

Understanding self-organization of ecosystems under disturbance using a microcosm study

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ABSTRACT

It is a key to success of ecological engineering to understand self-organization of a target ecosystem. Self-organizing patterns of ecosystems, however, become complicated due to a wide range of disturbance regimes in nature. We investigated how disturbances influence self-organization of ecosystems from energetic perspectives using 14 freshwater aquatic microcosms transplanted from lakes in Florida. We observed five different disturbance–productivity relationships from the microcosm tests and these variable relationships were attributed to the different initial states of the microcosms under the same input sequence of test plans and disturbance regimes. Through processes of self-organization, as the microcosms matured with time, *resistance* increased and *resilience* decreased. The microcosm study provided insights regarding restoration and management of ecosystems including the insight that initial seeds for restoration of an ecosystem should be carefully selected in consideration of typical disturbance regimes of the region. It is also suggested that consideration or manipulation of disturbance regimes in each successional stage is sometimes needed for maximum productivity or a designated goal of a restoration project because self-organizing patterns that result under disturbances vary depending on a system's maturity.

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1. Introduction

Understanding self-organization of a target ecosystem is an important element of successful ecological engineering (Odum and Odum, 2003). Practically speaking, when attempting restoration or some other form of engineering of ecosystems, one should observe the development of a system over time, to better understand how the system self-organizes during succession. Since this is not always possible, researchers or practitioners often obtain knowledge about the typical patterns of ecosystem self-organization from theoretical studies, or more commonly, implement an ecological engineering project on an ad hoc basis (Hobbs and Norton, 1996). Yet, seldom do researchers take into consideration that ecosystems are often disturbed by exogenous forces, the impact of which can drive self-organization to unexpected results (Attiwill, 1994), although there have been increasing efforts to analyze scenarios or test management decisions (e.g., Fuller et al., 2008) in restoration projects. In this study, using an energetic perspective, we explored how ecosystems self-organize under differing disturbance regimes.

1.1. Self-organization and productivity of ecosystems

Odum (1988) argued that the self-organization within systems is a trial-and-error process of species interactions where successful interactions (those that maximize power) are reinforced. He illustrated self-organization using the analogy of a balanced aquarium where the initial seeding with many species and abiotic components developed a steady-state ecosystem by selecting, at the system level, the necessary components. In a balanced ecosystem, as Odum (1969) suggested, the ecosystem-level ratio between production and respiration (P/R) approaches 1. In a similar context, Levin (2005) addressed an ecosystem as a complex adaptive system, where a whole selects parts and their interactions by feedback, adaptation, and regulation. As a measure of self-organization, Ulanowicz (1997) proposed “ascendency,” which is defined as the product of total system throughput and network average mutual information. According to ascendency theory, developing systems tend to increase total system throughput (total energy flow) and average mutual information (average amount of constraint between compartments) to some extent. Although it is unknown whether an ecosystem ultimately has a common goal in self-organizing processes, the maximum power principle (Lotka, 1922; Odum, 1983) hypothesizes a potential system-level strategy of maximum power (energy/time) acquisition for survival during self-organization. Because gross primary productivity (GPP), the rate of photosynthetic production, indicates the degree

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of active capture of light by autotrophs providing their ecosystems with directly usable energy resources for growth and enhancement of structures during self-organization, power-maximizing systems are likely to maximize GPP.

1.2. Ecological disturbance and productivity

For several decades, the Intermediate Disturbance Hypothesis (Connell, 1978; Grime, 1973) has been a dominant, yet somewhat controversial topic among ecologists as a way to explain the unimodal relationship between disturbance and species diversity. Mackey and Currie (2001) argued from analyses of previous literature on disturbance that the disturbance–diversity relationship is not always unimodal but may be variable. Upon the elusive disturbance–diversity relationship, the recent advance of disturbance theory has emphasized productivity and disturbance as two factors influencing species diversity (Cardinale et al., 2005; Haddad et al., 2008; Kondoh, 2001). However, the dependence of productivity on disturbance has been overlooked and has rarely been studied, due primarily to the less drastic change of productivity and difficulty of measuring it (Sprugel, 1985).

1.3. Maturity and stability of ecosystems under disturbance

Theories have supported the notion that systems develop complex structures by constructing and reinforcing interactions among components against external disturbances. Beyers (1962), using the microcosm study on the response of an ecosystem to temperature stresses, hypothesized that an integrated ecosystem with strong interdependence among system components is less affected by environmental extremes. Margalef (1963) argued that mature ecosystems tend to have higher complexity, more information, and higher efficiency (lower production/biomass) than less mature ones. Odum (1969) further suggested various ecosystem attributes between developmental and mature stages: mature stages are characterized by complex, well-organized, low-growth, and high-information structures. Sousa (1980) demonstrated in a study of intertidal algal community response to disturbance (overturning of boulders) that early successional communities are easily damaged by disturbance but recover more quickly from the damage than late successional communities. Recent studies using network theory (see a review by Albert and Barabási, 2002) confirmed the relationship between a system's maturity and its stability. Food-web networks in a mature ecosystem resemble scale-free networks (Barabási and Bonabeau, 2003) in that the food web shows a hierarchical structure where a few high-trophic-level species control the majority of low-trophic-level species (Odum, 1988). As they mature, these networks become more resistant to disturbance but less resilient under severe disturbance attacking high-linkage nodes. According to Halpern (1988), resistance can be defined as “the extent to which a system resists change by disturbance” and resilience as “the rate, manner, or degree to which initial community characteristics are restored following displacement.” Resistance and resilience have characterized stability of ecosystems.

1.4. Microcosm tests for disturbance studies

To study disturbance effects, researchers, possibly motivated by difficulty of measuring and controlling disturbance regimes in ecosystems, have often used microcosms (Buckling et al., 2000; Haddad et al., 2008; Jiang and Patel, 2008; Roelke et al., 2003; Sousa, 1980). Although an artificially selected combination of species shows how the species respond to given disturbance regimes (e.g., Buckling et al., 2000), a transplanted microcosm as a whole from an

ecosystem includes necessary components and their interactions for a balanced complex system resembling the sampled ecosystem and further eliminates unnecessary components or resuscitates dormant species through self-organization in a given environment (Beyers and Odum, 1993; Odum, 1988). Using a transplanted microcosm sampled from nature, one can benefit from the holistic approach of observing ecosystem-level phenomena emerging from complex interactions among biotic and abiotic components (Beyers, 1964). Some researchers have pointed out that microcosms do not fully represent phenomena occurring in ecosystems due to their isolation from seedling sources and their small capacity, which limits their ability to contain higher level species or more taxa (Carpenter, 1996; Frost et al., 2001; Ruth et al., 1994). Using microcosms, however, one can better control and accurately measure disturbance regimes and experimental parameters to test disturbance effects and quickly provide hypotheses that should be further demonstrated in ecosystems (Benton et al., 2007; Lawton, 1995).

