ants. The insects drown in the water, and this captured energy serves as the basis for a community of bacterial decomposers and bacterivorous mites (*Sarraceniopus gibsonii*), protozoa, and rotifers (esp. *Habrotrocha rosa*). The community also includes a specialist mosquito (*Wyeomyia smithii*) that consumes protozoa and rotifers, a specialist detritivorous midge (*Metriocnemus knabi*), and an omnivorous flesh fly (*Fletcherimyia fletcheri*). These communities rarely persist for more than a year, and complete successional sequences can be followed over the entire "lifetime" of a community.

Our study was conducted from 2004 through 2006 in a 20×20 m plot in a small pine savanna in the western portion of the Apalachicola National Forest in northwest Florida. Throughout 2004, the 267 plants in the plot were surveyed for new leaves every 2 weeks. Each month, 10 randomly chosen new leaves on separate plants were chosen and then censused biweekly until they no longer contained water. In each sampling period, the entire contents of each marked leaf were gently mixed, removed, and censused, and the abundances of all species in the community were recorded. The contents were then returned to their original host leaf, usually after less than 10 min. This sampling method may disturb the community by suspending sediments and insect parts in the bottom of the leaf; however, preliminary experiments found no change in bacterial abundances in sampled and unsampled leaves (T. Miller, unpublished data) and we believe the disturbance was minimal.

The prey items captured by the leaf and the larger organisms (e.g., mosquitoes, midges, mites) were counted in the field under a dissecting microscope at $\times 10$–40, using sterile equipment and aseptic methods. A 1-mL sample from each leaf was retained in a microcentrifuge tube on ice and transported to the laboratory for estimation of the abundances of smaller organisms. A 0.1-mL sample from each tube was placed on a Palmer counting cell, and abundances of all organisms (mostly protozoa and rotifers) were measured under a phase-contrast microscope at $\times 100$. Bacterial abundances were estimated from 0.05 mL of each sample diluted to 10^{-3} and 10^{-5} and then spread on plates with an LB agar medium. After 48 h of incubation in a growth chamber at 30 °C, bacterial colonies were counted by morphotypes based on colony size, color, and texture. In total, we identified 46 different colony morphotypes.

Quantification of bacterial abundance and diversity is challenging, as all methods have limitations. For example, many bacterial species are not culturable on agar media, whereas direct counts cannot distinguish live from dead cells or generally differentiate among types. Although the agar plate count method we used considerably underestimates both the total number of cells and the diversity of the bacterial community, it appears to be informative about community processes; for instance, Kneitel and Miller (2002) found that, as expected, the addition of dead ants to leaves resulted in increased bacterial abundance. The methodological limitations should be acknowledged in the interpretation of any study for bacterial communities; the patterns observed from our study represent only a subset of the entire bacterial community.

We used regression to determine whether the abundance of organisms in each trophic level (mosquitoes, bacterivores, bacteria, midges, ants) changed with successional age. Since data from each leaf age were not independent, we fit an Auto Regressive Integrated Moving Average (ARIMA) model for each variable to account for autocorrelation among data points, using "proc arima" in SAS (v.9.1; SAS Institute, Cary, NC, USA, 2002–2003) and performed linear and non-linear regressions within the best-fit (lowest AIC value) ARIMA model.

We used correspondence analysis (CA) in CANOCO 4.5 (ter Braak and Smilauer 2002) to compare community composition among leaves and through time. CA is a direct ordination technique that, relative to other multivariate techniques like principal components analysis, is more appropriate for analyzing the unimodal responses of many of our species. Rare species often have undue influence on CA results, so we did not use species present in fewer than 3 % of samples, but including rare species did not qualitatively change the results. Abundances of all species were transformed as $\ln(x + 1)$ before analysis. We then determined correlations between the CA axes and five environmental variables: the month of leaf opening, age of the community, the number of ants captured, other prey captured, and water volume.

We analyzed the change in three aspects of community structure with leaf age: stability, heterogeneity, and diversity. To determine community stability, we used the scores of the first and second CA axes to calculate the change in a community between successive 2-week time steps for each individual leaf. The average of the absolute value of biweekly change in each axis score (weighted by the % variance explained of that axis) was used as an

estimate of the change in community structure and an inverse measure of stability. To determine heterogeneity among communities, we used the average of the ln-transformed weights of all samples in each time step in the CA analysis (i.e., the distance of each sample from the centroid). Larger weights of samples represent more dispersion in CA space; smaller values indicate more similar communities. We estimated community diversity at each time step, by means of the Shannon–Wiener index (H′), separately for bacteria) and bacteriovores. For each variable (stability, heterogeneity, diversity), we performed linear and nonlinear regressions within the best-fit ARIMA model to test for a change in the variable with successional age. If the difference in AIC values between linear and non-linear fits (ΔAIC) was >2, we considered the lower value a significantly better fit. In cases where ΔAIC was <2, we used the linear fit. In addition, we used a repeated-measures ANOVA to test for an effect of month of opening on each variable over time (JMP v.4.0.4).

