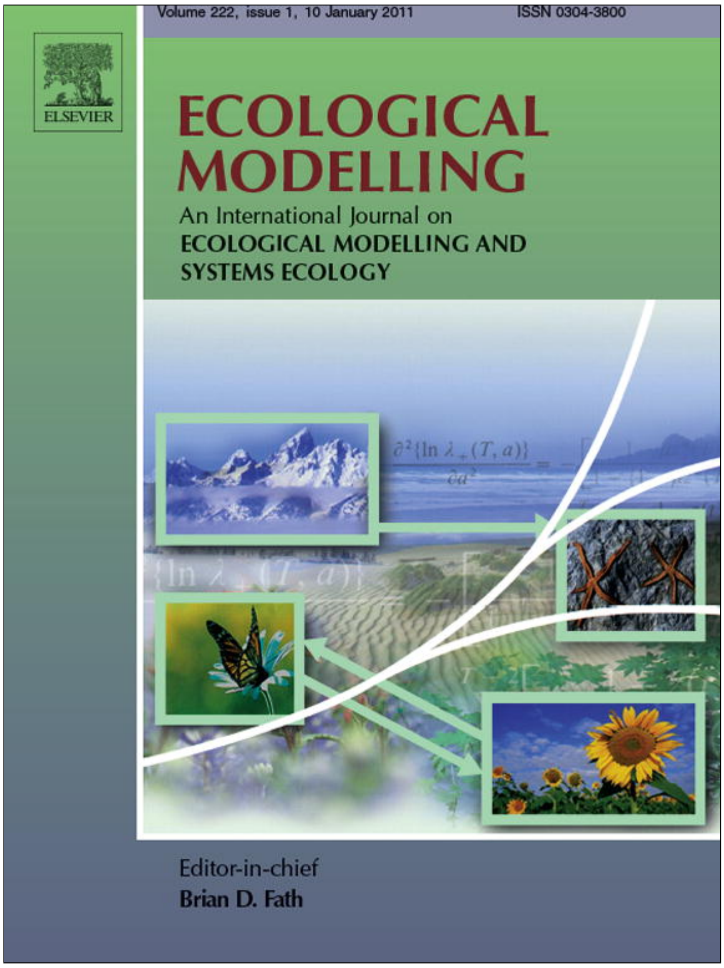
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An energetic perspective on the relationship between disturbance and ecosystem productivity

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ABSTRACT

Previous ecological models for disturbance from energetic perspectives have focused on destructive pulses by which storages in a system are quickly drained during disturbance events and recovered thereafter. However, considering the wide range of disturbance intensities, frequencies, and durations in nature, disturbance effects on ecosystem energetics would be better understood by diversifying the disturbance effects on specific system configurations or energy pathways. Based on two hypotheses, we built simulation models of the variable disturbance–productivity relationships observed in a fresh-water aquatic microcosm study. First, we hypothesized that disturbances will differentially alter the intrinsic rates of energy pathways in a system. Second, we hypothesized that there is a disturbance threshold where response of the intrinsic rates changes abruptly. Simulation results showed variable patterns of gross primary productivity (GPP) during the disturbance and post-disturbance periods under the diverse scenarios of disturbance effects on the intrinsic rates. Simulation results confirmed that the second hypothesis (i.e., disturbance threshold) was essential to achieve a U-shaped or peaked disturbance–productivity relationship. We evaluated the models by comparing them with the results of the microcosm tests, and suggested possible mechanisms of the variable disturbance–productivity relationships by varying parameters related to the disturbance effects on the intrinsic rates and the disturbance thresholds.

1. Introduction

Natural disturbance is a major source of ecosystem dynamics and heterogeneity (Sousa, 1984). For several decades, discussion of ecological disturbance has centered on the relationship between disturbance and species diversity. As an example, the Intermediate Disturbance Hypothesis (Connell, 1978; Grime, 1973; Roxburgh et al., 2004) has been controversial among ecologists as a core concept that explains the unimodal disturbance–diversity relationship. Recent studies have suggested variable disturbance–diversity relationships (Mackey and Currie, 2001) or further emphasized interactions between productivity and disturbance for species diversity (Haddad et al., 2008; Kondoh, 2001). However, disturbance may directly influence ecosystem productivity, which is rarely explored compared with the disturbance–diversity or diversity–productivity relationship. Despite the recent efforts to investigate the relationship among disturbance, diversity, and productivity (e.g., Cardinale et al., 2005), an energetic perspective has rarely been considered in the study of disturbance–productivity relationship. Sprugel (1985) pointed out that the scarcity of productivity-related disturbance studies is due to less prominent change of energetic parameters under disturbances and the difficulty of measuring these parameters.

Previous ecological models of disturbance from energetic perspectives have primarily focused on destructive pulses (Odum and Odum, 2000b; Reiners, 1983). In these destructive pulse models, disturbances quickly drain storages in a system and the system gradually rebuilds the storages after the disturbances (Fig. 1). Considering the wide range of disturbance regimes (intensity, frequency, and duration) in nature, disturbance effects on ecosystem energetics would be better understood by modeling potentially diverse disturbance effects on specific configurations or energy pathways of a system.

Recent studies on regime shift of ecosystems have suggested that many ecosystems have thresholds where an ecosystem quality abruptly changes (Carpenter et al., 2011; Scheffer et al., 2001). Scheffer et al. (2001) proposed in the alternative stable state hypothesis that an ecosystem changes to an alternative stable state when a disturbance regime exceeds a certain threshold and the threshold may be further altered by external perturbation. In environmental management, it is critical to identify a threshold for regime shift (Groffman et al., 2006).

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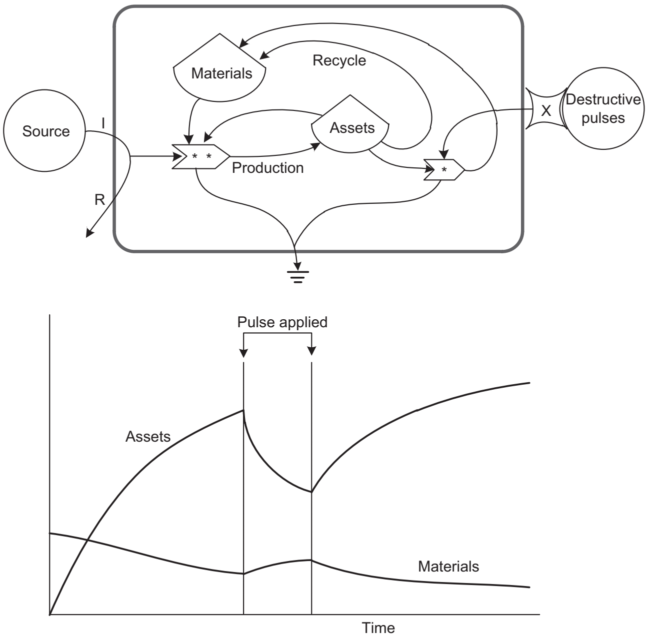

Fig. 1. Energy systems diagram and simulation results of a destructive pulse model (Odum and Odum, 2000b).

