Typhoons initiate predictable change in aquatic bacterial communities

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Abstract

We explored patterns of change in bacterioplankton and phytoplankton community composition in response to typhoons in a subtropical, subalpine freshwater humic lake in Taiwan. Thermal profiles with depth, near-surface dissolved oxygen, and meteorological conditions were measured at high temporal resolution using an instrumented buoy. We collected samples across a time series spanning two typhoon seasons and assessed bacterial community composition at each time point using a fingerprinting technique targeting the internal transcribed spacer region of the ribosomal RNA operon. Wind and rain associated with the typhoons mixed the otherwise stably stratified water column. After each of six typhoon-induced mixing events, the bacterial community composition was reset to similar conditions, revealing a surprisingly deterministic pattern of recovery that was reminiscent of secondary succession following large infrequent disturbances in terrestrial ecosystems. Distinct bacterial assemblages were associated with epilimnion and hypolimnion samples collected more than 80 d after a mixing event. These assemblages were also distinct from the communities observed in the generally unstratified water column within 7 d after a typhoon. Our results were surprising since bacterial communities are not expected to respond in such predictable ways because of their immense complexity and diversity. In contrast, phytoplankton communities did not recover in a predictable way after typhoons.

Disturbance regimes are an important factor in the maintenance of spatiotemporal heterogeneity in ecosystems

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(Sousa 1984). A disturbance is a discrete event that disrupts ecosystem, community, or population structure and changes resource availability or the physical environment (White and Pickett 1985). Disturbances can be either natural or anthropogenic in origin, can occur over a variety of spatial and temporal scales, and are characterized by their timing, frequency, intensity, and extent (White and Jentsch 2001; Shea et al. 2004). Examples of disturbance in terrestrial communities include fire, windthrow, pest outbreaks, and flooding. In lakes, examples of disturbance include introduction of nonnative species, chemical spills, and wind and rain events that cause vertical mixing of an otherwise stably stratified water column. Biological response to disturbance often takes the form of a "resetting" to a community consisting of early successional or pioneer species. Water column mixing has been identified as a disturbance that, depending on frequency and intensity, can maintain high diversity of phytoplankton species

(Reynolds et al. 1993). Bacteria, however, are expected to respond unpredictably to such disturbances, because of the immense diversity and complexity of bacterial communities (Yannarell et al. 2003).

Previous research suggests that predictable patterns of aquatic bacterial community change in response to disturbance are unlikely (Kent et al. 2004). Sloan et al. (2006) recently explained the occurrence patterns of 16 freshwater bacterial taxa in 96 lakes using a neutral community model. Neutral community models assume that all taxa are equal in their growth rates and that immigration and composition of the ''source'' community drive local community dynamics, suggesting that competition and environmental gradients, key assumptions underlying successional theory (Gleason 1927), are unimportant in structuring bacterial communities. In addition, bacterial communities in a temperate lake, similar in size and chemical composition to our study system, exhibited unpredictable, nonrepeated dynamics, and composition across seasonal mixing events (Newton et al. 2006). Dramatic shifts in bacterial community composition as a result of discrete disturbances have been demonstrated (Axelrood et al. 2002; Fierer et al. 2003), but no previous studies have indicated repeated, predictable responses to disturbance in natural bacterial communities.

Here we investigated the effect of typhoon-mediated disturbance on aquatic microbial communities in Yuan Yang Lake (YYL), a subalpine humic lake in northern Taiwan. Typhoons bring heavy rain and strong wind to the lake several times each summer and fall, dramatically altering the physical and chemical characteristics of the water column. The irregular frequency and short duration of these events creates an ideal system in which to study the disturbance and subsequent recovery of microbial communities in the lake.

YYL stratifies strongly between mixing events and does not mix appreciably during calm weather (Fig. 1). Temperature profiles with depth were monitored in near real time via an instrumented buoy over the deepest location in the lake to characterize physical structure of the water column. We sampled the phytoplankton and bacterioplankton communities in the warm mixed layer (the epilimnion) and bacterioplankton assemblages in the cold dark hypolimnion to study the changes in community composition initiated by disturbance during two typhoon seasons. Taken together, these physical and biological observations provided an intimate view of the effect of typhoon disturbance on the lake plankton community.