Results

In this northern Florida population, *S. purpurea* produces very few new leaves during winter months (January–March). During the remaining months, leaves were produced at a rate of approximately one leaf per plant per month. A few leaves held water for up to 18 months, but community life span could be as short as a few weeks. The most common causes for leaves to lose water included holes made by herbivorous grasshoppers and attacks by lepidopteran larvae that skeletonize the leaf (especially *Exyra fax*; Atwater et al. 2006). Communities have a Type I survivorship curve, in which leaf mortality is highest in older leaves, with a median life span of 40 weeks.

The successional patterns were fairly consistent across leaves. Ants were primarily captured by young leaves, resulting in high nutrient inputs to the community early in succession. Ant abundance peaked in 3-week-old communities and then declined significantly, as very few ants were captured in leaves older than 10 weeks (Fig. 1e). Other prey such as spiders and grasshoppers were rare and captured stochastically throughout a leaf's life span, showing no pattern with leaf age. The density of bacteria (based on agar plate counts) closely tracked the input of resources into the leaf. Bacterial densities peaked at 5 weeks and then declined with leaf age (Fig. 1d). Total bacterivore density (all protozoa + rotifers) showed a peak in abundance at intermediate ages (Fig. 1c), but different species showed different patterns with leaf age (Fig. 2). The abundance of mosquito larvae was highest in the youngest leaves and then declined significantly as larvae either died or eclosed and flew away from the community (Fig. 1b).
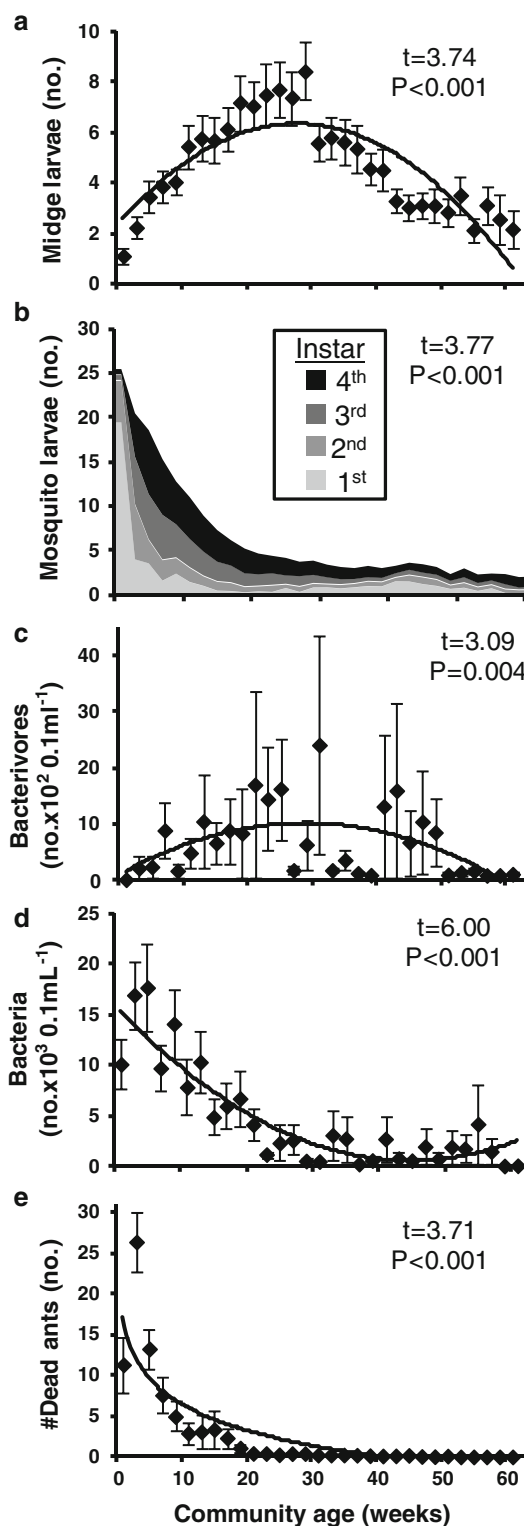

