Ecol Res (2007) 22: 214–219
DOI 10.1007/s11284-006-0304-5

MIYADI AWARD

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Regime shifts: catastrophic responses of ecosystems to human impacts

Received: 4 July 2006 / Accepted: 10 October 2006 / Published online: 18 November 2006

Abstract Evidence of abrupt changes in ecosystem states, such as sudden eutrophication in lakes, has been increasingly reported in a variety of aquatic and terrestrial systems. Ecosystems may have more than one state with a self-stabilizing mechanism, so that a shift between states does not occur frequently and is not readily reversible. These big changes are termed regime shifts where often one state is preferred over another. Thus, regime shifts are problematic for ecosystem managers, and the need exists for studies that lead to the identification of thresholds of key variables that trigger regime shifts. Regime shifts are currently difficult to predict and in many cases may be caused by the human pursuit of efficiency in land and water productivity in the last few decades. Here I briefly introduce a theoretical approach to predict the shift between a clear-water state and a turbid state in lakes, the best-studied example of regime shifts. This paper also discusses alternative states in other natural systems besides ecosystems to draw more attention to the research currently being performed on regime shifts.

Keywords Ecosystem · Human impact · Management · Mathematical model · Regime shift

Introduction

Regime shifts are increasingly reported in natural environments (Scheffer et al. 2001). Regime shifts are large system changes that are beyond the normal range seen at microscopic scales (e.g., stable points, limit cycles, and strange attractors). Any state in nature is not truly stable at a microscopic scale, because it fluctuates daily and seasonally depending on external forces such as temperature and light conditions. Nonetheless, these microscopic fluctuations are not problematic when natural systems are described on macroscopic scales, which are arguably the proper scales at which persistent states in natural systems should be described. Thus, the terms regime and regime shift are most appropriately used to describe the state of a natural system at a macroscopic scale and a large change in a macroscopically described system, respectively (Carpenter 2003).

Increased evidence of regime shifts seems related to the enhanced human pressure on ecosystems (Folke et al. 2004; Millennium Ecosystem Assessment 2005). Often regime shifts are not reversible, or can be reversed only slowly, with long time delays (Carpenter 2003). The irreversibility and time lags are related to the phenomenon called hysteresis. This phenomenon was first identified in magnetic materials by Ewing (1891). Because of its property that systems react slowly or do not return completely to their original state, hysteresis is problematic for people who depend on ecosystems, that is all of us.

In lake ecosystems, for example, nutrient loading from surrounding watersheds does not necessarily lead to turbid water or eutrophication, because the effect of nutrient loading on water clarity also depends on changes in biotic communities. Algal blooms are due to changes in biotic communities and may act as a buffer against alterations of ecosystems by humans, but may cause hysteretic phenomena (i.e., regime shifts) in nature. Thus ecosystem managers who neglect the indirect effects of biotic communities could fail at ecosystem restoration.

Nutrient loading and water clarity of a lake can be illustrated as a spring and weight diagram where the mass of the weight represents the amount of nutrient loading (Fig. 1a). The more mass, the more the spring stretches downward and the more turbid the lake water. The resilience of the spring to the weight corresponds to

Motomi Genkai-Kato is the recipient of the 10th Denzaburo Miyadi Award.

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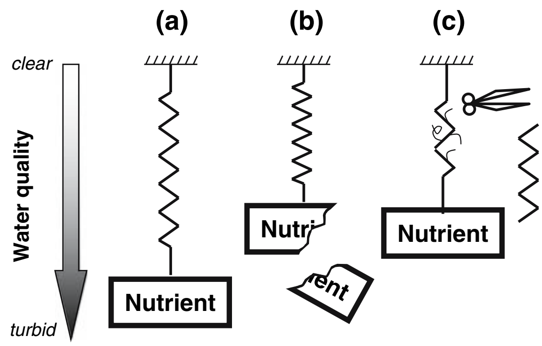