Methods

Site description—YYL is a 4-m-deep subalpine lake (1,700 m above sea level) located in the Chilan forest preserve in Ilan County, Taiwan (24°35′N, 121°24′E). The total area of the preserve and watershed is about 3.74 km², of which the lake is about 36,000 m². The surrounding hillsides are dominated by undisturbed *Chamaecyparis* forest. The year-round mild air temperature (daily mean temperature less than 21°C in summer and higher than −4°C in winter) and humid conditions (yearly precipitation >4,000 mm) hamper the decomposition of soil organic matter. Humic acids leach from the soil and are washed into the lake during rain events, leading to pH values in YYL of 4.8–5.5 (Wu et al. 2001). Typhoons contribute more than one-fourth of total annual precipitation. High-frequency water temperature profile measurements collected by an instrumented buoy indicate that the water column becomes isothermal and mixed during most typhoon events (Porter et al. 2005).

Sample collection—Integrated water column samples were collected over the deepest hole in the lake basin (4.5 m). Epilimnion samples were collected from 0–0.5 m and hypolimnion from 0.5–3.5 m. These depth ranges were used to define the two layers even after typhoons when the water column had not yet restratified, for sample collection purposes. Approximately 2 liters of lake water were collected from each layer and 150-mL aliquots were captured by vacuum filtration on 0.2-μm filters (Supor-200; Gelman). Temperature profiles and meteorological data were measured every 10 min by an instrumented buoy. The buoy was equipped with a Templine thermistor chain with sensors at 0, 0.5, 1.0, 1.5, 2.0, 2.5, and 3.0 m (Apprise Technologies), a Greenspan DO100 dissolved oxygen sensor at the surface, an RM Young wind vane, an anemometer to measure wind speed and direction (Campbell Scientific), and a Campbell CR10X data logger. Lake water level was measured at the lakeshore using a PS-9800 submersible pressure transducer (Instrumentation Northwest). Additional data were collected at a nearby meteorological station (around 500 m from the buoy) measuring air temperature, light intensity, relative humidity, soil temperature, and rainfall.

Sample processing—Bacterial samples were processed from integrated thermal layer samples and community profiles were created using ARISA, as described (Newton et al. 2006). Briefly, ARISA uses the variation in length of the intergenic spacer region between the 16S and 23S ribosomal RNA genes to distinguish operational taxonomic units (OTUs) within the bacterial community. DNA from a single filter from each sample was extracted using the FastPrep DNA purification kit (BIO101). Five to 10 ng of community DNA was included in each 30-cycle ARISA polymerase chain reaction using a 5′ phosphoramidite dye 6-FAM-labeled 1406f forward primer (5′ TGYACA-CACCGCCCGT 3′) and 23Sr reverse primer (5′ GGGTTBCCCCATTCRG 3′). Phytoplankton samples taken from the epilimnion were fixed with Lugol's solution. For enumeration, the samples were concentrated by centrifugation (3,500 × g, 10 min) and then stained with Coomassie blue (0.1% in phosphoric acid), and filtered through a cellulose nitrate membrane (pore size 0.45 μm) under reduced pressure. The relative abundance of each species was calculated on the basis of counting 1,000 phytoplankton cells per sample using a light microscope at ×200 magnification.