Fig. 1 Abundance of organisms in each trophic level as the community aged from 0 to 60 weeks: **a** midge larvae, **b** mosquito larvae (1st–4th instar), **c** bacterivores, **d** bacteria, and **e** dead ants, mean ± SE. Non-linear parameters (*t* values shown) were significant and fit the data better than linear models in each case
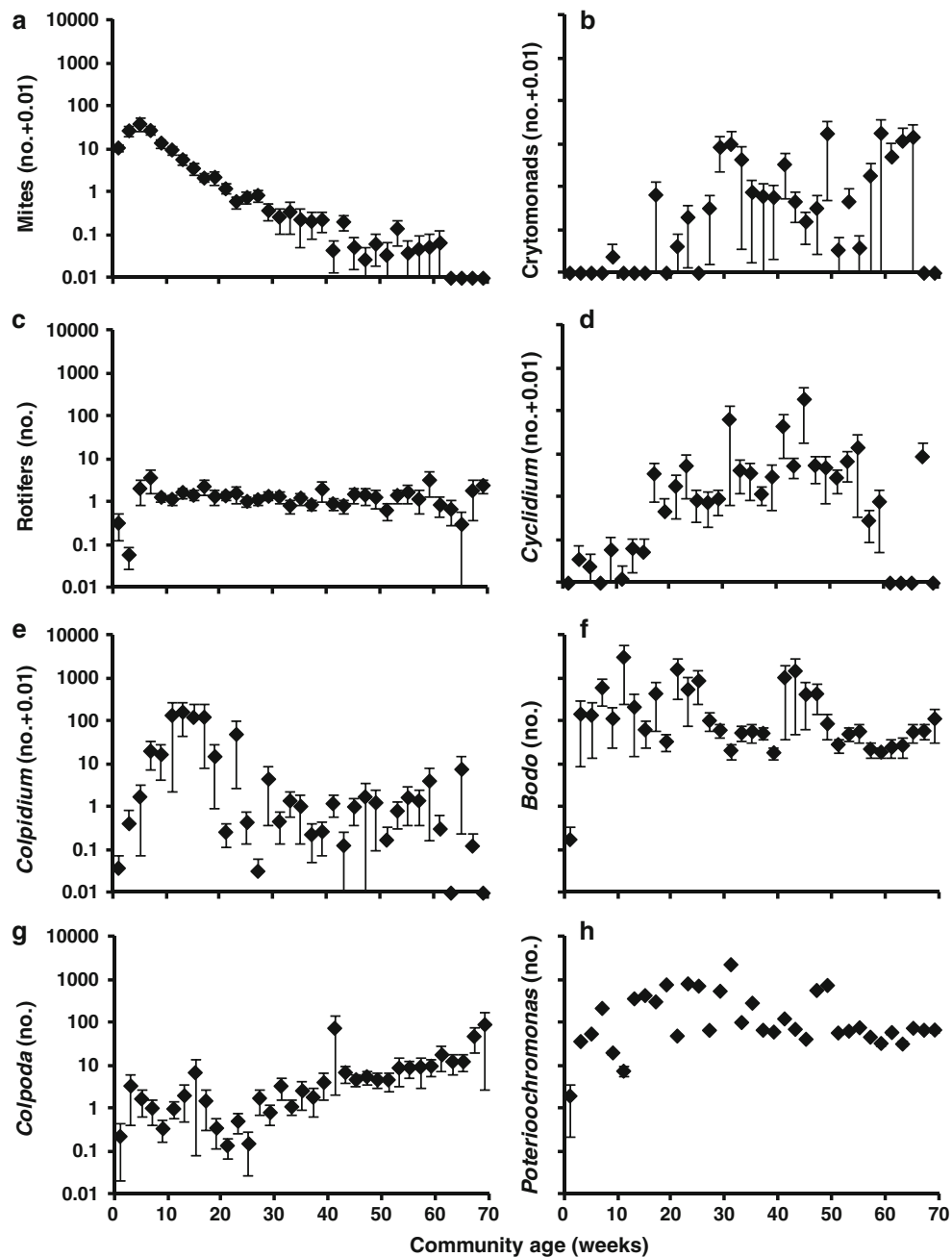
Fig. 2 Bacteriovores (mean number per 0.1 mL ± SE) in the community as a function of community age, arranged in order of decreasing body size. Note that the abundances are ln-transformed and the y-axes are on different scales

The abundance of midges peaked in 20- to 30-week-old leaves and declined thereafter (Fig. 1a). Flesh flies were typically rare in our communities (<0.04 per leaf) but peaked in abundance in 1- and 3-week-old leaves (0.11 per leaf) and declined thereafter.