Table 1
Test plans and regimes for the 14 microcosms.

Microcosm[a]	Sample lake	Test plan[b] (days)	Test regime
mNI5-10	Newnan	5-10-15	Intensity
mNI20-10	Newnan	20-10-15	Intensity
mAI5-10	Alice	5-10-15	Intensity
mAI20-10	Alice	20-10-15	Intensity
SI1-5	Santa Fe	1-5-15	Intensity
SF1-5	Santa Fe	1-5-15	Frequency
WI1-5	Wauberg	1-5-15	Intensity
WF1-5	Wauberg	1-5-15	Frequency
OI5-10	Orange	5-10-15	Intensity
OF5-5	Orange	5-5-15	Frequency
AI5-5	Alice	5-5-15	Intensity
AF5-5	Alice	5-5-15	Frequency
NI5-5	Newnan	5-5-15	Intensity
NF5-5	Newnan	5-5-15	Frequency

[a] Each pair of microcosms (e.g., mNI5-10 & mNI20-10, mAI5-10 & mAI20-10, etc.) was constructed using the same sample of water and sediment.

[b] Test plan is in the order of the three periods: (initial stabilization)–(disturbance)–(post-disturbance). Initial stabilization: the four sections in a microcosm were replicated by cross seeding. Disturbance: 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.

Ecosystem modeling based on hypotheses is used as a useful tool to identify critical aspects of ecosystems and understand complex ecosystem dynamics (e.g., Montague et al., 2001). Hypothesis-driven ecological models are partially validated by empirical tests. Because hypotheses cannot be proven but can only be disproven by validation (Rykiel, 1996), however, an alternative hypothesis may exist even if modeling and experimental results are consistent.

In this study, we built simulation models for the variable disturbance–productivity relationships observed in a microcosm study (Lee and Brown, 2011) under different hypotheses of the mechanisms of disturbance interaction. We show that the variable productivity response to disturbance can be attributed to disturbance effects on different energy pathways and we confirm the existence of a disturbance threshold, where system energy flow patterns abruptly change, leading to the peaked or U-shaped disturbance–productivity relationship. Finally, we synthesize the results of the microcosm tests and simulation models to evaluate the models and suggest hypothetic mechanisms of the five disturbance–productivity relationships: monotonic increase, monotonic decrease, peaked, U-shaped, and non-significant as defined by Mackey and Currie (2001).

2. Materials and methods

2.1. Microcosm tests

We tested the relationships between disturbance and gross primary productivity (GPP) in 14 freshwater aquatic microcosms constructed using water and sediment collected as a whole from lakes in Florida (Table 1). We divided a glass open-top microcosm tank (60 cm × 60 cm × 38 cm) into four equal sections (sub-microcosms) and applied a distinct pump-induced water motion disturbance regime in each sub-microcosm. We varied either intensity or frequency of disturbance in each microcosm test (Table 1). The microcosms were tested under an alternating fluorescent light regime (12 h light, 12 h darkness) and no nutrient subsidy was added. Ambient conditions (e.g., temperature) were maintained constant. By monitoring pH and alkalinity (Skirrow, 1965; Smith, 1973), we established a disturbance–GPP relationship from each microcosm test. The details of the microcosm study are summarized in Lee and Brown (2011).

2.2. Simulation models

2.2.1. Basic microcosm model and parameterization

A conceptual macroscopic model of a freshwater aquatic microcosm was built with flows of energy (carbon) and recycling of nutrient among the three functional groups: producers, consumers, and decomposers (Fig. 2). Light was the only energy source flowing into the microcosm. The modeled microcosm was assumed to be phosphorus (P) limited so that P was modeled as the nutrient of interest. Producers and consumers were assumed to reproduce by first-order autocatalytic feedback controls (Odum, 1994a). Organic matter from dead producers and consumers was decomposed and recycled by decomposers. Production functions in the model were written as multiplications of contributing state variables and coefficients based on Holling's type I functional response (Table 2). For numerical simulation, flows and storages of energy and nutrients were estimated from relevant literature or the microcosm tests under the steady-state assumption of the variables (producers, consumers, dead organic matter, nutrient, and GPP), and the coefficients for the production functions were back-calculated to satisfy the production functions and the steady-state values as suggested by Odum and Odum (2000a) (Table 3). This basic steady-state microcosm model without disturbance factors was simulated in 5 min intervals (dt = 5 min) for 50 days (14,400 time steps) using *R* (available at the R Project for Statistical Computing, http://www.r-project.org/) to verify the steady state of the variables.

2.2.2. Hypotheses on the mechanisms of disturbance–productivity relationships

We hypothesized two mechanisms of disturbance effects on system-level productivity by interpreting recent studies on disturbance from energetic perspectives. First, a disturbance alters characteristics of energy flow pathways in an ecosystem by filtering out certain species groups according to the type of disturbance and regime (Helmus et al., 2010). The altered characteristics may include configurations or intrinsic flow rates of energy pathways among functional species groups. Second, the alternative stable state hypothesis (Scheffer et al., 2001) proposes the existence of a disturbance threshold that determines a range of disturbance

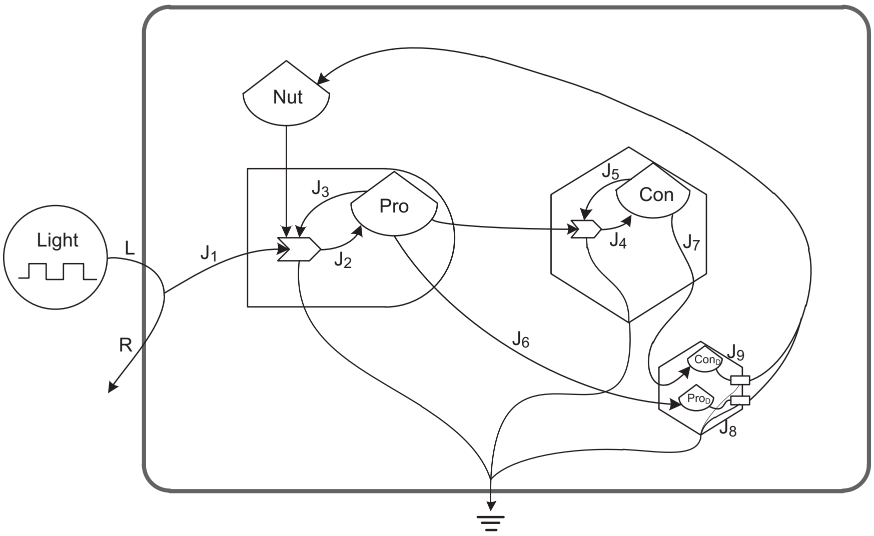

Fig. 2. Energy systems diagram of the basic aquatic microcosm model without disturbance (Pro, producers; Con, consumers; Nut, nutrients; Pro_D, dead organic matter of producers; Con_D, dead organic matter of consumers).

intensities causing abrupt changes to the characteristics of the energy pathways. The threshold is likely to be determined by vulnerability of an ecosystem under the influence of a disturbance (see the definition of disturbance severity in Sousa, 1984).