Statistical analyses—Bacterial and phytoplankton community similarity and dynamics were separately analyzed
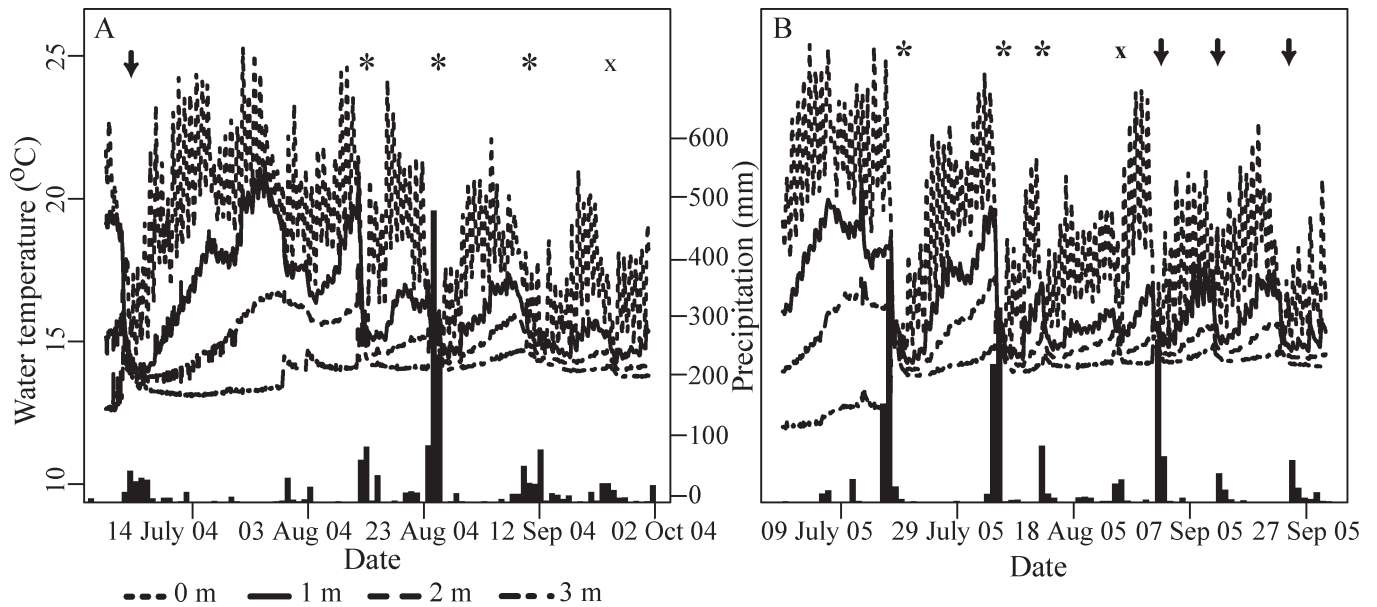
Fig. 1.   Yuan Yang Lake water temperature at four depths during the (A) 2004 and (B) 2005 stratified season. Arrows indicate typhoon events that caused water column mixing, asterisks mark water column mixing events for which we sampled bacterial and phytoplankton community composition, and x's indicate typhoons that did not result in water column mixis but for which we obtained samples before and after. Vertical black bars are daily total precipitation (mm).

using correspondence analysis and analysis of similarity (ANOSIM) (Clarke 1993; Legendre and Legendre 1998; Ter Braak and Similauer 2002). ANOSIM generates a test statistic, R, that indicates the degree of separation between groups of samples, a score of 1 indicating complete separation and 0 indicating no separation. Significance of the ANOSIM R statistic is assigned using permutation. Concordance between epilimnetic bacterial and phytoplankton community dynamics was investigated using Procrustean superimposition (Peres-Neto and Jackson 2001) on the first three axes of individual correspondence analyses. The sum of squared residuals between scaled and rotated configurations of each ordination solution is used as a metric of association (m^2) (Peres-Neto and Jackson 2001). The m^2 metric varies between 0 and 1, and smaller values of m^2 indicate stronger concordance between data sets. Significance was assessed by permutation tests (999 permutations) using the PROTEST package (Peres-Neto and Jackson 2001). Variability or dispersion of bacterial community data was also investigated using permutational analysis of multivariate dispersions (PERMDISP [Anderson 2006]). For this analysis, a centroid for a cloud of communities in an ordination was determined and distances from the centroid described the dispersion of the sample set. Significantly different levels of dispersion between sample subsets were determined by permutation.

To simplify the bacterial community and evaluate whether bacterial OTUs displayed repeatable occurrence patterns across the typhoon-induced disturbance time series we selected the 20 OTUs contributing the highest relative fluorescence on each sample date from both the epilimnion and hypolimnion. This resulted in a list of 98 OTUs from a total of 169 observed ARISA-defined OTUs; only OTUs occurring in more than one sample were

considered in subsequent analyses. This resulting final list of "dominant" bacterial community members included 80 bacterial OTUs. We then calculated the proportion of occurrence of each OTU in four time–space categories on the basis of days since mixing and lake layer: mixed (<7 d since mixing) versus successional (>80 d since mixing), and epilimnion versus hypolimnion. The resultant 4 by 80 matrix was used along with the heat map function in the R statistics package (R Development Core Team 2006) to visually represent OTU occurrence patterns and to conduct a hierarchical cluster analysis on the samples and bacterial OTUs.

Results

Typhoons disrupt the physical structure of the water column—Between 01 July 2004 and 30 September 2005 the Taiwan Central Weather Bureau recorded 14 typhoon and tropical storm events (Table 1). Because of the small and protected nature of the YYL watershed, wind speeds during typhoon events were high, but not severe at the lake (maximum observed over the study period: 16.4 m s^{-1}). Lake mixing was presumably caused by the large amount of precipitation. High spatial (with depth) and temporal resolution thermal profiles of the lake showed that storm events often resulted in complete mixing of the water column (Fig. 1). Twelve of the 14 events caused complete mixing, and we were able to sample the bacteria and phytoplankton communities before and after eight of the events (Fig. 1; Table 2).