The first two CA axes explained 28 % of the variation in the species data (CA1: 18 %; CA2: 10 %). Community age explained more variation in the samples than any other environmental variable, with a weight more than twice as high as the next most explanatory variable—

water volume (Fig. 3). Stability (as measured by a lack of change in community structure between sample times) changed with the successional age of the community (Fig. 4; $t = 4.97$, $P < 0.001$); the polynomial fit was significantly better than the linear fit (ΔAIC 8.12). Thus, stability was highest in young and old communities; communities changed most at an intermediate age of approximately 40 weeks. Month of leaf opening did not affect the change in community structure over time ($F_{45,58} = 0.67$, $P = 0.92$).
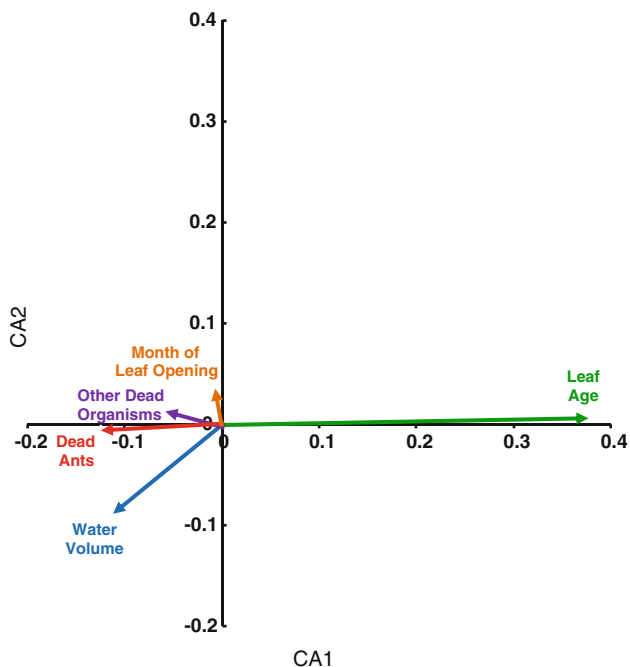
Fig. 3 The weights of five environmental variables on CA1 (*x*-axis) and CA2 (*y*-axis): leaf age, water volume, dead ants, other dead organisms, and month of leaf opening. Length of the *arrow* is proportional to the variance explained by each variable
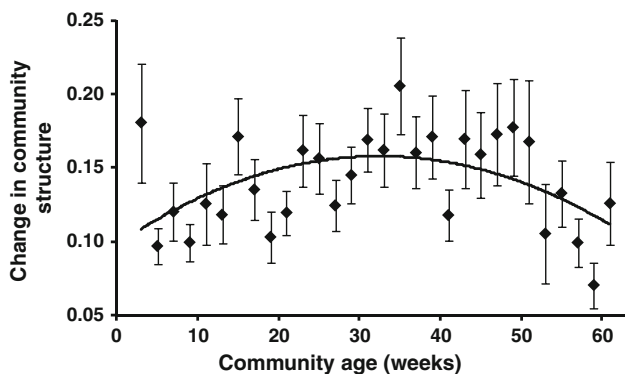

Fig. 4 The absolute value of the change in community structure, represented by the weighted average of the first two correspondence analysis (CA) axis scores over the age of the community (mean ± SE)

Fig. 5 Heterogeneity (mean ± SE) estimated as the average distance of each community from the CA centroid for that age as the community aged from 0 to 60 weeks

Fig. 6 Diversity (Shannon–Wiener index, mean ± SE) of **a** bacteria and **b** bacterivores as a function of community age. Bacterial diversity marginally declined with leaf age ($t = 1.73$, $P = 0.095$), while bacterivores increased significantly with community age ($t = 10.4$, $P < 0.001$)

Among-leaf heterogeneity decreased significantly with leaf age (Fig. 5; $t = 7.04$, $P < 0.001$), indicating that communities became more similar over time. There was no significant difference between linear and non-linear fits (ΔAIC 1.1). The month in which a leaf opened had no effect on the change in heterogeneity over time ($F_{30,30} = 0.99$, $P = 0.50$).