2.2.3. *Embodying disturbances in the model*

We embodied disturbance factors in the basic steady-state simulation model using the hypothetic mechanisms of disturbance effects on energy flows of the microcosm. First, disturbances alter the intrinsic rates of energy flows, which are represented by the coefficients (c_i) of the production functions. We established the equations for the changing coefficients under disturbances (Table 4). We assumed disturbances always increase the intrinsic rates of the density-dependent death pathways of producers (c_6) and consumers (c_7) but may increase, decrease, or not affect those of the net reproduction pathways of producers ($c_2 - c_3$) and consumers ($c_4 - c_5$) depending on the traits of microcosm samples, such as species' compositions, interactions, and life histories (Sousa, 1980). Second, the changing patterns of the coefficients are dependent on a threshold of disturbance intensity. For this second hypothesis, we assumed the intrinsic rates of the energy flow pathways ($c_2 - c_3$, $c_4 - c_5$, c_6, c_7) change temporarily during disturbances and return to initial states when disturbance intensity is below a threshold, whereas they change permanently above the threshold (Table 4).

As represented in the equations in Table 4, we assigned the unit disturbance factors, f_{dl} and f_{dh}, which indicate percent change of each coefficient per unit time (5 min) by disturbances. Thus the unit disturbance factors imply vulnerability of the intrinsic rate of a pathway to disturbance. If a certain system's energy pathways are altered more than another system's under the same disturbance regime, the former will have higher unit disturbance factors. In each simulation for distinct disturbance effects on $c_2 - c_3$ and $c_4 - c_5$, values of f_{dl} and f_{dh} were selected on a 5 min basis.

2.2.4. *Disturbance regimes*

We followed the concept of intensity, frequency, and duration of disturbance defined by Shea et al. (2004). As in the microcosm tests, we varied either intensity or frequency of disturbances as a gradient of disturbance regimes in the simulation models (Table 5). The same disturbance frequencies and durations as in the microcosm tests were applied to the simulation models. Disturbances were applied for 10 days (Day 20–29) in the intensity-varied tests and 5 days (Day 20–24) in the frequency-varied tests of simulation models.

Table 2
Equations of the basic steady-state model for the microcosm.

Equation	Description	Unit
$L = 0$ (6 pm–6 am)/45 (6 am–6 pm)	Fluorescent light energy	mmol × m^{-2} $(5\,min)^{-1}$
$R = 0.1\,L$	Remaining light not involved in reproduction	mmol × m^{-2} $(5\,min)^{-1}$
$J_1 = c_1 \cdot R \cdot \mathrm{Nut} \cdot \mathrm{Pro}$	Rate of incoming light energy for primary production	mmol × m^{-2} $(5\,min)^{-1}$
$J_2 = c_2 \cdot R \cdot \mathrm{Nut} \cdot \mathrm{Pro}$	Reproduction rate of producers (GPP)	mg-C $(5\,min)^{-1}$
$J_3 = c_3 \cdot R \cdot \mathrm{Nut} \cdot \mathrm{Pro}$	Energy consumption rate of producers for autocatalytic production	mg-C $(5\,min)^{-1}$
$J_4 = c_4 \cdot \mathrm{Pro} \cdot \mathrm{Con}$	Reproduction rate of consumers	mg-C $(5\,min)^{-1}$
$J_5 = c_5 \cdot \mathrm{Pro} \cdot \mathrm{Con}$	Energy consumption rate of consumers for autocatalytic production	mg-C $(5\,min)^{-1}$
$J_6 = c_6 \cdot \mathrm{Pro}$	Death rate of producers (density dependent)	mg-C $(5\,min)^{-1}$
$J_7 = c_7 \cdot \mathrm{Con}$	Death rate of consumers (density dependent)	mg-C $(5\,min)^{-1}$
$J_8 = c_8 \cdot \mathrm{Pro_D}$	Release rate of decomposed organic matter from producers	mg-C $(5\,min)^{-1}$
$J_9 = c_9 \cdot \mathrm{Con_D}$	Release rate of decomposed organic matter from consumers	mg-C $(5\,min)^{-1}$
$d(\mathrm{Pro})/dt = J_2 - J_3 - J_4 - J_6$	Change of storage of producers	mg-C $(5\,min)^{-1}$
$d(\mathrm{Con})/dt = J_4 - J_5 - J_7$	Change of storage of consumers	mg-C $(5\,min)^{-1}$
$d(\mathrm{Pro_D})/dt = J_6 - J_8$	Change of storage of dead organic matter from producers	mg-C $(5\,min)^{-1}$
$d(\mathrm{Con_D})/dt = J_7 - J_9$	Change of storage of dead organic matter from consumers	mg-C $(5\,min)^{-1}$
[a]$\mathrm{Nut} = \mathrm{TN} - f_P\,(\mathrm{Pro} + \mathrm{Pro_D}) - f_C\,(\mathrm{Con} + \mathrm{Con_D})$	Nutrient (P) in the water column	mg-P

[a] Nut indicates available phosphorus concentration in the water column, while TN is total phosphorus in the microcosm system. f_P and f_C indicate phosphorus/carbon in producers and consumers, respectively.

Table 3
Steady-state values of the variables and coefficients of the basic steady-state model for the 30 L microcosm.