Fig. 1 Weight and spring model for eutrophication in a lake. The weight and its position represent the amount of nutrient loading and the resultant water quality, respectively. A bigger weight represents heavier nutrient loading to the lake. A heavy weight results in a lower position, indicating turbid water (**a**). The spring represents biotic communities in the lake and can play a role in mitigating the effect of nutrient loading on lake eutrophication. **b** Restoration of clear water by means of a management with reduction in nutrient loading. **c** Restoration by a management using technological methods (the scissors correspond to, for example, application of chemical agents) that have the potential to impair the biotic communities in the lake

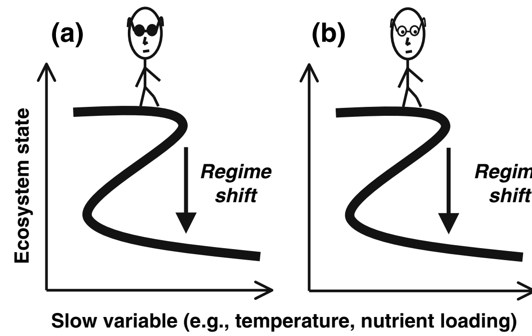

Fig. 2 Schematic diagram showing the state of an ecosystem potentially subject to a regime shift. The position of a man walking on a landscape with an overhanging cliff (*vertical axis*) represents an ecosystem state such as water quality in lakes and fish catch in fisheries. The horizontal axis represents a variable that changes gradually such as temperature and nutrient loading. **a** A man with blind glasses cannot look forward. The man corresponds to a society where ecological research on regime shifts is undeveloped. **b** A man with clear glasses is looking ahead. Replacing the blind glasses with clear glasses can be accomplished by intensive research on ecosystem regime shifts

the response of biotic communities to nutrient loading. Managers who consider biotic communities, while reducing human impacts on ecosystems, may restore water quality without the loss of biotic integrity (Fig. 1b). On the other hand, managers who ignore the effects of biotic communities and instead adopt technological methods, such as dredging and application of chemical agents, may restore water quality but irreversibly alter the natural state of biotic communities. In such cases, biotic communities cannot react in response to reduced nutrient loading, like a dead spring (Fig. 1c).

This paper presents ecological theory as an application tool for ecosystem management. As an example, I describe a mathematical model to predict the threshold values of drivers such as nutrient loading in lakes. In doing so, I show how mathematical models are powerful tools to prevent ecological surprises such as regime shifts in ecosystem management. While the paper starts with a case study on the prediction of the possibility of regime shifts in lakes, I then draw attention, as an important ecological issue as well as a biodiversity issue (Perrings et al. 1995; Millennium Ecosystem Assessment 2005), to regime shifts in ecosystems by giving some examples of regime shifts in other systems.

Model for ecosystem management

In ecology, since repeatable and prospective research has been emphasized, studies with experiments and microcosms have been promoted. However, regime shifts do not occur frequently or repeatedly, and are large phenomena involving ecosystem modifications. Standard ecological methods such as experiments and small-scale observations may not be applicable to such large, infrequent phenomena. Studies on regime shifts have just begun and there are many unknown issues to be challenged (e.g., the prediction of thresholds and possibility of restoration). Triggers for regime shifts are often slow variables such as global warming and nutrient loading (Carpenter 2003). Regime shifts currently have three problematic issues that can be described as a man with blind glasses walking on a Cartesian landscape shown in Fig. 2a: (1) when the key variable, although it changes very slowly, exceeds a threshold even slightly, a regime shift occurs abruptly; (2) the shift is discontinuous; (3) after the regime shift, it is difficult to restore the state to the original one because of hysteresis. Mathematical models are now being applied to predictions of thresholds and practical restoration of degraded ecosystems (Scheffer and Carpenter 2003; Suding et al. 2004). Theoretical approaches are a useful tool to substitute clear glasses for blind glasses (Fig. 2b).