Typhoons initiate repeated bacterial community succession—Surprisingly, the bacterial community was repeatedly and predictably reset after the six typhoon

Table 1.   Dates of typhoons occurring near the island of Taiwan from 01 Jul 2004 to 01 Oct 2005. Total precipitation (mm) for each typhoon is also presented.

Start date	End date	Name	Total precipitation (mm)	Mixed water column
01 Jul 2004	04 Jul 2004	Mindulle	160	Yes
11 Aug 2004	14 Aug 2004	Rananim	205	Yes
23 Aug 2004	25 Aug 2004	Aere	817	Yes
09 Sep 2004	12 Sep 2004	Haima	206	Yes
23 Sep 2004	25 Sep 2004	Meari	80	No
24 Oct 2004	26 Oct 2004	Nock-ten	241	Yes
03 Dec 2004	04 Dec 2004	Nanmadol	215	Yes
17 Jul 2005	18 Jul 2005	Haitang	623	Yes
03 Aug 2005	05 Aug 2005	Matsa	645	Yes
12 Aug 2005	13 Aug 2005	Sanvu	278	Yes
24 Aug 2005	25 Aug 2005	Mawar	75	No
31 Aug 2005	01 Sep 2005	Talim	380	Yes
10 Sep 2005	13 Sep 2005	Khanun	285	No
22 Sep 2005	23 Sep 2005	Damrey	103	Yes

events (Fig. 2a). After each event, the similarity between hypolimnetic and epilimnetic bacterial communities was high, but as time increased since mixing the communities diverged along separate trajectories (Fig. 2a). The pattern of convergence after disturbance and repeated divergence as time passed after a mixing event was evident when pairwise similarities between bacterial community composition in epilimnion and hypolimnion samples taken on the same day were compared (Fig. 2b). Bray–Curtis similarity between communities collected from the two layers was strongly related to the number of days since water column mixis ($n = 18$, $R^2 = 0.83$, $p < 0.001$). ANOSIM was used to test the hypothesis that bacterial communities from the

same layer were more similar in composition to each other than to communities in different layers. The mixed epilimnion and hypolimnion (within 7 d of a typhoon), successional epilimnetic, and successional hypolimnetic bacterial communities were all significantly distinct from each other (ANOSIM, $n = 38$, global $R = 0.72$, $p = 0.001$). Significantly different levels of community dispersion were also observed between the mixed water column, stratified epilimnion, and stratified hypolimnion (PERMDISP, $n = 38$, $p < 0.001$). The stratified epilimnion communities were most variable, followed by the mixed condition, and the stratified hypolimnion was least dispersed in ordination space (38, 34, 24; respective mean centroid Bray–Curtis distances).

When evaluated separately the epilimnion and hypolimnion bacterial communities displayed repeated patterns of succession in response to typhoons. A plot of days since mixing and the sample score along the first axis from separate correspondence analysis ordinations (Fig. 3) for epilimnion and hypolimnion samples revealed moderate to strong linear relationships (Fig. 4, epilimnion: $R^2 = 0.59$, $p < 3.2 \times 10^{-5}$, $n = 22$; hypolimnion: $R^2 = 0.82$, $p < 2.7 \times 10^{-7}$, $n = 18$). Late successional communities were somewhat distinct across years (Fig. 3). However, these communities were separated mainly along the second correspondence analysis axis, indicating that the amount of time passed since mixing explained more of the variation in bacterial community composition.

Table 2.   Dates samples were collected from the epilimnion and hypolimnion of Yuan Yang Lake, Taiwan. Days since last water column mixis when samples were taken is also indicated.

Date of sample	Days since last mixing
08 Jul 2004	98
13 Jul 2004	103
19 Jul 2004*	109
22 Jul 2004	112
26 Jul 2004	116
29 Jul 2004	119
04 Aug 2004	125
17 Aug 2004	3
01 Sep 2004	7
06 Oct 2004*	42
24 Oct 2004*	60
05 May 2005	34
22 Jun 2005	82
28 Jun 2005	88
30 Jun 2005	90
12 Jul 2005	102
25 Jul 2005	6
26 Jul 2005	7
01 Aug 2005*	13
03 Aug 2005	15
09 Aug 2005	4
16 Aug 2005	2

* No hypolimnion sample collected on this date.