1.5. Estimation of ecosystem-level energetic parameters

Species exchange materials with surrounding environments through metabolic processes. For example, primary producers exchange carbon dioxide and oxygen with environments through photosynthetic or respiratory processes. In aquatic ecosystems, assuming material exchange between organisms and their environments, ecosystem-level metabolic processes can be estimated by measuring the change of carbon dioxide or oxygen concentration in the water column. Odum (1956) and Copeland and Dorris (1964) measured oxygen concentration to estimate primary production in flowing waters. Carbon dioxide metabolism has been estimated either by using the C-14 method (see Peterson, 1980) or by monitoring water column pH (e.g., Beyers and Gillespie, 1964). Beyers and Gillespie (1964) used the CO₂ water titration method to obtain a pH-[CO₂] curve, but the method cannot provide the pH-[CO₂] relationship when pH is continuously monitored or alkalinity changes. In a theoretical study, Skirrow (1965) provided a thermodynamic relationship among pH, alkalinity, and total CO₂ concentration in a carbonate system. The water column [CO₂] change occurring by photosynthesis and respiration is calculated from [TCO₂] by correcting [CO₂] changes by CaCO₃ precipitation or resolution and CO₂ gas exchange across the air–water interface (Smith, 1973).

1.6. Study plan

We investigated how disturbances influence self-organization of ecosystems using freshwater aquatic microcosms sampled as a whole from lakes. In this study, we regarded self-organization of microcosms as a developing process, where sampled biotic and abiotic components adapt to a new environment and interact to build new connections of material, energy, and information without external control. Different intensity or frequency regimes of water motion disturbance were applied to initially replicated microcosms, and ecosystem-level gross primary productivity (GPP) and respiration rate (ER) values were estimated from metabolic [CO₂] change in the water column by continuously monitoring pH and alkalinity. First, we demonstrate that the disturbance–productivity relationship can be variable depending on the initial states of the microcosms. Second, we show from the results of the microcosm tests that an ecosystem self-organizes to balance between system-level production and consumption and to construct internal stability (resistance and resilience) against external disturbances. We provide insights from the results of the microcosm tests in light of restoration and management of ecosystems under disturbance.

2. Materials and methods

2.1. Design of microcosms

We tested self-organization of ecosystems under disturbance using 14 freshwater aquatic microcosms. Seven different sets of water and sediment were serially collected from five lakes (Alice [2], Newnan [2], Orange [1], Santa Fe [1], and Wauberg [1]) in central Florida to set up the 14 microcosms. Sample lakes were selected based on a wide range of chemical and biological properties (Table 1). Water was collected in 20 L plastic buckets within 5 m littoral zone (shallower than 50 cm) from the shoreline of the sampling point in each lake. Sediments were collected from the top 10 cm layer to minimize the anaerobic metabolism of microcosms. The collected sediments were filtered through a 2 mm mesh to maximize the homogeneity of sediments in each microcosm. We constructed two microcosms each time using each sample of water and sediment and they lasted 22–46 days depending on a designated test plan (Table 2). We varied the duration of initial stabilization and disturbance periods among microcosm tests as an additional treatment because duration of each period may also influence disturbance–productivity relationship. For the microcosm tests, two open-top glass microcosm tanks were constructed to hold 120 L water and 4 L sediment (2 mm sieved) sample in each tank (Fig. 1). The interior of each tank was divided into four equal sections by sealing acrylic panels on the bottom and sides of the tank with 100% silicone to make four replicated sub-microcosms. A rectangular hole was made in the middle of each acrylic panel to facilitate cross-seeding. After an initial stabilization period, we tested the disturbance–GPP relationship in each microcosm by applying four different disturbance regimes of intensity or frequency (Table 3) to the four replicated sub-microcosms. We also tested how a system's maturity influences stability of the system under disturbance using two sets of microcosms (mNI5-10/mNI20-10 and mA15-10/mA120-10). In these maturity tests, the two microcosms in each microcosm set were cross-seeded several times by moving approximately 300 ml water each time for replication during the initial stabilization period. Two microcosm pairs in each set were disturbed at different times (Day 6–15 for mNI5-10 and mA15-10, Day 21–30 for mNI20-10 and mA120-10) with the same disturbance regimes. We regarded mNI5-10 and mA15-10 as less mature systems and mNI20-10 and mA120-10 as mature systems.

2.2. Measurements and maintenance

System-level daily metabolic rates (GPP and ER) of each sub-microcosm were estimated by continuously monitoring pH (Oakton double-junction gel-filled electrode, pH 0–14; Artisan PH2000, resolution 0.01, accuracy ± 0.02) and total alkalinity (end-point titration with 0.2 N H₂SO₄ at pH 4.5 using Hach digital titrator, 1.25 μ L/digit) during the whole test period. We used double-junction pH electrodes for long-term monitoring and pH usually drifted less than 0.03 a week. The pH meters were calibrated at 4.01, 7.00, and 10.01 every week. We rinsed pH electrodes with deionized water once a day to minimize organic matter coating. Eight 20 W, 60 cm cool-white fluorescent bulbs (PAR 150–160 μ mol m⁻² s⁻¹, LI-190 quantum sensor and LI-1400 data logger) were set up 23 cm above the water surface of each tank with the alternating light regime of 12 h light (6:00–18:00) and 12 h darkness (18:00–6:00). The exterior of each tank was enclosed by aluminum foil to maximize the capture of light energy in the tank (PAR 20% increased). Temperature of the dark room was maintained at 24 \pm 1 °C. We maintained the microcosm water level

by adding filtered deionized water (Barnstead NANOpure Infinity Water Purification System).

2.3. Disturbance regimes

We adopted the definition of intensity, frequency, and duration provided by Shea et al. (2004). A water pump (Aquarium Systems Mini-Jet 404, flow rate adjustable), which was centered vertically and offset from the center horizontally about 7 cm on one side of each sub-microcosm, generated horizontal circular water motion by ejecting water sucked up from surroundings. Power (energy/time) of outflowing water from a pump was regarded as the intensity of a water motion disturbance and we defined disturbance intensity as a dimensionless value by eliminating the unit (ml/s) of an outflow rate of pumped water under the assumption that the power is proportional to the outflow rate.

We applied either different intensity or frequency regimes of water motion disturbance to the four replicated sub-microcosms in each microcosm (Table 3). For the intensity-varied tests, different intensities with the same frequency and duration of disturbance were applied to the four sub-microcosms. For frequency-varied tests, different combinations of frequency and duration of disturbance were applied to satisfy the same total disturbance energy among sub-microcosms. In the frequency-varied tests, one of the sub-microcosms (regime 1) was disturbed continuously so the intensity was set at one seventh of the other sub-microcosms (regimes 2, 3, and 4).