Patterns of diversity across community age depended on trophic level. Bacterial diversity marginally declined with leaf age (Fig. 6a; $t = 1.73$, $P = 0.095$), while the diversity of bacterivores increased strongly and significantly with
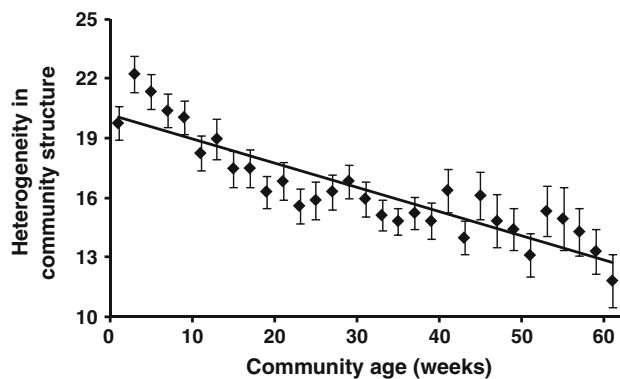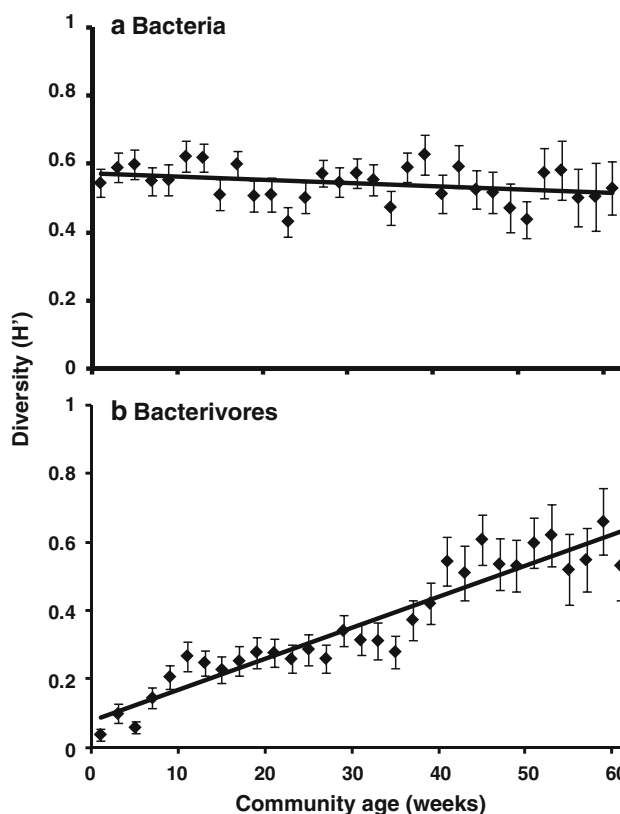
community age (Fig. 6b; $t = 10.4$, $P < 0.001$). In both cases, there was no significant difference in the fit of linear and non-linear models (bacteria: ΔAIC 1.9; bacterivores: ΔAIC 1.3). The month in which a leaf opened had no significant effect on how diversity at either trophic level changed with succession (bacteria: $F_{31,27} = 1.23$, $P = 0.29$; bacterivores: $F_{30,26} = 1.02$, $P = 0.48$).

Discussion

Succession is a dominant paradigm in ecology yet has seldom been documented in a detailed, replicated manner sufficient for hypothesis testing. Using the small aquatic communities in pitcher-plant leaves, we found significant changes in stability, heterogeneity, and diversity over successional time, but these changes did not always match our predictions.

The expected top-down and bottom-up drivers of community structure in this system, namely predation by mosquito larvae and resources in the form of dead insects (e.g., Kneitel and Miller 2002; Hoekman 2011), changed dramatically with the age of the community within a pitcher-plant leaf (Fig. 1). Despite considerable differences in climate between northern Florida and Massachusetts, the patterns shown in Fig. 1 are very similar to patterns observed in pitcher plants in the northeastern United States (Fish and Hall 1978). The number of predators (mosquito larvae) was greatest in young communities but, by 9 weeks, had fallen to less than half of peak abundance (Fig. 1b), which is likely to have reduced the predation pressure on protozoa and rotifers over this period. First instar larvae were most abundant in young leaves, but the remaining larvae in older communities tended to be fourth instar larvae (Fig. 1b). Bottom-up forces also changed over this period; dead ants were most abundant in young leaves and had decreased by nearly an order of magnitude in 11-week-old communities (Fig. 1e).

The strength of these top-down and bottom-up forces was probably driven by both extrinsic and intrinsic factors. At the bottom, pitcher-plant leaves produce nectar that attracts ants to the leaf (Bennett and Ellison 2009), but nectar production declines rapidly with leaf age (K. Reuter, unpublished data). Older leaves continue to act as pitfall traps for other insects, garnering low but highly variable resource input in older leaves. At the top, mosquito larval abundance is largely driven by adult oviposition behavior. Adult mosquitoes preferentially oviposit in young leaves, laying virtually no eggs in leaves older than a few weeks (Fish and Hall 1978; Miller and Kneitel 2005). However, this oviposition behavior may be stimulated by resource levels, as adult mosquitoes preferentially oviposit in leaves with an intermediate number of ants (Hoekman et al. 2007). The decline in the number of predators over time resulted from the lack of further oviposition and the development of larvae into adults over the course of weeks to months, depending on food availability (Bradshaw and Johnson 1995). The variance in both top-down and bottom-up drivers of community structure over successional time underscores the importance of understanding how successional dynamics at one trophic level alter dynamics at other trophic levels.