Typhoons interrupt but do not reset phytoplankton community succession—The phytoplankton community succession was also disturbed by each typhoon. However, unlike the bacterial community it did not repeatedly reset to a similar community composition (Fig. 5). Concordance between epilimnetic bacterial and phytoplankton community dynamics was investigated using Procrustean superimposition (Peres-Neto and Jackson 2001) on the first three axes of individual correspondence analyses. Although the successional trajectories of both bacterial and phytoplankton communities were both affected by typhoon-induced mixing, there was no temporal concordance between these
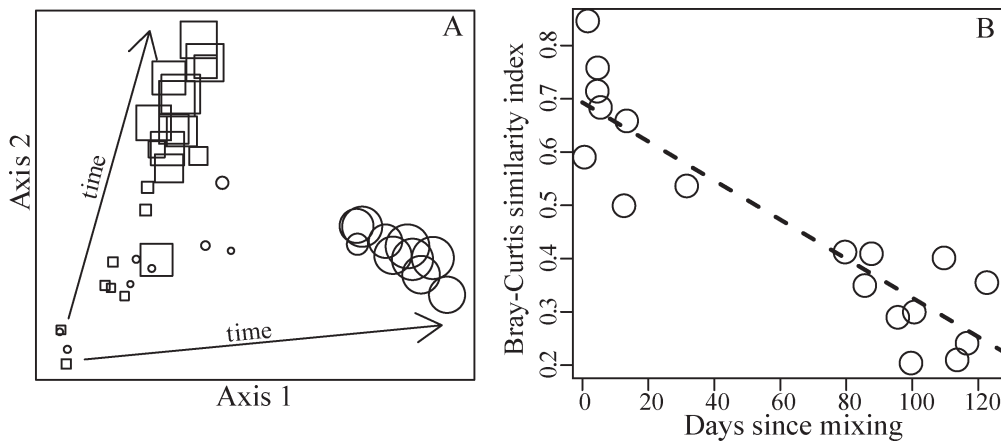
Fig. 2. Changes in bacterial community composition in the epilimnion and hypolimnion of YYL during the stratified seasons of 2004 and 2005. (a) A correspondence analysis ordination of community composition in the two thermal layers collected as a time series. Squares represent epilimnetic bacterial communities and circles represent the hypolimnetic communities. The symbol size is proportional to days since the last mixing event (2–125 d). (b) Scatter plot of pairwise Bray–Curtis similarity index between the hypolimnetic and epilimnetic bacterial communities on a given date versus the number of days passed since the last mixing event. "Days since mixing" explains much of the variability in hypolimnion and epilimnion community similarity (linear regression, $n = 18$, $R^2 = 0.83$, $p < 0.001$).

two communities (PROTEST, $n = 17$, $m^2 = 0.61$, $p = 0.006$), indicating that the two communities change asynchronously after disturbances.

Discrete bacterial OTU occurrence patterns were present—Our reduction in complexity of the bacterial community by selecting for further analysis the 20 ARISA-defined OTUs with the highest relative fluorescence in each sample did not appear to affect the overall relationship between samples. Mantel tests indicated that the Bray–Curtis similarity matrix of the entire bacterial community was greater than 98% similar to a similarity

matrix calculated with the 80 "dominant" bacterial taxa (Mantel $R = 0.984$, $p < 0.001$). In addition, the sum of the relativized fluorescence of the top 20 OTUs in each sample averaged 91% across all samples (min. = 75%, max. = 100%).