2.4. Data analyses

Total CO₂ concentration in the water column ([TCO₂]) was calculated using the following thermodynamic equation (Skirrow, 1965):

$$[\text{TCO}_2] = [\text{CA}] \frac{1 + (K'_2/a_{\text{H}}) + (a_{\text{H}}/K'_{1,1})}{1 + (2K'_2/a_{\text{H}})} \quad (1)$$

where [CA] is the carbonate alkalinity, a_{H} is the hydrogen ion activity (we assumed $a_{\text{H}} = 10^{-\text{pH}}$), $K'_{1,1}$ is the Lyman's first apparent dissociation constant, and K'_2 is the second apparent dissociation constant.

We estimated [CA] by assuming the following equations of total alkalinity ([TA]) and [CA] of the microcosms:

$$[\text{TA}] = [\text{HCO}_3^-] + 2[\text{CO}_3^{2-}] + [\text{OH}^-] - [\text{H}^+] \quad (2)$$

$$[\text{CA}] = [\text{HCO}_3^-] + 2[\text{CO}_3^{2-}] \quad (3)$$

Water column CO₂ concentration from ecosystem-level photosynthesis and respiration ([PCO₂]) was calculated from [TCO₂] by correcting water column CO₂ concentration change caused by CaCO₃ precipitation or resolution ([CCO₂]) (Smith, 1973). We did not correct change of [CO₂] by diffusion across the air–water interface ([GCO₂]) for [PCO₂] calculation, but theoretically analyzed uncertainty of disturbance–productivity relationships from [GCO₂] change using the gas flux equation (MacIntyre et al., 1995) and variable CO₂ gas transfer velocity k (Borges et al., 2004; Cole and Caraco, 1998; Crusius and Wanninkhof, 2003).

We obtained a nighttime respiration rate of each day by the slope connecting the minimum and maximum points of a nighttime [PCO₂] plot on a 12 h basis and a daytime respiration rate by averaging two adjacent nighttime respiration rates. Nighttime and daytime respiration rates were summed to estimate a daily ecosystem-level respiration rate (ER). GPP of each day was calculated by subtracting a daytime [PCO₂] slope from a calculated daytime respiration rate. We calculated average GPP (M_{GPP}) values (temporal average) of the disturbance

Table 1
Chemical and biological properties of the sample lakes (Florida LAKEWATCH, 2005).

Properties	Lake Alice	Newnan's Lake	Orange Lake	Lake Santa Fe	Lake Wauberg
Total phosphorus concentration ($\mu\text{g/L}$)	454	121	68	11	120
Total nitrogen concentration ($\mu\text{g/L}$)	627	3362	1698	449	1805
PH	7.5	6.9	7.1	5.9	7.6
Alkalinity (mg/L CaCO_3)	85.0	12.4	19.4	1.8	19.7
Secchi depth (m)	1.5	0.3	0.8	2.3	0.6
Chlorophyll concentration ($\mu\text{g/L}$)	13	208	51	7	92

Table 2
Test plan, disturbance regime, and sample lake for the 14 microcosms.

Microcosm ^a	Test plan ^b (days)	Varied regime (disturbance)	Sample lake	Location	Sampling date
mNI5-10	5-10-15	Intensity	Newnan	+29°38'11", -82°14'25"	April 30, 2009
mNI20-10	20-10-15	Intensity	Newnan	+29°38'11", -82°14'25"	April 30, 2009
mAI5-10	5-10-15	Intensity	Alice	+29°38'36", -82°21'45"	April 17, 2010
mAI20-10	20-10-15	Intensity	Alice	+29°38'36", -82°21'45"	April 17, 2010
SI 1-5	1-5-15	Intensity	Santa Fe	+29°42'49", -82°03'48"	October 5, 2009
SF1-5	1-5-15	Frequency	Santa Fe	+29°42'49", -82°03'48"	October 5, 2009
WI1-5	1-5-15	Intensity	Wauberg	+29°32'06", -82°18'13"	February 20, 2010
WF1-5	1-5-15	Frequency	Wauberg	+29°32'06", -82°18'13"	February 20, 2010
OI5-10	5-10-15	Intensity	Orange	+29°28'16", -82°11'59"	March 16, 2010
OF5-5	5-5-15	Frequency	Orange	+29°28'16", -82°11'59"	March 16, 2010
AI5-5	5-5-15	Intensity	Alice	+29°38'36", -82°21'45"	June 20, 2010
AF5-5	5-5-15	Frequency	Alice	+29°38'36", -82°21'45"	June 20, 2010
NI5-5	5-5-15	Intensity	Newnan	+29°38'11", -82°14'25"	July 17, 2010
NF5-5	5-5-15	Frequency	Newnan	+29°38'11", -82°14'25"	July 17, 2010

^a Each character or number in a label indicates: (lake initial)(intensity or frequency test)(initial stabilization period)-(disturbance period). Microcosms also used for a maturity test were labeled with "m" in front of each microcosm label.

^b Test plan is in the order of the three periods: (initial stabilization)-(disturbance)-(post-disturbance). Initial stabilization: sub-microcosms were allowed to cross-seed each other through the rectangular holes and we additionally cross-seeded among sub-microcosms several times by moving approximately 300 ml water each time. Disturbance: rectangular holes were blocked and water motion disturbances were applied according to the designated disturbance regimes. Post-disturbance: microcosms were not altered or manipulated except to take measurements and to add make-up water.