A long-held hypothesis about ecological succession is that dynamics are controlled from the bottom up by resource levels (Lindeman 1942; Odum 1969; Tilman 1985). The mechanisms by which top-down forces (predation) can stabilize communities have been demonstrated in a variety of natural communities (e.g., Paine 1966; Schmitz et al. 2004), but virtually nothing is known about how these controlling forces change over successional time. Although several studies document the effect of predators or resources on successional patterns (e.g., Hixon and Brostoff 1996; Olito and Fukami 2009; Nelson and Craig 2011), the ways in which succession in one trophic level interacts with succession in another is not clear. The successional models of Connell and Slatyer (1977), for example, might predict that predators will alter succession of prey, but these models do not address how that succession of prey will in turn inhibit particular predators. Previously, few data were available with which to evaluate the strength of top-down and bottom-up forces during succession (but see Schmitz et al. 2006). Our results confirm that simultaneous changes in top-down and bottom-up forces can interact to affect successional pathways.

These strong changes in top-down and bottom-up drivers of community structure with community age might also affect that stability of communities during succession. We predicted that communities that approach a stable climax should become more stable (i.e., show a decrease in the change in community structure over time). This was not the case in these inquiline communities, where the rate of change in community structure initially increased with time, demonstrating an initial decrease in stability with successional time (Fig. 4). However, after a peak in the rate of change at about 40 weeks into succession, communities began to increase in stability (Fig. 4). Predation can alter successional trajectories (e.g., Olito and Fukami 2009) and the decline in predation may have caused the initial decrease in stability. The decline in predation cannot explain the increase in stability in older communities though, since mosquitoes are rare in communities more than 20 weeks old (Fig. 1b). However, the decline in resources, accompanied by an increase in consumer abundance and richness (Figs. 1, 5), may result in increased competition in older communities. Stability may arise from more diffuse competition in species-rich older communities (Pianka 1974; Chesson 2000).

Despite the change in stability, the heterogeneity among replicate communities decreased with community age, as predicted, indicating that communities became more similar over successional time (Fig. 5). This result is expected of communities converging on a similar climax community. The existence of a climax state allows for predictions about both stability and heterogeneity, but our results highlight that stability and heterogeneity can be independent of one

another. This independence is particularly important for detecting alternate stable communities (sensu Lewontin 1969), where both heterogeneity and stability must be considered in the detection of multiple climax states. Replicated and complete successional sequences, such as those from these pitcher-plant communities, are required for evaluation not only of the average successional pathway but also of the variance in those pathways.

The strong patterns in predation and resource levels with community age (Fig. 1), along with a trade-off between predator tolerance and competitive ability associated with differences in size among bacterivorous species (Kneitel 2002; Leibold and Miller 2004) suggest that predator-tolerant species should be most successful in young communities, whereas strong competitors should be most successful in older communities. Densities of the largest bacterivorous species, such as mites, rotifers (*Habrotrocha rosa*), and *Colpidium* sp., peaked in young communities when predation pressure was strongest and began to decline as resources declined (Fig. 2). Intermediate-sized species, such as *Colpoda*, *Cyclidium*, and cryptomonads, were not abundant when predators were present but increased with declining resources (Fig. 2). The abundances of the smallest bacterivorous species, *Bodo* and *Poterioochromonas*, changed little over successional time (Fig. 2). Despite patterns of change in individual species that are consistent with a mid-successional peak in diversity, we found no evidence for such a pattern, as bacterivore diversity increased throughout succession (Fig. 6b). This result suggests that competitive exclusion of consumer species was rare and that pitcher-plant leaves accumulated more and more species as the leaf aged.

Bacterial diversity declined slightly over time, although this pattern was only marginally significant (Fig. 6a). This is surprising, as we might expect that a decline in resources over succession would result in lower bacterial diversity. However, it is important to interpret this result with caution, as our method of quantifying bacterial diversity using morphotype growth on agar plates is crude and underestimates the number of species in the community. Additionally, the biweekly removal of fluid from the pitcher plant may have disturbed the bacterial species. If disturbance maintains diversity (e.g., Eggeling 1947; Connell 1978), our sampling regime may have influenced the static pattern in bacterial diversity over time.

Finally, our successional sequences may be too long to interpret as such. Because most of the resources (dead prey) come into this community in the first few weeks, most of the successional processes may occur only during the earliest part of life of the individual pitcher plant leaf. An alternate view is that the long-term patterns we observe are due to ecosystem retrogression, which can occur when nutrients are depleted or reduced in the absence of a rejuvenating disturbance (Peltzer et al. 2010). The pitcher-plant inquiline community is similar to other detritus-based communities, such as insect communities on carrion or leaf-litter communities, in that a large peak in resources early in succession is followed by a rapid decline of the basal resource in the community that is likely to affect community structure and successional patterns. We would argue against these views, simply because pitcher-plant communities at 60 weeks are still changing (Figs. 4, 6b), even as the host leaves are dying. Instead, we suggest that, collectively, these views illustrate that different successional patterns need to be interpreted in light of strong drivers, such as resource and top-predator availability.