Variable	Value	Unit	Steady-state flow	Meaning	Source references
Pro	72	mg-C	–	Producers	Wetzel (2001)[a]
Con	270	mg-C	–	Consumers	Wetzel (2001)[a]
$\mathrm{Pro_D}$	72	mg-C	–	Dead organic matter of Producers	Rodgers and DePinto (1983)[b]
$\mathrm{Con_D}$	72	mg-C	–	Dead organic matter of Consumers	Estimate from $\mathrm{Pro_D}$
Nut	3.85	mg-P	–	Water column P (Phosphorus)	Florida LAKEWATCH (2005)[c]
c_1	3.25×10^{-2}	$(\text{mg-P} \times \text{mg-C})^{-1}$	40.5	Ratio of incoming to remaining light per nutrient per producers	Estimate
c_2	2.00×10^{-4}	$\text{m}^2\,(\text{mmol} \times \text{mg-P})^{-1}$	0.25	Producers' reproducing proportion per light energy per nutrient	Microcosm M1-A
c_3	6.01×10^{-5}	$\text{m}^2\,(\text{mmol} \times \text{mg-P})^{-1}$	0.075	Producers' consuming proportion per light energy per nutrient	Estimate from Lindeman (1942)[d]
c_4	3.21×10^{-6}	$(\text{mg-C} \times 5\,\text{min})^{-1}$	0.0625	Consumers' reproducing proportion per producers	Estimate[e]
c_5	1.93×10^{-6}	$(\text{mg-C} \times 5\,\text{min})^{-1}$	0.0375	Consumers' consuming proportion per producers	Estimate from Lindeman (1942)[d]
c_6	3.47×10^{-4}	$(5\,\text{min})^{-1}$	0.025	Specific rate of death of producers	Steady state
c_7	9.26×10^{-5}	$(5\,\text{min})^{-1}$	0.025	Specific rate of death of consumers	Steady state
c_8	3.47×10^{-4}	$(5\,\text{min})^{-1}$	0.025	Specific rate of decomposition of dead producers	Steady state
c_9	3.47×10^{-4}	$(5\,\text{min})^{-1}$	0.025	Specific rate of decomposition of dead consumers	Steady state
f_P	0.025	–	–	Phosphorus/Carbon (P/C) in Pro and $\mathrm{Pro_D}$	Redfield ratio[f]
f_C	0.025	–	–	Phosphorus/Carbon (P/C) in Con and $\mathrm{Con_D}$	Estimate

[a] The storages of producers and consumers were calculated based on the two day and 15 day turnover rates, respectively.
[b] Ten-day turnover rate for decomposition.
[c] Water column P was assumed to be 128 μg/L (Newnan's Lake).
[d] J_3 was assumed to be 30% of J_2 (considering a new container environment that species need to adapt to, we assumed a higher percentage than the one Lindeman suggested). J_5 was assumed to be 60% of J_4 (a higher percentage was assumed with the same reason for J_3).
[e] Half of GPP (J_2).
[f] Mass ratio of C/P = 41 from Redfield ratio of C:N:P = 106:16:1.

Table 4
Equations for the new coefficients under disturbances.

New coefficient	$p <$ threshold		$p \geq$ threshold	
	Disturbed[a]	Undisturbed[a]	Disturbed[a]	Undisturbed[a]
$(c_2 - c_3)'_t$	$(1 + \alpha \cdot p \cdot f_\mathrm{dl})\,(c_2 - c_3)$[b]	$(c_2 - c_3)$	$(1 + \alpha \cdot p \cdot f_\mathrm{dh} \cdot T)\,(c_2 - c_3)$[b]	$(c_2 - c_3)'_{t-1}$
$(c_4 - c_5)'_t$	$(1 + \alpha \cdot p \cdot f_\mathrm{dl})\,(c_4 - c_5)$[b]	$(c_4 - c_5)$	$(1 + \alpha \cdot p \cdot f_\mathrm{dh} \cdot T)\,(c_4 - c_5)$[b]	$(c_4 - c_5)'_{t-1}$
$(c_6)'_t$	$(1 + p \cdot f_\mathrm{dl})\,(c_6)$	(c_6)	$(1 + p \cdot f_\mathrm{dh} \cdot T)\,(c_6)$	$(c_6)'_{t-1}$
$(c_7)'_t$	$(1 + p \cdot f_\mathrm{dl})\,(c_7)$	(c_7)	$(1 + p \cdot f_\mathrm{dh} \cdot T)\,(c_7)$	$(c_7)'_{t-1}$

[a] "Disturbed" indicates only the time water motion disturbances operate in a microcosm, while "Undisturbed" means the rest of the experimental period.
[b] $\alpha = 1$ (positive effect), $\alpha = -1$ (negative effect), or $\alpha = 0$ (no effect) depending on the designated disturbance effects on the intrinsic rates of the pathways. (c_i) is the coefficient, $(c_i)'_t$ is the new coefficient at time t, p is the disturbance intensity, f_dl is the unit (5 min) disturbance factor at $p <$ threshold, f_dh is the unit (5 min) disturbance factor at $p \geq$ threshold, and T is the total duration of disturbances until t ($T = 1$ for 5 min). In simulations, the time interval of 1 is equivalent to 5 min.

Table 5
Disturbance regimes applied to intensity- or frequency-varied tests in simulation models.

Disturbance regime #	Intensity[a]	Frequency (h)	Duration[b] (h)	Total energy[c]
Intensity-varied tests (Day 20–29)				
0	0	–	–	0
1	1	24	1[d]	10
2	2	24	1[d]	20
3	3	24	1[d]	30
4	4	24	1[d]	40
Frequency-varied tests (Day 20–24)				
0	0	–	–	0
1	1	Continuous	105	105
2	7	4	0.5[e]	105
3	7	8	1[f]	105
4	7	24	3[g]	105

[a] In the microcosm tests, intensity was defined as a dimensionless value by eliminating the unit (ml/s) from the outflow rate of a pump.
[b] Per each disturbance event.
[c] Calculated by multiplying intensity (power) and total duration (time) of disturbances as a dimensionless value.
[d] 11:00–12:00.
[e] 2:00–2:30, 6:00–6:30, 10:00–10:30, 14:00–14:30, 18:00–18:30, and 22:00–22:30.
[f] 2:00–3:00, 10:00–11:00, and 18:00–19:00.
[g] 10:00–13:00.

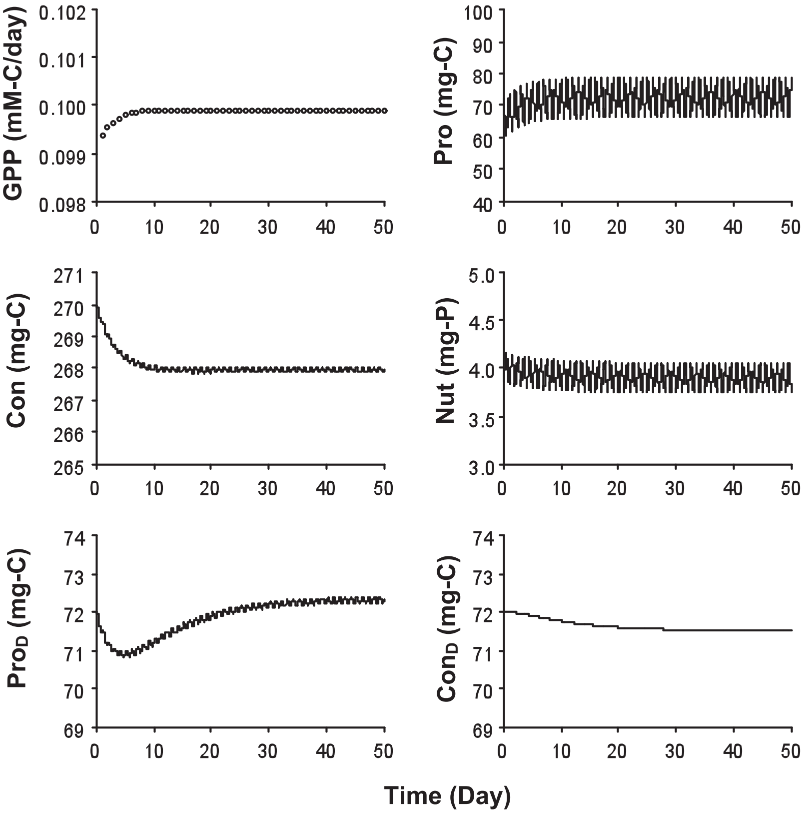

Fig. 3. Simulation results of the basic steady-state microcosm model showing GPP and the five state variables: Pro, producers; Con, consumers; Nut, nutrients; Pro$_D$, dead organic matter of producers; and Con$_D$, dead organic matter of consumers. (GPP was calculated by averaging all GPP values in each day.)