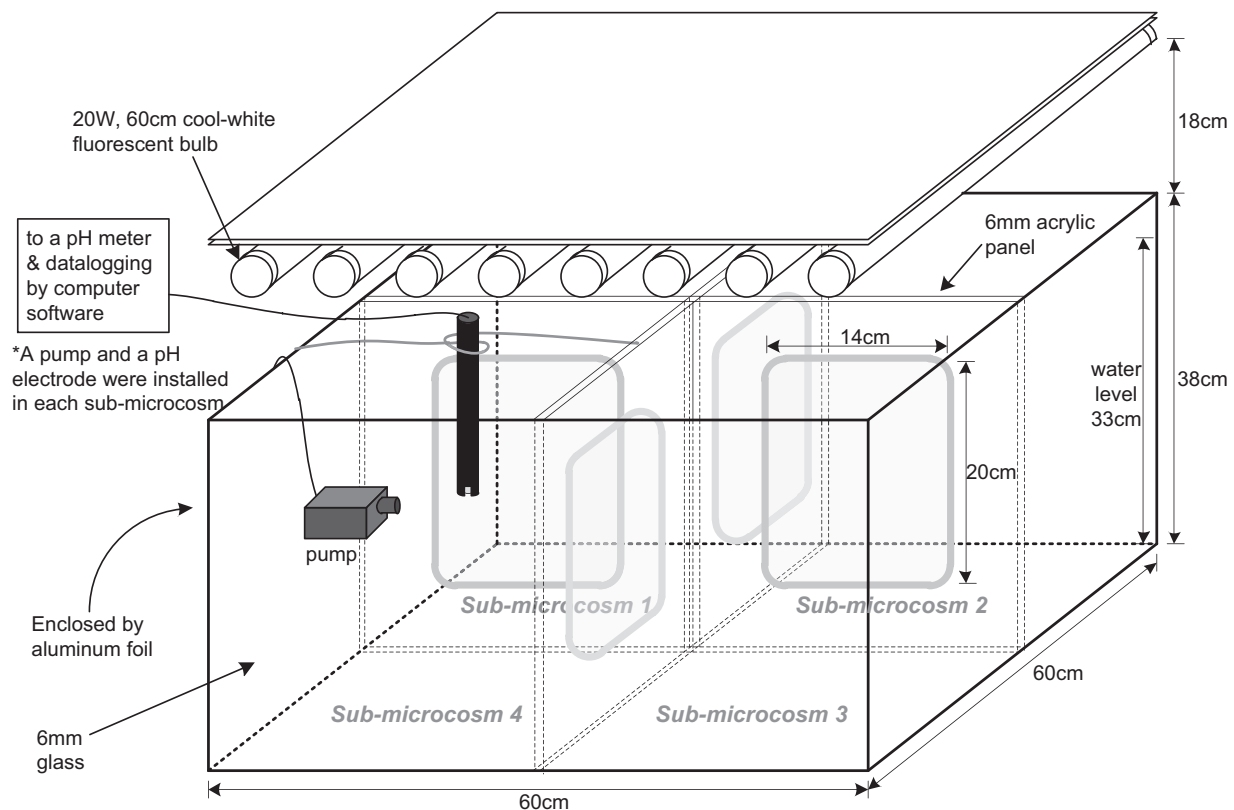


Fig. 1. Design of a microcosm system.

Table 3
Disturbance regimes applied to microcosms for intensity- or frequency-varied tests.

Sub-microcosm	Intensity	Frequency (h)	Duration ^a (h)	Total energy ^b
For intensity-varied tests (10 day or 5 day disturbance period)				
1	0	–	–	0
2	28	24	1 or 2 ^c	280
3	50	24	1 or 2 ^c	500
4	62	24	1 or 2 ^c	620
For frequency-varied tests (5 day disturbance period)				
1	8	Continuous	105	840
2	56	4	0.5 ^d	840
3	56	8	1 ^e	840
4	56	24	3 ^f	840

^a Per each disturbance event.

^b Calculated by multiplying intensity (power) and total duration (time) of disturbances as a dimensionless value.

^c 1 h (11:00–12:00) for 10 day disturbance or 2 h (11:00–13:00) for 5 day disturbance period.

^d 2:00–2:30, 6:00–6:30, 10:00–10:30, 14:00–14:30, 18:00–18:30, 22:00–22:30.

^e 2:00–3:00, 10:00–11:00, 18:00–19:00.

^f 10:00–13:00.

and post-disturbance periods because difference of GPP levels among the four sub-microcosms under different disturbance regimes was not always obvious from GPP time series graphs. We obtained disturbance– M_{GPP} graphs of the disturbance and post-disturbance periods for each microcosm test and categorized them according to the five disturbance–traits relationships: monotonic increase, monotonic decrease, peaked, U-shaped, and non-significant (Mackey and Currie, 2001).

2.5. Resistance and resilience

Following the definition by Halpern (1988), we defined new indices for resistance (RS) and resilience (RL) different from those provided by Orwin and Wardle (2004), although the concepts of resistance and resilience are the same. RS was used as an indicator of how much GPP or ER of a disturbed sub-microcosm (sub-microcosm 2, 3, or 4) deviates from that of the reference sub-microcosm (sub-microcosm 1). RS was calculated using the following equation:

$$RS_{(Sub-x)} = 1 - \frac{\sum_i^m |(GPP_{i(Sub-x)}/GPP_{i(Sub-1)}) - 1|}{m} \quad (4)$$

where $GPP_{i(Sub-x)}$ is the GPP at time i in sub-microcosm x ($x=2, 3, 4$), and m is the number of days in the disturbance period. The maximum $RS_{(Sub-x)}$ is 1 when $GPP_{(Sub-x)}$ does not deviate from $GPP_{(Sub-1)}$, and $RS_{(Sub-x)}$ decreases as the $GPP_{(Sub-x)}$ deviates from $GPP_{(Sub-1)}$.

RL was used as an indicator of how much GPP or ER, once deviated from that of the reference sub-microcosm during the disturbance period, recovers during the post-disturbance period. RL was calculated using the following equation:

$$RL_{(Sub-x)} = 1 - \frac{\sum_j^n |(GPP_{j(Sub-x)}/GPP_{j(Sub-1)}) - 1|/n}{1 - RS_{(Sub-x)}} \quad (RS_{(Sub-x)} \neq 1) \quad (5)$$

where $GPP_{j(Sub-x)}$ is the GPP at time j in sub-microcosm x ($x=2, 3, 4$), and n is the number of days during the post-disturbance period. The maximum $RL_{(Sub-x)}$ is 1 when the post-disturbance $GPP_{(Sub-x)}$ returns to the $GPP_{(Sub-1)}$, and $RL_{(Sub-x)}$ decreases as the $GPP_{(Sub-x)}$ deviates from $GPP_{(Sub-1)}$ during the post-disturbance period. We calculated RS and RL in terms of GPP and ER for mNI5-10, mNI20-10, mAI5-10, and mAI20-10.

Our RS and RL indices are consistent with those by Orwin and Wardle (2004) in that the maximal resistance and full recovery are defined by +1 and that they give identical values for positive and negative effects (i.e., higher or lower GPP than $GPP_{(Sub-1)}$). Unlike the indices by Orwin and Wardle (2004), however, our indices can

have negative infinite numbers depending on how far GPP deviates from a reference state.