The classic predictions about diversity over successional time (see, e.g., Eggeling 1947; Connell 1978) generally do not consider how changes at one trophic level are affected by changes at other trophic levels. During primary succession, changes occur at all trophic levels and are likely to influence dynamics at other trophic levels (Quesada et al. 2009). Although resource availability and competition might be important for determining bacterivore diversity, declining abundances of predators might be equally or even more important. Future successional models should incorporate these complex and dynamic interactions among trophic levels during future attempts to predict community-wide patterns.

References

Addicott JF (1974) Predation and prey community structure: an experimental study of the effect of mosquito larvae on the protozoan communities of pitcher plants. Ecology 55:475–492

Atwater DZ, Butler JL, Ellison AM (2006) Spatial distribution and impacts of moth herbivory on northern pitcher plants. Northeast Nat 13:43–56

Bennett KF, Ellison AM (2009) Nectar, not colour, may lure insects to their death. Biol Lett 5:469–472

Blatt SE, Crowder A, Harmsen R (2005) Secondary succession in two south-eastern Ontario old-fields. Plant Ecol 177:25–41

Bradshaw WE, Johnson K (1995) Initiation of metamorphosis in the pitcher-plant mosquito: effects of larval growth history. Ecology 76:2055–2065

Cadotte MW, Fukami T (2005) Dispersal, spatial scale, and species diversity in a hierarchically structured experimental landscape. Ecol Lett 8:548–557

Chesson P (2000) Mechanisms of maintenance of species diversity. Annu Rev Ecol Syst 31:343–366

Christensen NL, Peet RK (1984) Convergence during secondary forest succession. J Ecol 72:25–36

Clements FE (1936) Nature and structure of the climax. J Ecol 24:252–284

Connell JH (1978) Diversity in tropical rain forests and coral reefs: high diversity of trees and corals is maintained only in a non-equilibrium state. Science 199:1302–1310

Connell JH, Slatyer RO (1977) Mechanisms of succession in natural communities and their role in community stability and organization. Am Nat 111:1119–1144

Cowles HC (1899) The ecological relations of the vegetation on the sand dunes of Lake Michigan. Bot Gaz 27:95–117 167–202, 281–308, 361–391

del Moral R (2009) Increasing deterministic control of primary succession on Mount St. Helens, Washington. J Veg Sci 20:1145–1154

Drake JA (1991) Community assembly mechanics and the structure of an experimental species ensemble. Am Nat 137:1–26

Eggeling WJ (1947) Observations on the ecology of the Budongo rain forest, Uganda. J Ecol 34:20–87

Egler FE (1954) Vegetational science concepts. I. Initial floristic composition, a factor in old-field vegetation development. Vegetatio 4:412–417

Facelli JM, D'Angela E (1990) Directionality, convergence, and rate of change during early succession in the Inland Pampa, Argentina. J Veg Sci 1:255–260

Fish D, Hall DW (1978) Succession and stratification of aquatic insects inhabiting leaves of insectivorous pitcher plant, *Sarracenia purpurea*. Am Midl Nat 99:172–183

Foster BL, Tilman D (2000) Dynamic and static views of succession: testing the descriptive power of the chronosequence approach. Plant Ecol 146:1–10

Gleason HA (1926) The individualistic concept of the plant association. Bull Torrey Bot Club 53:7–26

Hixon MA, Brostoff WN (1996) Succession and herbivory: effects of differential fish grazing on Hawaiian coral-reef algae. Ecol Monogr 66:67–90

Hoekman D (2011) *Sarracenia purpurea* pitcher communities at disparate latitudes: a field study of the relative importance of top-down and bottom-up forces in food webs. Oecologia 165:1073–1082

Hoekman D, terHorst CP, Bauer A, Braun S, Gignac P, Hopkins R, Joshi S, Laskis K, Sanscrainte N, Travis J, Miller TE (2007) Oviposition decreased in response to enriched water: a field study of the pitcher-plant mosquito, *Wyeomyia smithii*. Ecol Entomol 32:92–96

Johnson EA, Miyanishi K (2008) Testing the assumptions of chronosequences in succession. Ecol Lett 11:419–431

Kardol P, Bezemer TM, van der Putten WH (2006) Temporal variation in plant-soil feedback controls succession. Ecol Lett 9:1080–1088

Kneitel JM (2002) Species diversity and trade-offs in pitcher plant (*Sarracenia purpurea*) inquiline communities. PhD dissertation, Florida State University, Tallahassee

Kneitel JM, Miller TE (2002) The effects of resource and top-predator addition to the inquiline community of the pitcher plant *Sarracenia purpurea*. Ecology 83:680–688

Kuiters AT, Kramer K, Van der Hagen HGJM, Schaminee JHJ (2009) Plant diversity, species turnover and shifts in functional traits in coastal dune vegetation: results from permanent plots over a 52-year period. J Veg Sci 20:1053–1063