Many models in ecology can be classified into two extremes in terms of predictive aim. Some models are abstract and provide qualitative predictions. Other models perform exact calibration to make precise predictions. Abstract models tend to involve parameters that do not directly represent observable properties of ecosystems, while exact models tend to be applicable only to a single target ecosystem because of their exact calibration. For the purpose of ecosystem management, models with parameters that are well based on empirical data, so as to provide precise predictions, are preferred. Empirically based models also need to be rather simple to be applicable to broader conditions of the target ecosystem such as temperature and ecosystem size.

Example of realistic prediction: sudden eutrophication in lakes

Lakes may have two contrasting states in water clarity due to excessive phosphorus (P) input: a clear-water state versus turbid one (Jeppesen et al. 1998; Scheffer 1998). The clear-water state is often characterized by dense macrophytes in the littoral area and the turbid one by algal blooms in the pelagic area (Timms and Moss 1984). Macrophytes are suggested to reduce P recycling from lake bottoms to the water column by stabilizing sediments; and provide refuge for zooplankton against fish predation, thus increasing grazing pressure on phytoplankton (Scheffer et al. 1993). As long as a lake is clear, the clear-water state is self-maintained by these feedback mechanisms (Fig. 3a). On the other hand, once phytoplankton are dominant due to excessive P input, rooted macrophytes become sparse because of shading by dense phytoplankton. In this case, the nutrient resource for phytoplankton growth is recycled from sediments and grazing pressure from zooplankton is diminished, self-maintaining the turbid state (Fig. 3b). Thus the interaction between pelagic and littoral areas through competition between phytoplankton and macrophytes is crucial for regime shifts, and the vulnerability of lakes to regime shifts and water quality are likely to depend on lake morphometry such as lake area and lake depth (Fig. 4).

Here I pick up a theoretical approach by Genkai-Kato and Carpenter (2005) where a mathematical model was used to predict the possibility of regime shifts in relation to basic limnological characteristics such as area

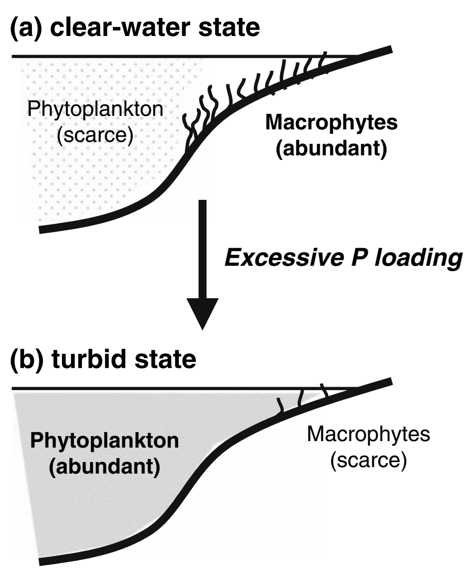

Fig. 3 Two alternative states in water quality in a lake. **a** A clear-water state is often characterized by abundant macrophytes in the littoral area and scarce phytoplankton. **b** A turbid state is often characterized by phytoplankton blooms in the pelagic area and scarce macrophytes. Excessive phosphorus loading to a lake is suggested to cause a shift from a clear-water state to a turbid state

and mean depth of lakes, and water temperature. The frame of the model is composed of the dynamics of algal density and phosphorus concentration (Fig. 5, see Genkai-Kato and Carpenter 2005 for the model and results in detail). The algal density in the model represents the mean chlorophyll concentration in the epilimnion in summer. We incorporated into the frame model the relationships between lake area and epilimnion depth (Hanna 1990), between chlorophyll concentration and the maximum distribution depth of macrophytes (Carlson 1977; Duarte and Kalff 1990), between hypolimnion thickness, temperature at hypolimnion, chlorophyll concentration, and P recycling rate from sediments (Charlton 1980). The role of macrophytes was embedded in the model by preventing P recycling from sediments (Kufel and Kufel 2002), and thus P recycling was assumed to occur from sediments where macrophytes were absent (i.e., pelagic area). The shape of lake basin was modeled by quadric surfaces (Carpenter 1983).