3. Results

3.1. Self-organization of microcosms

Each microcosm went through a rapid change in GPP and ER during the first 5 days after initial setup and GPP and ER stabilized thereafter. The suspended sediments during initial setup stabilized on the bottom of each tank after 3–5 days. Microcosms generally culminated in a combination of algal clusters and heterotrophic species primarily composed of zooplankton. Three to five individuals of snail or freshwater shrimp with body lengths of less than 1 cm were usually observed at the end of the microcosm tests. Regardless of initial states of autotrophy ($GPP/ER > 1$) or heterotrophy ($GPP/ER < 1$) of the microcosms, average GPP/ER values approached 1 from the disturbance in the post-disturbance period with some exceptions (Table 4). This tendency of GPP/ER to

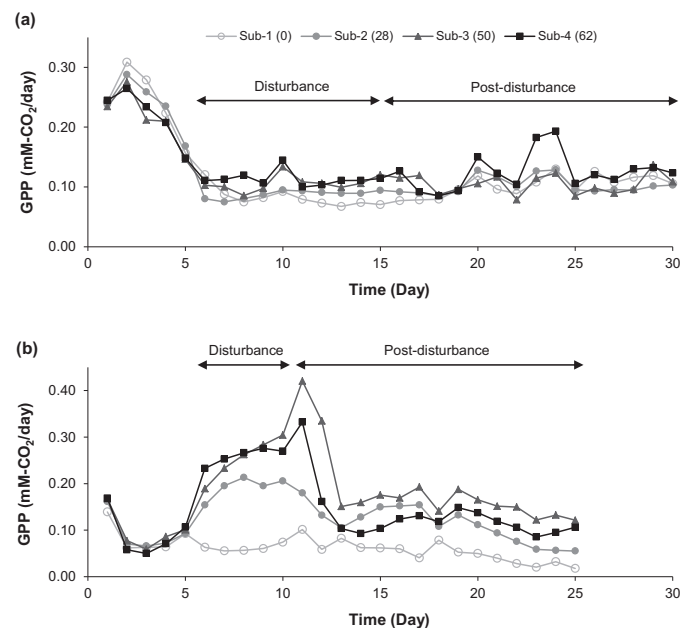


Fig. 2. Examples of GPP time series (the number in each parenthesis of the legend indicates disturbance intensity): (a) GPP of mNI5-10; (b) GPP of NI5-5.

Table 4
Average GPP/ER in the four sub-microcosms of each microcosm during the disturbance and post-disturbance periods.

Microcosm	Average GPP/ER (disturbance)				Average GPP/ER (post-disturbance)			
	Sub-1	Sub-2	Sub-3	Sub-4	Sub-1	Sub-2	Sub-3	Sub-4
mNI5-10	0.86	0.89	0.90	0.90	0.94	0.93	0.91	0.94
mNI20-10	0.90	0.92	0.90	0.91	0.93	0.92	0.91	0.92
mAI5-10	0.91	0.89	0.87	0.89	1.01	0.99	1.02	0.95
mAI20-10	1.06	1.06	1.06	1.06	1.04	1.04	1.03	1.03
SI 1-5	1.28	1.48	1.40	1.80	1.07	1.11	1.15	1.05
SF1-5	1.64	1.40	1.45	1.37	1.03	0.99	1.04	1.05
WI1-5	1.10	1.21	1.15	1.13	1.06	1.20	1.00	1.04
WF1-5	1.06 ^a	1.09	1.09	1.14	1.13 ^a	1.02	1.01	1.05
OI5-10	1.06	1.14	1.21	1.16	1.01	1.00	1.00	1.01
OF5-5	1.51	1.50	1.63	1.48	1.01	0.99	0.99	0.99
AI5-5	1.37	1.28	1.25	1.27	1.01	0.98	1.06	1.04
AF5-5	1.22	1.18	1.14	1.24	1.11	1.06	1.09	1.03
NI5-5	0.96 ^a	0.97 ^a	0.96	0.97	0.90 ^a	0.94 ^a	0.98	0.97
NF5-5	1.00 ^a	0.99 ^a	0.98 ^a	0.95	0.90 ^a	0.97 ^a	0.96 ^a	0.99

^a Exceptions in the self-organizing pattern where GPP/ER approaches 1 over time.

converge to 1 over time occurred in both undisturbed (Sub-1) and disturbed microcosms (Sub-2, Sub-3, Sub-4).

3.2. Disturbance–productivity relationships

We obtained GPP time series of each microcosm. Fig. 2 shows the two examples of GPP time series from microcosms mNI5-10 and NI5-5. Each microcosm test represented unique time series of the four sub-microcosms. In some microcosms, GPP rank among the four sub-microcosms was inconsistent over time as shown in the GPP time series of mNI5-10 (Fig. 2a). NI5-5, however, represented clear difference of GPP among the sub-microcosms over time (Fig. 2b). To clarify GPP difference among sub-microcosms in a microcosm, we calculated average GPP (M_{GPP}) as a temporal average for disturbance and post-disturbance periods.

Intensity of disturbance had variable effect on microcosm GPP both during and following disturbance (Fig. 3a). In some cases during the period of disturbance increasing intensity caused increases in GPP (mNI5-10, mNI20-10, AI5-5, NI5-5), in others there was a decrease in GPP with increased intensity (mAI5-10, mAI20-10, OI5-10). Following disturbance, the effects of water motion disturbance intensity on M_{GPP} were variable as well, with some microcosms exhibiting a monotonic increase (mNI5-10), monotonic decrease (mAI5-10), U-shaped (mNI20-10, OI5-10, AI5-5), peaked (mAI20-10, NI5-5), and non-significant (SI1-5, WI1-5). The same intensity- M_{GPP} relationships remained through the disturbance and post-disturbance periods only in mNI5-10 and OI5-10. In these intensity-varied microcosm tests, disturbance- M_{GPP} relationships of the post-disturbance period were variable with different initial samples under the same input sequence of a test plan and disturbance regimes (mNI5-10 & mAI5-10 & OI5-10, mNI20-10 & mAI20-10, SI1-5 & WI1-5, AI5-5 & NI5-5). For example, mNI5-10, mAI5-10, and OI5-10 were sampled from Lake Newnan, Alice, and Orange, respectively, but tested under the same test plan of 5-10-15 (days) and the same disturbance regimes (Table 2). These three microcosms showed different disturbance- M_{GPP} relationships: monotonic increase in mNI5-10, monotonic decrease in mAI5-10, and U-shaped in OI5-10 during both the disturbance and the post-disturbance periods. In the frequency-varied tests (Fig. 3b), there were few clear trends in the relationship between disturbance frequency and GPP, although in three of the five microcosms (OF5-5, AF5-5, and NF5-5) M_{GPP} values were higher under the discrete disturbances (regimes 2, 3, and 4) than the continuous one (regime 1) during both the disturbance and the post-disturbance periods.

Uncertainty of the data used to compute disturbance- M_{GPP} relationships was analyzed in terms of potential pH measurement error, alkalinity measurement error, and GCO_2 corrections. According to the error bars, the disturbance- M_{GPP} relationship from each microcosm test remained consistent with potential ± 0.02 pH measurement error applied to the whole test period (Fig. 3). We also analyzed the consistency of disturbance- M_{GPP} relationship under potential alkalinity measurement error. Regardless of the volume of water sample (either 100 ml or 50 ml) for alkalinity titration, a minimum accuracy of ± 0.005 meq (± 0.005 meq for 50 ml sample, ± 0.0025 meq for 100 ml sample) was guaranteed per each digit of the titrator. According to our analysis, at least 5 digit error (± 0.025 meq) in alkalinity measurement should occur to represent the similar error range shown in the M_{GPP} graphs (Fig. 3) estimated from potential ± 0.02 pH measurement error. Potential changes of the disturbance- M_{GPP} relationships of the post-disturbance period were analyzed by including GCO_2 corrections (Fig. 4). The disturbance- M_{GPP} relationships were altered with increasing k (cm/h) in SI1-5 and WF1-5 (Fig. 4a and b). The fluctuating $[PCO_2]$ diel pattern, a phenomenon occurring in a self-sustaining system, however, disappeared with the theoretical GCO_2 corrections when k values were equal to or greater than 1 cm/h in SI1-5 (Fig. 4c).