2.2.5. Model output and manipulation of disturbance parameters

Model output was a GPP time series from which we calculated average GPP (M_{GPP}) of the disturbance and post-disturbance periods (15 days after disturbance). Using the disturbance–productivity relationships found in the microcosm tests, we developed approximate models of the disturbance–M_{GPP} relationships by manipulating the disturbance-related parameters in each simulation. We varied the disturbance-related parameters, such as f_{dl}, f_{dh}, disturbance threshold, and disturbance effects on $c_2 - c_3$ and $c_4 - c_5$, to examine how they influence patterns of the GPP time series. Manipulation of disturbance-related parameters (i.e., f_{dl}, f_{dh}, disturbance threshold, and disturbance effects on $c_2 - c_3$ and $c_4 - c_5$) and observation of the resulting disturbance–M_{GPP} relationships, lead to hypotheses regarding the mechanisms of disturbance influence on systems.

3. Results

3.1. Basic steady-state model

The basic steady-state microcosm model was simulated for 50 days (Fig. 3). The time interval of simulation (dt = 5 min) was small enough not to change the simulation results with a smaller dt. The state variables of GPP, Pro, Con, and Nut leveled off after the approximate initial transient time of 10 days. This initial transient time was necessary to achieve the steady state of the state variables because the selection of decimal places in the coefficients limited the accuracy of coefficient values for steady states during the initial transient time.

3.2. Effects of disturbance parameters

We examined GPP time series patterns by varying nine combinations of disturbance effects on the intrinsic rates of the net reproduction pathways of producers ($c_2 - c_3$) and consumers ($c_4 - c_5$) for the intensity- and frequency-varied disturbance tests under disturbance intensities below and above a threshold (Fig. 4). Increasing or decreasing patterns of GPP time series during the disturbance or post-disturbance period were variable depending on the combination of disturbance effects on $c_2 - c_3$ and $c_4 - c_5$. Some combinations of disturbance effects on $c_2 - c_3$ and $c_4 - c_5$ represented similar GPP time series patterns. For example, GPP time series patterns were similar when disturbance decreases or does not affect $c_2 - c_3$ if disturbance increases $c_4 - c_5$ (i.e., (−,+) and (0,+)). Disturbance effects on $c_2 - c_3$ and $c_4 - c_5$ causing similar patterns of GPP time series were grouped together (Fig. 4).

The second hypothesis (i.e., disturbance threshold) was necessary to generate M_{GPP}–disturbance relationships other than monotonic increase or decrease as exemplified in Fig. 5. In Fig. 5c, a U-shaped disturbance–M_{GPP} relationship was possible when a threshold of disturbance intensity is in-between the maximum and minimum intensities with proper f_{dl} and f_{dh} values. Under a designated combination of disturbance effects on $c_2 - c_3$ and $c_4 - c_5$, an increase of the disturbance intensity (p) maintained patterns of GPP time series but increased the distance of GPP from a reference GPP as in Fig. 5a and b. Thus, in the example of Fig. 5, the disturbance–M_{GPP} relationship was a monotonic decrease (Fig. 5a and b) when the disturbance thresholds were out of the tested disturbance intensity range (0 or 5).

3.3. Results of microcosms and simulation models

Fig. 6 shows graphs of M_{GPP} of the microcosm studies (mNI5-10 though NF5-5) and simulation results of the macroscopic mini-model of disturbance (MI1 through MF5). The simulation results were matched with the microcosm results based on overall similarities of model response during the disturbance and during