We conducted numerical simulations using the model described above to determine the possibility of discontinuous change of algal density in the eutrophication process (i.e., regime shift) and the possibility of restoration in the restoration process. Based on Lathrop et al. (1998), the P loading rate (term *l* in Fig. 5) was increased from 0.02 to 0.5 μg P l^{-1} day^{-1} in the eutrophication process, and this procedure was reversed in the restoration process.

There were three types of lake response to eutrophication: *reversible*, eutrophication is gradual and recovery is proportional to the reduction in P input; *hysteretic*, eutrophication involves a regime shift and recovery requires severe reductions in P input for a period of time; *irreversible*, eutrophication involves a regime shifts and recovery is impossible by means of reductions in P input alone. The model predicted that lakes with intermediate mean depth and higher temperature at hypolimnion were most vulnerable to regime shifts and restoration cannot be accomplished in such lakes (Fig. 6). Macrophytes were effective in the reduction of P recycling from sediments in shallow lakes; while the volume of water contained within the hypolimnion of large, deep lakes greatly diluted nutrients coming in from the watershed. Thus, the model predicted that lakes with intermediate mean depth and higher hypolimnion temperature were most vulnerable to regime shifts making restoration very difficult in such lakes (Fig. 6). The model clarified the existence of peculiar depths in an intermediate range where neither the macrophyte nor dilution effect worked. Notably, lake area did not help predict the possibility of regime shifts or restoration.

The model showed that the vulnerability of lakes to regime shifts can be categorized by mean depth and temperature at hypolimnion. Here let me give an example for each type (Fig. 6). Lake Biwa in central Japan (north basin, mean depth: 43 m, temperature at hypolimnion: 7°C, lake area: 613 km^2) is categorized as reversible, Lake Mendota in Wisconsin, USA (12.7 m, 12°C, 40 km^2) as hysteretic, and Lake Suwa in central

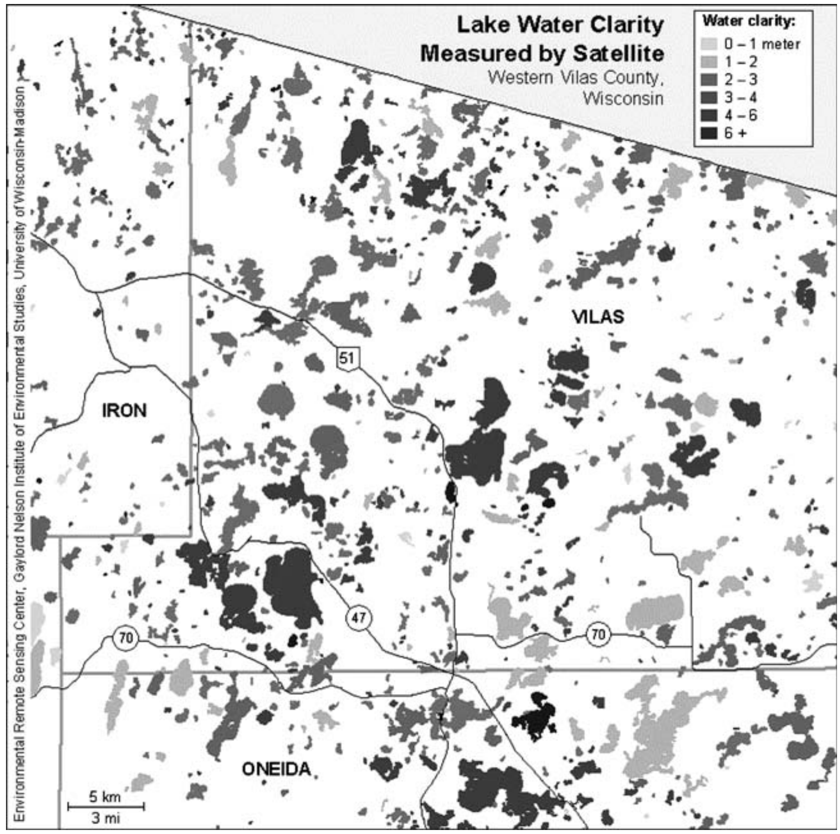

Fig. 4 Map of lake water quality for western Vilas County, Wisconsin, USA, created by Chipman et al. (2004). This map was derived from satellite imagery in combination with field observations of water clarity (Reprinted from www.lakesat.org by permission of the senior author.)