3.3. Stability of microcosms under disturbance

The two microcosm sets (mNI5-10/mNI20-10 and mAI5-10/mAI20-10) showed higher resistance (RS) and lower resilience (RL) in mature systems than less mature ones in terms of both GPP and ER with an exception of RS in the ER of Sub-3 of the mAI5-10/mAI20-10 set (Table 5). The difference of RS of GPP between a less mature system and a mature one ranged 0.10–0.24 in the mNI5-10/mNI20-10 set and 0–0.01 in the mAI5-10/mAI20-10 set. The difference of RL of GPP between a less mature system and a mature one ranged 0.18–1.16 in the mNI5-10/mNI20-10 set and 6.90–13.53 in the mAI5-10/mAI20-10 set.

4. Discussion

4.1. Disturbance–productivity relationships from microcosm tests

We selected lake ecosystems as the ecosystem type for the microcosms and water motion as the disturbance agent. Disturbance is generally regarded as an unusual event that stresses a system (Sousa, 1984; White and Pickett, 1985). Thus a certain external force regarded as a disturbance in a system may not be a

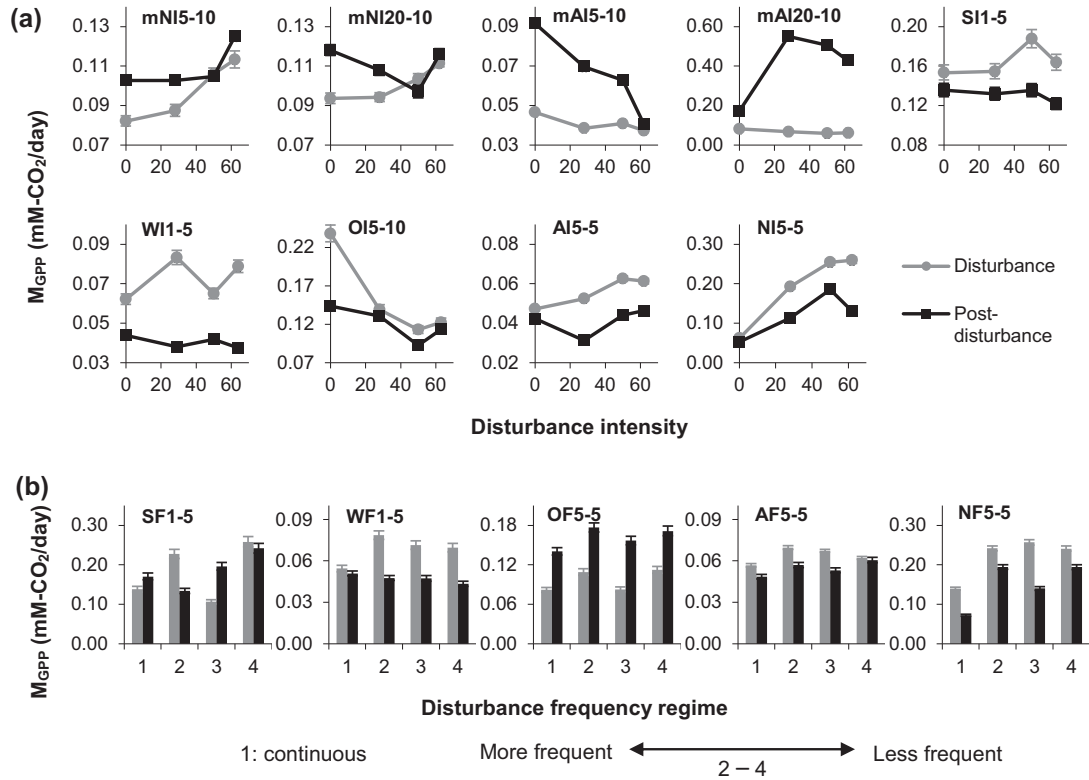


Fig. 3. Relationships between disturbance regimes and average GPP (M_{GPP}) in the 14 microcosm tests (the error bars indicate possible error ranges of M_{GPP} under potential ± 0.02 pH measurement error). (a) Intensity-varied tests (each data point represents the M_{GPP} in one of the four sub-microcosms within a microcosm in the period of disturbance or post-disturbance). (b) Frequency-varied tests (each regime number is equivalent to each sub-microcosm number).

disturbance in another system depending on vulnerability of a system to the force. We assumed water motion acts as a disturbance on the organisms of the microcosms that have been well adapted to the near still-water condition of the lakes where the microcosm samples were collected.

We intended to test system-level responses to various disturbance regimes. It should be noted that our disturbance regimes were intermediate and expected to change part of the system configurations, which differs from the large destructive disturbances that might disorder the entire ecosystem driving it close to primary succession.

Variation among the initial microcosm samples was the most reasonable factor for the variable disturbance–productivity relationships, identified in the intensity-varied tests. The sampled lakes represented remarkable differences in chemical and biological properties, such as total phosphorus and nitrogen concentrations, pH, alkalinity, turbidity, and chlorophyll concentration (Table 1). Even if samples were collected at the same location of a lake, the

trajectories of pH and alkalinity were different between the two microcosms collected at different times of the year (e.g., mAI5-10 and AI5-5 from Lake Alice) likely because of seasonal variation (Staeher and Sand-Jensen, 2007) or anthropogenic management (e.g., spraying chemicals to control an algal bloom). The sensitivity of the disturbance–productivity relationship to initial samples was also identified in the frequency-varied tests, although the difference between the effects of continuous and discrete disturbances on productivity was consistent in OF5-5, AF5-5, and NF5-5.

The disturbance–productivity relationship was variable even within a microcosm test depending on the time period over which M_{GPP} was calculated. Microcosm tests represented different disturbance– M_{GPP} relationships between the disturbance and post-disturbance periods (Fig. 3). When we calculated M_{GPP} over the whole period from the disturbance to the post-disturbance, disturbance– M_{GPP} relationships of this combined period were generally close to those of the 15 day post-disturbance period. Although we calculated M_{GPP} of the post-disturbance period using

Table 5
Resistance (RS) and resilience (RL) of GPP and ER.