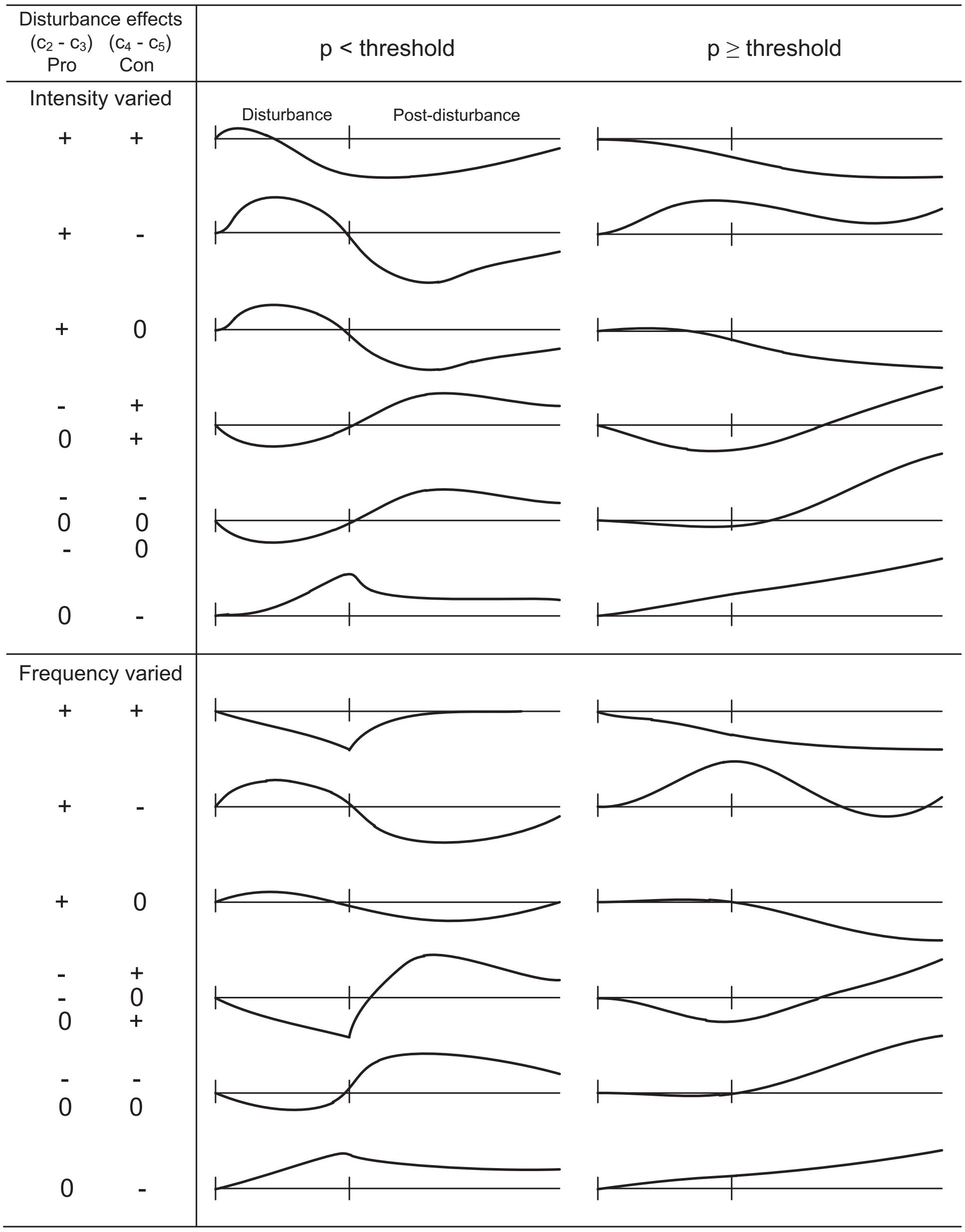

Fig. 4. Simulated patterns of GPP time series under different disturbance effects on the intrinsic rates of the reproduction pathways. (The horizontal lines indicate the reference GPP at disturbance intensity 0. The signs for $(c_2 - c_3)$ and $(c_4 - c_5)$ indicate disturbance effects on the intrinsic rates of the net reproduction pathways for producers and consumers: increasing (+), decreasing (−), or no effect (0). In the first column of graphs, the disturbance is assumed less than the threshold and therefore coefficients are reset to pre-disturbance values. In the second column the disturbance is assumed greater than the threshold and therefore coefficients are not reset.)

the post-disturbance period. By matching the simulation outputs we then provide possible mechanisms (i.e., disturbance threshold, f_{dl}, f_{dh}, disturbance effects on $c_2 - c_3$ and $c_4 - c_5$) for microcosm response to disturbance. Nine combinations of disturbance parameters under the intensity regime yielded simulation results similar to those of the microcosms (Fig. 6a), while three combinations of the disturbance parameters under the frequency regime yielded similar simulation results (Fig. 6b). We represented M_{GPP} versus disturbance frequency regime with bar graphs in Fig. 6b because frequency regimes are categorical data. The *y*-axis values in the simulation results (MI1 through MF5) do not agree with those in the microcosms (mNI5-10 through NF5-5) because the basic simulation model was built with parameters referred from literature, microcosm, or our estimation. We defined the similarity between the results of microcosm and simulation model by the five M_{GPP}–disturbance relationships (monotonic increase, monotonic decrease, U-shaped, peaked, non-significant). By applying the second hypothesis on disturbance threshold, we simulated U-shaped (MI2, MI7, MI8) or peaked (MI9) M_{GPP}–disturbance relationships during the post-disturbance (Fig. 6a). We also simulated M_{GPP}–disturbance relationships resulted from the microcosms during both the disturbance and post-disturbance periods with the parameters we selected in each microcosm simulation. The simulation result of MF3, MF4, and MF5 in Fig. 6b shows the similar M_{GPP}–disturbance relationship to OF5-5, AF5-5, and NF5-5, where the M_{GPP} values of the discretely disturbed systems are higher than those of the continuously disturbed system under the same total disturbance energy, although the simulation result could not represent the M_{GPP} rank among the frequency regimes 2, 3, and 4 in OF5-5, AF5-5, and NF5-5.