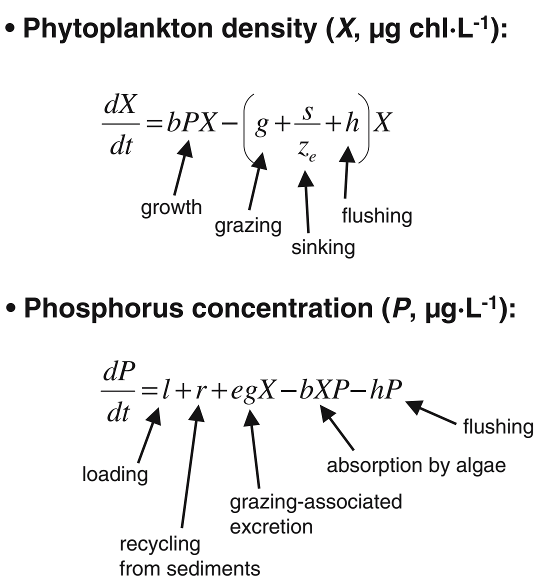

Fig. 5 Basic model for predicting sudden eutrophication in lakes due to phosphorus recycling in relation to lake morphometry, temperature and macrophytes (after Genkai-Kato and Carpenter 2005)

Japan (4.7 m, 20°C, 13.3 km^2) as irreversible. As the region of the hysteretic type is small, most lakes in the world would fall into either reversible or irreversible type.

The existence of lakes vulnerable to regime shifts at intermediate mean depths is worthy of note. The value of a lake in terms of recreational utility such as fishing and drinking water is considered to increase with its size. In contrast, the number of lakes decreases in general with lake size (i.e., there are many small lakes, while large lakes are sporadically scattered). Thus lakes with intermediate sizes may be most valuable for us in terms of easy accessibility and considerable utility. The model results suggest that more cautious management may be necessary for such lakes, rather than naturally protected shallow (i.e., macrophyte effect) or deep lakes (i.e., dilution effect).

Regime shifts as phenomena happening at hand

Regime shifts in ecosystems other than lakes

In ecosystems the term regime shift was originally used for fisheries in oceanography (Francis and Hare 1994). Hare and Mantua (2000) showed that the physical and biological environments in the North Pacific remarkably shifted several times in the past, in which the physical environments included mostly climatic characteristics and the biological ones included biomass, recruitments and catches of oceanic species ranging from zooplankton to salmon. Scheffer et al. (2001) reported other examples of regime shifts: coral reefs (state with corals

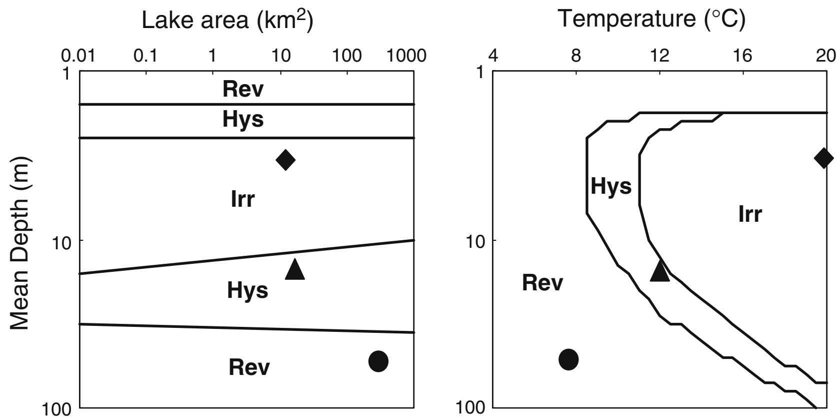

Fig. 6 Prediction of lake response types to eutrophication by the model shown in Fig. 5 (after Genkai-Kato and Carpenter (2005; Genkai-Kato 2005). In the *left panel* (lake area versus mean depth), water temperature is set at 12°C. In the *right panel* (water temperature versus mean depth), lake area is set at 40 km^2. *Rev* reversible type, *Hys* hysteretic type, *Irr* irreversible type. An example of each type of lake response was also indicated: *filled circle*, North Basin of Lake Biwa (Shiga, Japan); *filled triangle*, Lake Mendota (Wisconsin, USA); *filled diamond*, Lake Suwa (Nagano, Japan)