Stability index	Microcosm	Maturity	GPP			ER		
			Sub-2	Sub-3	Sub-4	Sub-2	Sub-3	Sub-4
RS	mNI5-10	Less mature	0.81	0.65	0.57	0.89	0.75	0.66
	mNI20-10	Mature	0.91	0.89	0.81	0.93	0.90	0.83
	mAI5-10	Less mature	0.80	0.73	0.76	0.80	0.80 ^a	0.75
	mAI20-10	Mature	0.81	0.74	0.76	0.82	0.74 ^a	0.77
RL	mNI5-10	Less mature	0.38	0.52	0.47	−0.20	0.38	0.33
	mNI20-10	Mature	0.03	−0.64	0.29	−0.29	−0.61	0.25
	mAI5-10	Less mature	−0.33	0.08	−1.00	−0.31	−0.14	−0.83
	mAI20-10	Mature	−13.86	−8.76	−7.90	−16.18	−9.63	−9.03

^a An exception in the pattern of higher resistance in a mature system than a less mature one.

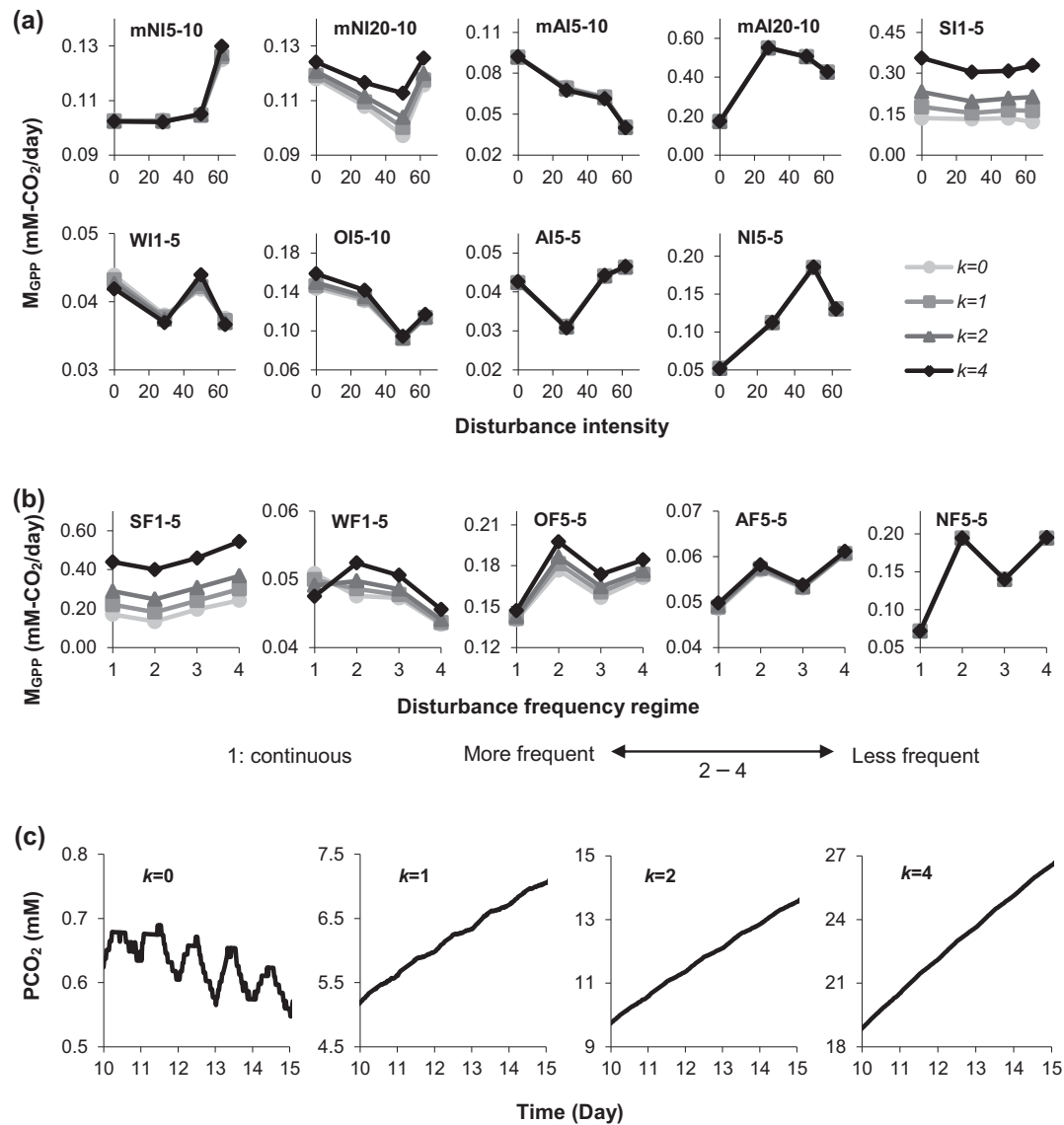


Fig. 4. Sensitivity analyses of disturbance- M_{GPP} relationships of the 14 microcosm tests under GCO₂ corrections (in each microcosm, sensitivity of disturbance- M_{GPP} relationship of the 15 day post-disturbance period was analyzed with CO₂ transfer velocity k (cm/h) of 0, 1, 2, and 4). (a) Intensity-varied tests; (b) frequency-varied tests; (c) PCO₂ diel patterns of microcosm SI1-5 under the four k values.

15 day GPP data in Fig. 3, in some microcosms disturbance- M_{GPP} relationships were variable when we calculated M_{GPP} for different periods. For example, from our analyses, mAI5-10 showed an increasing disturbance- M_{GPP} relationship in the early post-disturbance period (Day 16–17) but a decreasing relationship in the whole post-disturbance period (Day 16–30). The post-disturbance period was standardized to 15 days for the purposes of comparisons among microcosms. We determined the 15 day post-disturbance period as a minimum duration for one generation of higher-trophic-level species (zooplankton) to represent disturbance effects under complex interactions with lower-trophic-level species (phytoplankton) and a maximum duration to observe the change of GPP affected mainly by disturbances. We speculated that effects of certain disturbances do not remain long because other endogenous or exogenous factors may also influence self-organization of the microcosms (Connell and Slatyer, 1977; Turner et al., 1998).