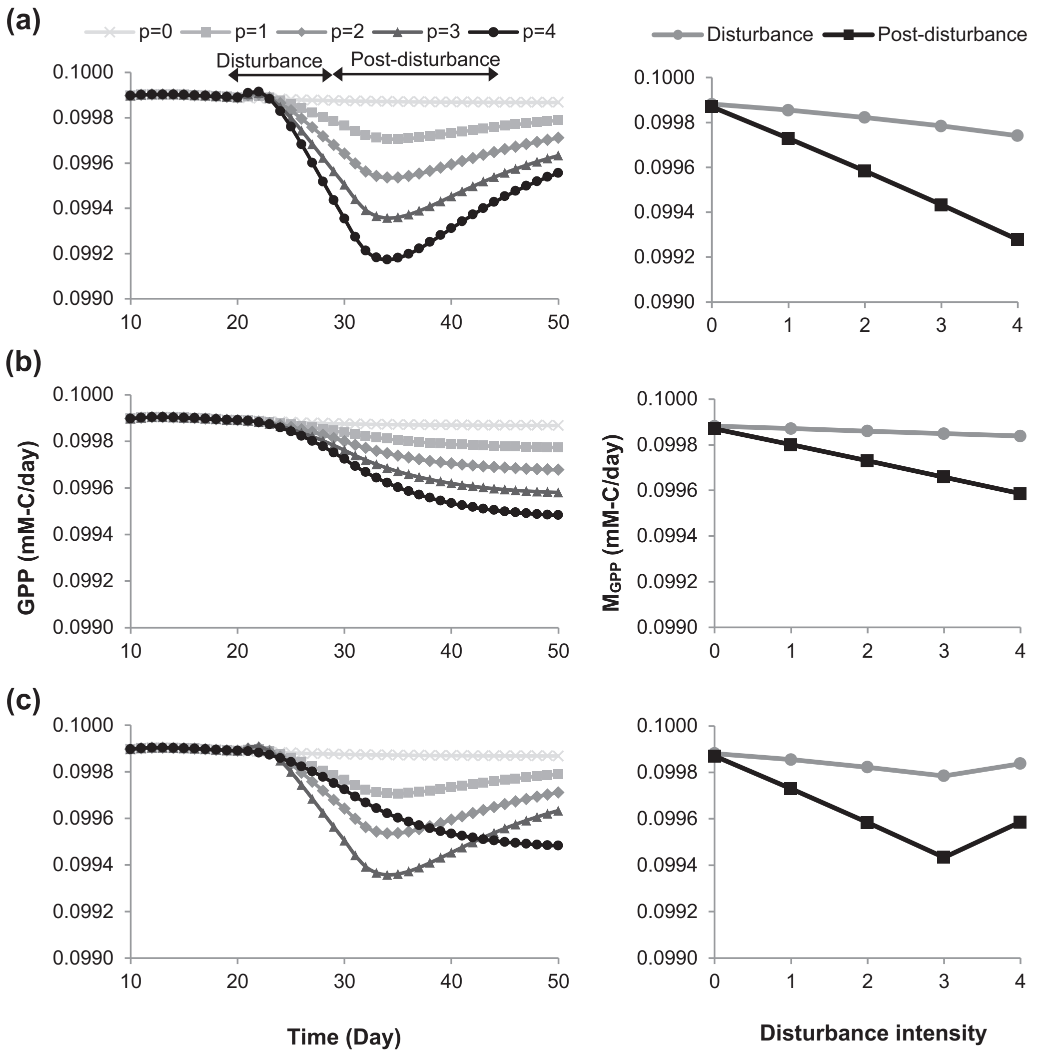

Fig. 5. An example showing the necessity of a disturbance threshold for disturbance–M_{GPP} relationships other than monotonic increase or decrease. (Simulation of the intensity-varied test, disturbance during Day 20–29, post-disturbance during Day 30–44, disturbance effect on $(c_2 - c_3, c_4 - c_5) = (+,+)$ at both $p <$ threshold and $p \geq$ threshold, $f_{\mathrm{dl}} = 0.4$, $f_{\mathrm{dh}} = 0.0001$). (a) threshold = 5, (b) threshold = 0, and (c) threshold = 4.

4. Discussion

The variable disturbance–M_{GPP} relationships resulted from the microcosms under different initial samples but the same input sequence of disturbance regimes and test plans. Those variable relationships may imply that components of a microcosm and their interactions are characterized by unique energy flow pathways and that disturbance alters GPP patterns by differentially influencing these pathways. If so, GPP patterns will be determined by specific effects of disturbances on different energy flow pathways. We speculated that the energy flow pathways between functional groups in our microcosms had intrinsic rates and that disturbance can alter those rates. From this perspective, we established the isomorphism between the change of coefficients in the simulation models and the change of intrinsic rates of energy flow pathways in the microcosms under the suite of disturbances.

4.1. *Mechanisms for the disturbance–productivity relationships*

We suggested possible mechanisms for the disturbance–productivity relationship of each microcosm test using the disturbance parameters assigned for each simulation model by choosing the simulation results that best matched the microcosm behavior during and after disturbance (Fig. 6). For example, suggested mechanisms for the changes in M_{GPP} of NI5-5 was that disturbance intensities 0, 28, and 50 did not affect the intrinsic rate of net reproduction pathways of producers but decreased that of consumers (see the disturbance factors of MI9 in Fig. 6a). Disturbance intensity 62 increased the intrinsic rate of reproduction of producers but decreased that of consumers (also see the disturbance factors of MI9 in Fig. 6a). In NI5-5, disturbance threshold would be between disturbance intensities of 50 and 62.

A meaningful result from the simulation study is that an ecosystem's response in GPP to disturbance may be variable depending on how a specific disturbance affects intrinsic rates of diverse pathways. From the analyses of GPP patterns under disturbance (Fig. 4), we identified that the negative effects of disturbance on the intrinsic rates of the net reproduction pathways of both producers and consumers decreased GPP during the disturbance period but ultimately increased GPP during the post-disturbance period as simulated by Odum and Odum (2000b). On the other hand, the positive effects of disturbance on the intrinsic rates of the net reproduction pathways of both producers and consumers

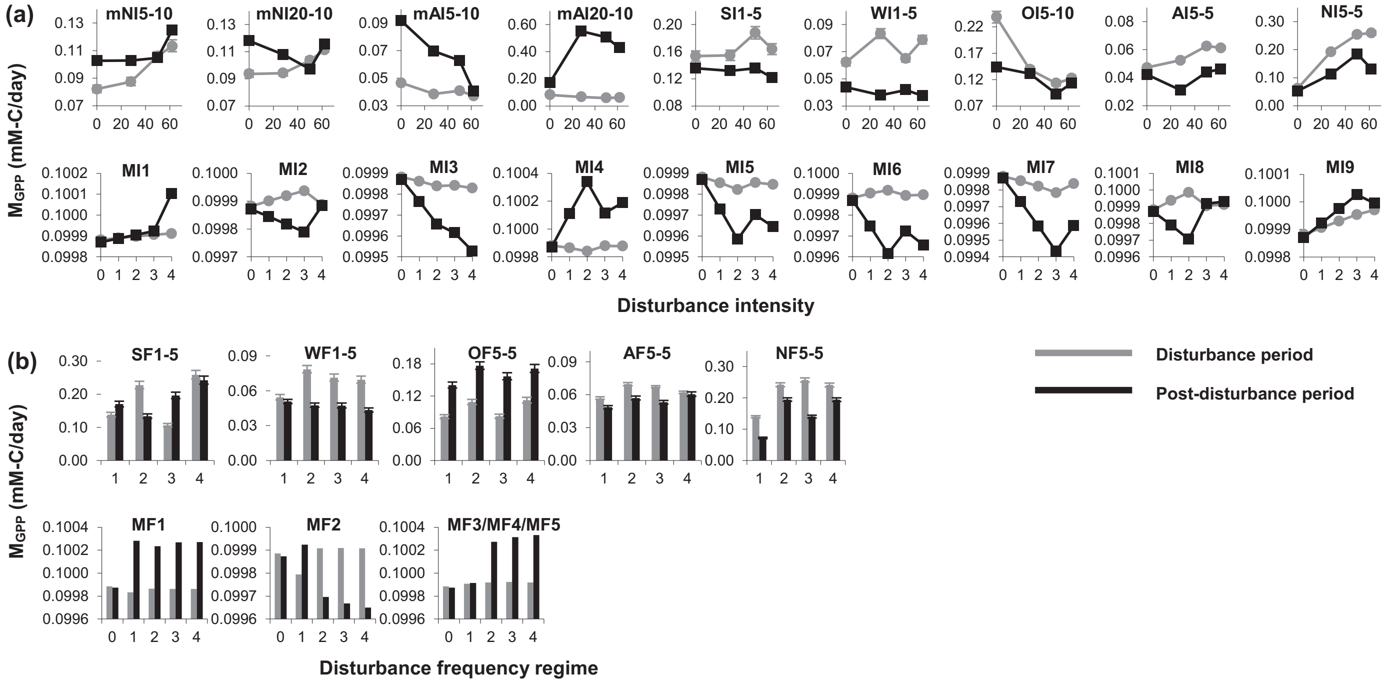

Fig. 6. Comparison of disturbance–M_{GPP} models between the results of microcosm tests and simulation models (a) Intensity-varied tests. Upper: microcosm tests (mNI5-10 through NI5-5), lower: simulation models (MI1 through MI9). MI1: 4, 0.1, 0.0001, (0,−)/(0,−) (in the order of disturbance threshold, f_{dl}, f_{dh}, disturbance effects on ($c_2 - c_3$, $c_4 - c_5$) at $p <$ threshold/at $p \geq$ threshold). MI2: 4, 0.1, 0.00001, (+,−)/(+,−). MI3: 3, 0.3, 0.00012, (+,+)/(+,+). MI4: 3, 0.4, 0.0001, (−,−)/(−,−). MI5: 3, 0.4, 0.00008, (+,+)/(+,+). MI6: 3, 0.4, 0.0002, (+,0)/(+,0). MI7: 4, 0.4, 0.0001, (+,+)/(+,+). MI8: 3, 0.3, 0.00005, (+,−)/(+,−). MI9: 4, 0.3, 0.00015, (0,−)/(+,−). (b) Frequency-varied tests. Upper: microcosm tests (SF1-5 through NF5-5), lower: simulation models (MF1 through MF5). MF1: 2, 0.1, 0.00008, (−,−)/(−,−). MF2: 2, 0.02, 0.0001, (−,+)/(+,0). MF3, MF4, MF5: 2, 0.02, 0.0001, (0,−)/(0,−).