Hierarchical clustering of the "dominant" bacterial OTUs revealed distinct clusters with well-defined occurrence patterns in response to disturbance (Fig. 6). We observed taxa that were perpetually present in all time–space periods (cluster A), taxa that were repeatedly present in primarily one layer during the late successional time frame (clusters C, D, and F), and OTUs that were found
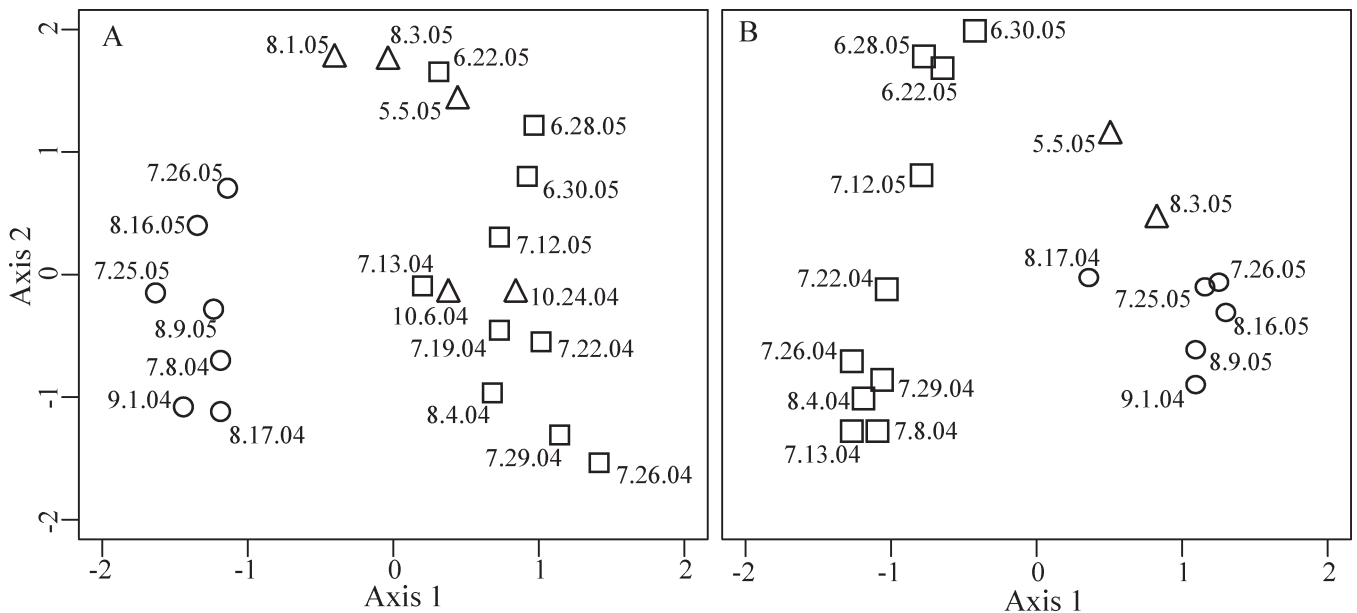

Fig. 3. A correspondence analysis ordination of the (A) epilimnetic and (B) hypolimnetic bacterial community composition in Yuan Yang Lake during the stratified seasons of 2004 and 2005. Samples collected within 7 d of a mixing event are coded as circles; samples collected after more than 80 d since a mixing event are coded as squares; samples collected between 7 and 80 d of mixing are coded as triangles.
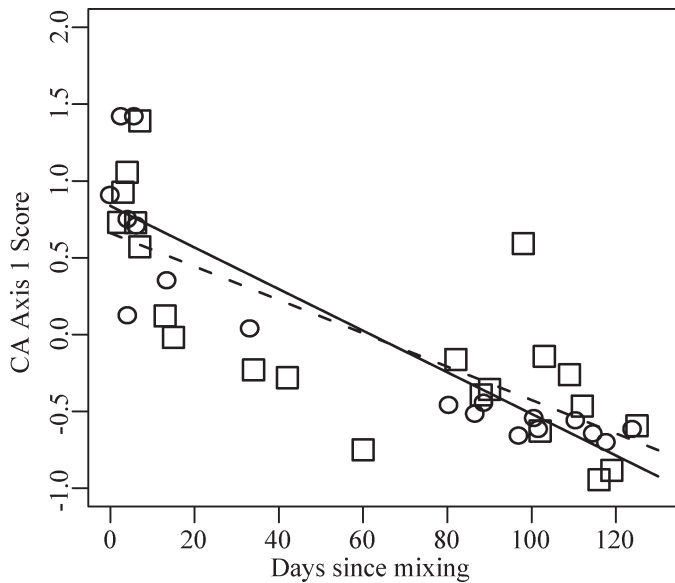
Fig. 4. A plot of axis one scores from separate correspondence analysis ordinations for the epilimnion and hypolimnion of Yuan Yang Lake against days since last mixing. This plot reveals that axis one of both ordinations is correlated with the number of days between the sample and last lake column mixing (epilimnion: $R^2 = 0.59$, $p < 0.001$, $n = 22$; hypolimnion: $R^2 = 0.82$, $p < 0.001$, $n = 18$). Squares represent epilimnion samples and circles are hypolimnion samples. The dashed line is the linear fit for the epilimnion and solid line for the hypolimnion.