We analyzed the reliability of the results in terms of potential pH measurement error and GCO₂ corrections. Disturbance- M_{GPP}

relationships remained with potential ± 0.02 pH error, the accuracy of the pH meters. The disturbance- M_{GPP} relationship of SI1-5 was most uncertain under higher potential pH errors (>0.02 or <-0.02). In the GCO₂ corrections, the loss of [PCO₂] diel fluctuation patterns in SI1-5 with k (cm/h) of 1, 2, and 4 may indicate that appropriate k values are lower than 1 cm/h if a microcosm is self-sustaining without any subsidy (Fig. 4c). We did not subsidize any material or energy except the fluorescent light throughout the tests, and self-organization generally drove the GPP/ER of the microcosms to 1. If the k value is less than 1 cm/h, CO₂ gas exchange across the air-water interface does not alter the disturbance- M_{GPP} relationships in the controlled laboratory environment (no wind). Flow-induced CO₂ exchange across the air-water interface during the water motion would be also minor because water motion was only applied during the disturbance period and maximum 2 h a day in the intensity-varied tests or 3 h a day in the frequency-varied tests. The estimated average circulation velocity of microcosm water under the highest disturbance intensity (62) was approximately 5 cm/s. An estimated k value under the highest disturbance

intensity was approximately 1.1 cm/h assuming that k is proportional to the square root of circulation velocity (Borges et al., 2004). Potential error might come from chemically enhanced diffusion of CO₂ under high pH conditions (Bade and Cole, 2006). The pH temporarily reached up to 10 in mAI20-10 in the diel fluctuations. However, surface slicks in the stagnant microcosm water might reduce CO₂ diffusion (MacIntyre et al., 1995). Maintenance of microcosms, such as refilling water and cleaning electrodes, did not affect pH or alkalinity of water.

The multiple experiments (Heath, 1979), where we tested microcosms with different initial samples but the same input sequence of disturbance regimes and test plans, were indispensable in discovering the variable responses of GPP to the same disturbance regimes. Our experimental design focused more on the multiple experiments than replication of the tests under the trade-offs among time, space, and resources. In terms of replication of microcosm tests from the same initial sample, we observed similar trajectories of pH and alkalinity among replicated microcosms from our preliminary studies when the microcosms were initially cross-seeded through the holes in a tank.

4.2. Self-organization of the microcosms and their applicability

It was intriguing that the system-level response was quite sensitive to initial sample condition even in the relatively simple microcosm systems (compared with natural ecosystems). We expected a consistent disturbance–productivity relationship that was a characteristic of the system type, even with different initial sample conditions. We reasoned that similar ecosystem types may have typical responsive patterns under the same input sequence of test plans and disturbance regimes, even if their initial properties are different. However, we learned that the response of the microcosms to disturbance appears to be sensitive to the initial states of microcosms since no clear, consistent pattern emerged. The sensitivity of the system-level response to initial states within one type of ecosystem leads us to conclude that the disturbance–productivity relationship may be more influenced by initial state of the system than by the ecosystem type. In this regard, the results of the microcosm tests may be applicable to other ecosystems if certain external forces can be regarded as disturbances to the systems.

From the results of resistance and resilience tests (Table 5), we confirmed that a mature system shows higher resistance but lower resilience than a less mature counterpart. We speculate that the microcosms used in the maturity tests self-organized over time to build complex networks that could resist disturbance, but once they were disturbed in the mature state they showed much different GPP and ER trajectories from the reference systems. As argued in network theory, mature systems tend to become less resilient when disturbance attacks high linkage nodes in the systems. We suppose that mAI5-10/mAI20-10 microcosms did not build stronger linkage than mNI5-10/mNI20-10 microcosms did because resistance almost remained constant but resilience changed significantly in mAI5-10/mAI20-10 microcosms over time.

In contrast to our expectation that the microcosm systems' responses would be fairly consistent, self-organization of the microcosms was as inconsistent and complex as that of real ecosystems. Given the complexity of the response of these microcosm systems to disturbance, might these results apply to restored or constructed ecosystems that do not have a full composition of species and are in early stages of self-organization? Although the microcosms do not fully represent the complexity of natural ecosystems occurring from interactions among diverse hierarchical species groups, the restricted composition of species resulting from the microcosms' small capacity may become an analogy of

early stages of restored or constructed ecosystems. Thus our microcosm study would not be just limited in its applicability by its scale but may provide useful insights for the management of ecosystems (restored or constructed) and disturbance regimes (natural or anthropogenic).

4.3. Insights from the microcosm tests for restoration and management of ecosystems

Depending on initial conditions of an ecosystem, disturbance may or may not be necessary for maximum power acquisition. That is, disturbance neither always reduces productivity nor always increases it. For example, all disturbance intensities increased productivity in mNI5-10, but decreased it in mAI5-10 (Fig. 3). Regarding ecological engineering for ecosystem restoration, this implies that the selection of initial seeds is critical for future productivity, or power acquisition, and that it needs to be determined by disturbance regimes prevalent in the system. Disturbance timing is also important. As an example, productivity patterns under all disturbance intensities were opposite between mAI5-10 (disturbed early) and mAI20-10 (disturbed late), which were initially sampled from the same lake and replicated during the initial stabilization period (Fig. 3). The importance of the disturbance timing was also identified from the analyses of resistance and resilience. Our data from preliminary studies as well as mNI5-10, mNI20-10, mAI5-10, and mAI20-10 showed that microcosms become less resilient but more resistant to disturbances as they mature, which supports the theory on ecosystems' stability under different maturities (Beyers, 1962; Margalef, 1963; Odum, 1969).

It is also worth noting that the degree of self-organization over time is different among different systems. The test of mNI5-10/mNI20-10 pair showed more change in resistance but less change in resilience than that of mAI5-10/mAI20-10 pair (Table 5). This may imply that mNI5-10 and mNI20-10 built stronger internal networks against disturbances than mAI5-10 and mAI20-10. In the microcosm tests, average GPP/ER approached 1 over time in most microcosms, while NI5-5 and NF5-5 represented some exceptions where GPP/ER slightly diverged from 1 during the post-disturbance period (Table 4). The slight divergence of the average GPP/ER in NI5-5 and NF5-5 may indicate the adaptability of the initial samples of NI5-5 and NF5-5 to their environments at the initial setup. Here we mean by "adaptability" the required time for restored systems to reach final states of ecosystem organization and complexity depending on the beginning states. As an analogy, we expect some restored systems will need a significant degree of self-organization due to a discrepancy between initial and final states appropriate to their environments while others require minimum degree of self-organization by their initial adaptability to their environments. In this regard, restoration success depends on the selection of initial sources and monitoring of self-organizing patterns.

5. Conclusions

Gross primary productivity is a process of maximum power acquisition for the resource availability in a food web of an ecosystem. The microcosms, transplanted as a whole from lakes, self-organized to balanced production–consumption systems. From the 14 microcosm tests, we identified five different disturbance–productivity relationships under the same input sequence of test plans and disturbance regimes. These variable relationships were attributed to initial states of the microcosms. Analyses of resistance and resilience in terms of productivity and respiration rate revealed that resistance increased and resilience decreased as the microcosms matured. The microcosm tests provided insights on the restoration of ecosystems that initial seeds

for restoration of an ecosystem should be carefully selected in consideration of typical disturbance regimes of the region and that consideration or manipulation of disturbance regimes in each successional stage is sometimes needed for maximum productivity or a designated goal of a restoration project because self-organizing patterns under disturbances are variable depending on a system's maturity.

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