decreased GPP through the disturbance and post-disturbance periods. In this regard, our disturbance simulation models provided new insights into variable mechanisms of disturbance in ecosystems.

The response of the simulation model under intensity-varied and frequency-varied simulations was similar (Fig. 4) suggesting that the model was less sensitive to these parameters and changes in behavior were dominated by disturbance effects on intrinsic rates of net reproduction. The various GPP time series patterns (Fig. 4) show why disturbance study needs to be considered from an energetic perspective by assigning possible specific effects of a disturbance on different energy pathways. The second hypothesis related to disturbance threshold was critical to generate a U-shaped or peaked disturbance–productivity relationship as exemplified in Fig. 5c.

4.2. *Long-term simulation*

The patterns of GPP time series show the disturbance–M_{GPP} relationship is dependent on the length of the post-disturbance period (Fig. 4). When disturbance intensity (p) is lower than a threshold, we expect GPP to eventually approach a reference state as ecosystems generally return to their reference states following weak disturbances. Thus disturbance effects on productivity will gradually fade out as the post-disturbance period is elongated. When disturbance intensity (p) is higher than a threshold, productivity will diverge from a reference state as the post-disturbance period is elongated. In a real ecosystem, however, it is difficult to expect long-term response of the system to disturbances because other endogenous or exogenous factors than the disturbances may continuously influence the trajectory of succession of the system over time (Connell and Slatyer, 1977; Turner et al., 1998).

4.3. *Inconsistencies between the results of microcosms and simulation models*

We identified a few inconsistencies in the disturbance–M_{GPP} relationships between the results of microcosms and simulation models (Fig. 6). When disturbance intensity was higher than a threshold, the simulation models failed to generate a decreasing M_{GPP} pattern above a reference GPP or an increasing M_{GPP} pattern below the reference GPP with increasing disturbance intensity. If the model is correct, however, we may need to extend the range of disturbance intensity in the microcosm tests. That is, intensity 4 of the simulation models may be higher than intensity 62 of the microcosm tests. The simulation models of OF5-5, AF5-5, and NF5-5 failed to generate the different M_{GPP} levels among the three discrete disturbance regimes (regimes 2, 3, and 4). A more detailed model may be needed to improve the monotonically increasing or decreasing M_{GPP} patterns with the gradient of disturbance regimes.

Unlike the microcosm tests, the simulation models generated the same M_{GPP} at disturbance intensity 0 between the disturbance and post-disturbance periods because they were built under the steady-state assumption. In the simulation models, we assumed the steady state of the state variables to clearly compare GPP levels and time series patterns under different disturbance regimes. In the microcosms where ambient conditions (e.g., temperature) were maintained constant, however, the time series of GPP under disturbance intensity 0 rarely leveled off as GPP generally oscillated over time.

The M_{GPP} values were not the same between the microcosms and simulation models because the parameters and configurations of the basic model do not agree with those of each microcosm. While a certain variable such as the steady-state value of GPP was estimated from microcosm mNI5-10, we obtained other parameter values from the relevant literature or our experience. In the simulation model study, we focused more on the patterns of the variable disturbance–productivity relationships than the exact representation of the microcosm results.

4.4. Challenges of the simulation models

We identified several challenges of the simulation models in resolving the inconsistencies between the results of the models and microcosms. First, the alternative stable state hypothesis (Scheffer et al., 2001) suggests that a threshold of disturbance may change over time as a result of interactions between disturbances and a microcosm. Depending on resilience of a microcosm in a given sequence of disturbance regimes, the threshold will dynamically change. The challenge is that resilience of the microcosm may be altered after a disturbance event so that it is difficult to determine the trajectory of dynamic thresholds in a simulation model. Second, the current simulation models represent a static system configuration over time. In ecosystems or microcosms, biotic and abiotic components self-organize to build complex system structures over time (Levin, 2005; Odum, 1988). We face the challenge of how to represent the emerging or disappearing energy pathways and time-dependent complexity of the network among the functional species groups. Finally, we did not consider change in the configuration of the energy pathways by disturbances in the model. Under a severe disturbance, we might expect the configuration of the energy network to change. In addition, systems may adapt to the disturbed and undisturbed environments by flip–flop action (Odum, 1994b). Yet the network configuration and short temporal scale in our macroscopic mini-model did not have the capacity to change. If a more detailed model is built in the future, the change of network configurations as well as that of pathway characteristics should be considered.

4.5. Definition of disturbance from an energetic perspective

We may need another definition of disturbance applicable to the energetic perspective we discussed in this study. The most common definitions of disturbance earlier proposed by Sousa (1984) and White and Pickett (1985) show that current ecologists implicitly agree that a disturbance is a discrete damage that creates new opportunities for new individuals. Because damage of individuals or communities results in the change of energy configurations or characteristics of pathways, we may define disturbance as an external energy source that partially or collectively alters a system's energy configurations or characteristics of pathways in an unprecedented way.

5. Conclusions

We built simulation models of variable disturbance–productivity relationships observed in a freshwater aquatic microcosm study using two hypotheses related to energy pathways and disturbance thresholds. The first hypothesis stated that disturbance differentially affects intrinsic rates of energy flow on pathways of exchange between system components and that depending on the configuration of the system, response during and following disturbance is the result of changes in these rates. The second hypothesis stated that there are resilience thresholds which if exceeded result in permanent changes to intrinsic rates of energy flow on system pathways. Simulation of GPP based on the first hypothesis showed that GPP patterns of the disturbance and post-disturbance periods are determined by disturbance effects on the intrinsic rates of the net reproduction pathways of producers and consumers. The second hypothesis on the disturbance threshold was essential to explain a U-shaped or peaked disturbance–productivity relationship. Although the simulation models represented a freshwater aquatic microcosm under various disturbance regimes, they may also be applicable to many ecosystems and disturbance types by correcting critical energy pathways and their parameter values.

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