primarily during early succession, but in both layers (cluster B). The time–space designations also clustered in a way that would be expected, with the epilimnion and hypolimnion <7 d since mixing being most similar and the late-successional communities being less similar (Fig. 6).
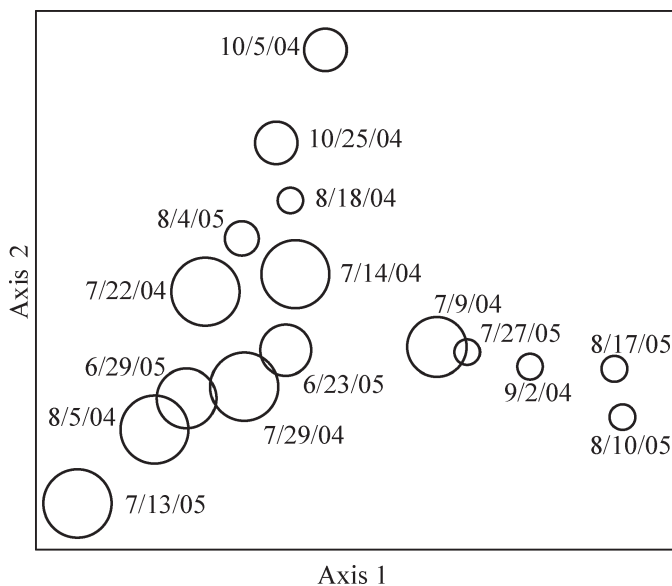

Fig. 5. A correspondence analysis ordination of the epilimnetic phytoplankton community in Yuan Yang Lake during the stratified seasons of 2004 and 2005. The symbol size is proportional to days since the last mixing event.

Discussion

Ecologists studying disturbance and succession in terrestrial plant communities have contributed many useful conceptual frameworks with which to interpret the effect of discrete disruptive events on community structure and diversity (Horn 1974; Connell and Slatyer 1977; White and Jentsch 2001). Several of these are particularly useful in the interpretation of our results. Disturbances can be categorized on the basis of their abruptness, magnitude, and duration (White and Jentsch 2001). Large infrequent disturbances (LIDs) are unique in their magnitude and scale relative to habitat patch size (Turner et al. 1998). Class II disturbances as defined by White and Pickett (1985) are large in scale relative to habitat patch size, and postdisturbance communities are not dominated by species present in predisturbance communities. We propose that typhoons affecting YYL could be characterized as LIDs, which resemble class II disturbances, and therefore initiate secondary succession in the lake microbial community.

The bacterial communities in YYL displayed an interesting response to the chemical and physical changes following a typhoon, which we propose have many of the characteristics that define LIDs. During the days immediately after a typhoon, communities in the two lake layers resembled a combination of the two distinct predisturbance communities, with additional taxa that were characteristic only of this time period (represented by cluster B) (Fig. 6). The latter populations likely were immigrants carried into the lake by rainfall and surface runoff. Landscape ecologists have noted the important role played by competition between residual species and immigrants in shaping community development after disturbances (Turner et al. 1998). Immigration and chance, rather than competitive sorting, are expected to be the dominant drivers of succession after LIDs (Turner et al. 1998). We note that virtually nothing is known about rates and patterns of microbial immigration and dispersal within and among ecosystems; we suggest this as a potentially very promising area of future research in our efforts to parse out the relative roles played by immigration and competition in aquatic bacterial community assembly processes.