Leibold MA, Miller TE (2004) From metapopulations to metacommunities. In: Hanski I, Gaggiotti O (eds) Ecology, genetics, and evolution of metapopulations. Academic, San Diego, pp 133–150

Lewontin RC (1969) The meaning of stability. Brookhaven Symp Biol 22:13–24

Lindeman RL (1942) The tropic-dynamic aspect of ecology. Ecology 23:399–418

Margalef R (1963) On certain unifying principles in ecology. Am Nat 97:357–374

Margalef R (1968) Perspectives in ecological theory. University of Chicago Press, Chicago

McIntosh RP (1999) The succession of succession: a lexical chronology. Bull Ecol Soc Am 80:256–265

Miller TE, Kneitel JM (2005) Inquiline communities in pitcher plants as prototypical metacommunities. In: Holyoak M, Leibold MA, Holt RD (eds) Metacommunities: spatial dynamics and ecological communities. University of Chicago Press, Chicago, pp 122–145

Myster RW, Walker LR (1997) Plant successional pathways on Puerto Rican landslides. J Trop Ecol 13:165–173

Nelson ML, Craig SF (2011) Role of the sea anemone *Metridium senile* in structuring a developing subtidal fouling community. Mar Ecol Prog Ser 421:139–149

Neutel AM, Heesterbeek JAP, van de Koppel J, Hoenderboom G, Vos A, Kaldeway C, Berendse F, de Ruiter PC (2007) Reconciling complexity with stability in naturally assembling food webs. Nature 449:599–602

Odum EP (1969) The strategy of ecosystem development. Science 164:262–270

Olito C, Fukami T (2009) Long-term effects of predator arrival timing on prey community succession. Am Nat 173:354–362

Paine RT (1966) Food web complexity and species diversity. Am Nat 100:65–75

Peltzer DA, Wardle DA, Allison VJ, Baisden WT, Bardgett RD, Chadwick OA, Condron LM, Parfitt RL, Porder S, Richardson SJ, Turner BL, Vitousek PM, Walker J, Walker LR (2010) Understanding ecosystem retrogression. Ecol Monogr 80:509–529

Pianka ER (1974) Niche overlap and diffuse competition. Proc Natl Acad Sci USA 71:2141–2145

Pickett ST, Collins SL, Armesto JJ (1987) A hierarchical consideration of causes and mechanisms of succession. Vegetatio 69:109–114

Quesada M, Sanchez-Azofeifa GA, Alvarez-Añorve M, Stoner KE, Avila-Cabadilla L, Calvo-Alvarado J, Castillo A, Espírito-Santo MM, Fagundes M, Fernandes GW, Gamon J, Lopezaraiza-Mikel M, Lawrence D, Morellato LPC, Powers JS, Neves FD, Rosas-Guerrero V, Sayago R, Sanchez-Montoya G (2009) Succession and management of tropical dry forests in the Americas: review and new perspectives. For Ecol Manag 258:1014–1024

Schmitz OJ, Krivan V, Ovadia O (2004) Trophic cascades: the primacy of trait-mediated indirect interactions. Ecol Lett 7:153–163

Schmitz OJ, Kalies EL, Booth MG (2006) Alternative dynamic regimes and trophic control of plant succession. Ecosystems 9:659–672

Sousa WP (1979) Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. Ecol Monogr 49:227–254

Srivastava DS, Kolasa J, Bengtsson J, Gonzalez A, Lawler SP, Miller TE, Munguia P, Romanuk T, Schneider DC, Trzcinski MK (2004) Are natural microcosms useful model systems for ecology? Trends Ecol Evol 19:379–384

ter Braak CJF, Smilauer P (2002) CANOCO software for canonical community ordination (version 4.5). Microcomputer Power, Ithaca, New York

Tilman D (1985) The resource-ratio hypothesis of plant succession. Am Nat 125:827–852

Van der Putten, WH, Mortimer SR, Hedlund K, Van Dijk C, Brown VK, Leps J, Rodriguez-Barrueco C, Roy J, Len TAD, Gormsen D, Korthals GW, Lavorel S, Santa-Regina I, Smilauer P (2000) Plant species diversity as a driver of early succession in abandoned fields: a multi-site approach. Oecologia 124:91–99

Walker LR, del Moral R (2003) Primary succession and ecosystem rehabilitation. Cambridge University Press, Cambridge

Warren PH, Law R, Weatherby AJ (2003) Mapping the assembly of protist communities in microcosms. Ecology 84:1001–1011

Wassenaar TD, van Aarde RJ, Pimm SL, Ferreira SM (2005) Community convergence in disturbed subtropical dune forests. Ecology 86:655–666