Although typhoons represent extensive LIDs from the perspective of bacteria in the YYL water column, the remarkable repeatability of bacterial community assembly following such disturbances (Fig. 3) suggests that competition supersedes the influence of immigration and chance in this system. Similar predictability has been seen on annual scales in other aquatic ecosystems (Crump and Hobbie 2005; Fuhrman et al. 2006; Kent et al. 2007). In contrast with many LIDs affecting terrestrial plant communities (Turner et al. 1998), typhoons destroy patchiness in the water column of YYL by mixing the lake. Heterogeneity is restored as rapid thermal restratification creates two distinct islandlike compartments within the water column and succession begins. Thus, the mixing events caused by typhoons at YYL represent a unique kind of LID that influences lake bacteria in ways that are consistent with previously developed theories about secondary succession, but with some striking differences
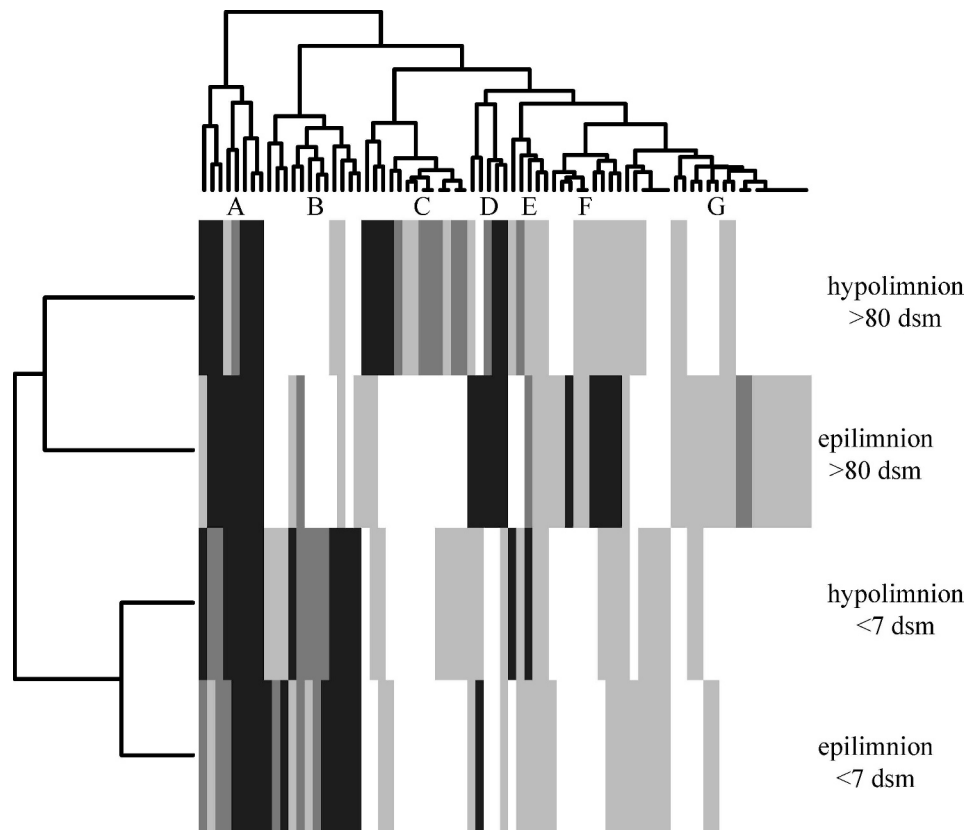
Fig. 6. Occurrence patterns of the 20 most highly represented bacterial taxa in ARISA profiles, as assessed using relative fluorescence. Only taxa observed in more than one sample across the 2-yr time series were included in the analysis. A higher proportion of occurrence in a given time–space category is represented by black to dark gray and lower levels of occurrence are light gray to white. Hierarchical cluster dendrograms are included for bacterial OTUs and time–space categories. dsm = days since mixing.

relative to patterns observed in other ecosystems. Our results therefore bring us closer to a more unified paradigm for disturbance ecology (White and Jentsch 2001).

We expect that dramatically different biotic and abiotic proximate drivers acting in each layer drove divergent development of the bacterial communities. Epilimnion dynamics are likely driven by immigration, competition, and food web interactions (Kent et al. 2004; Sloan et al. 2006) and may exemplify the inhibition model for succession proposed by Connell and Slatyer (1977). In the hypolimnion, sequential depletion of electron acceptors should promote the development of highly structured and characteristic anaerobic communities (Lehours et al. 2005); this mechanism is reminiscent of Connell and Slatyer's (1977) facilitation model for succession. These contrasting mechanisms could partly explain the observed differences in the patterns of successional trajectories in the two layers (Fig. 2); the late-succession epilimnetic bacterial commu-nity was more variable (as measured by higher dispersion in ordination space) than the hypolimnion community. We speculate that this higher degree of variability results from the fact that the epilimnion is open to the atmosphere and surrounding landscape, whereas the hypolimnion is largely isolated from such extrinsic drivers of change.

In summary, we show, for the first time, strikingly predictable patterns of bacterial community change in a natural system in response to large-scale disturbance events. Community development in the two thermal layers of YYL exhibited many of the characteristics of secondary succession initiated by large infrequent disturbances, with some interesting differences. We found this to be surprising given the immense diversity and complexity of bacterial communities. In light of these results, we propose that bacterial communities in stratified lakes are particularly intriguing and promising model systems, the study of which should provide a much needed, more generalized set of hypotheses for disturbance ecology.

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