versus state with fleshy macroalgae), woodlands (woodlands versus open landscape with grasses), and deserts (vegetation cover versus arid desert). In addition to these, river ecosystems may have abrupt transitions in river channel (wide, shallow valleys with converted flow versus entrenched arroyos with divergent flow) associated with vegetation (Dent et al. 2002).

Regime shifts in non-ecological systems

Brock (2006) describes examples of multistable economic and social systems. Economy displays two contrasting phases, prosperity and depression, and fluctuates between these phases. This fluctuation is often referred to as the economic or business cycle. Although the fluctuation is called a cycle, they are different from regular cycles such as seasonal fluctuation in temperature; they do not necessarily repeat at regular time intervals or are not mechanical in their regularity. In the state of depression, for example, an excess of goods supply leads to: (1) a decrease in the average price level, (2) a decrease in the producers' interests, (3) a reduction in money income, and (4) a reduction in the consumers' purchasing power. These negative-feedback effects often set off a so-called deflationary spiral. Actually unemployment does display a hysteretic phenomenon (Blanchard and Summers 1987). As unemployment is closely related to the economic negative feedbacks addressed above, unemployment tends to last for a long time and the recovery of employment is difficult.

Human health also has two alternative states: healthy and sick conditions. Sickness such as cold and fever usually results from lack of sleep, malnutrition, and overwork. Once a person gets sick, recovery is not immediately accomplished even he/she takes sufficient rest and nutrition. The problem of overweight of humans may be viewed as a regime shift. Weight of humans is dependent upon the balance between the magnitude of exercise and dietary calories gained from foods. As overweight generally makes it more difficult to exercise (e.g., the load on knees increases with weight) and reduced calories sometimes result in a reduction in metabolic rate, recovery from overweight conditions is hard to accomplish healthily (i.e., without rebounds). Also, the gradual reduction of the metabolic rate as humans age is similar to slow ecosystem variables, such as nutrient input and global warming, which have the potential to trigger regime shifts. Perhaps regime shifts unexpectedly lie in our own backyard.

Concluding remarks

The biodiversity issue is associated with problems such as species extinction, and stability and functioning of ecosystems (Kinzig et al. 2002). It is difficult for non-ecologists to realize how the loss of such biodiversity is actually harmful to human life. In contrast, regime shifts, such as toxic algal blooms, losses of forests and coral reefs, desertification, and so on, are issues easily perceivable to non-ecologists. Regime shifts are increasingly being reported on in the last few decades. These shifts, whether ecological, economic or human health, could be caused by the human pursuit of efficiency in agriculture and industrial production. It is likely that human alterations to ecosystems in many cases change the natural self-stabilizing mechanisms inherent in ecosystems such as those that resist daily and seasonal changes in temperature and light conditions. The key variables for regime shifts such as global warming and nutrient loading originate from emissions of CO_2 and polluted water from industrial and agricultural activities. Automobiles and computers have greatly improved efficiency in human activities; on the other hand, they have led to decreased physical activity of humans. Fast food allows more time for productive activities and less time required to eating, but tends to contain high amounts of fat and therefore high energetic calories. On the other hand, fast food is often poor in nutrition and leads to malnutrition problems; combined with reduced exercise this causes the current obesity epidemic seen in many areas of the globe.

We realize the preciousness of health when we lose it. Health is a problem for each individual and treatment for sickness has been well established due to the dramatic progress in medical science. On the other hand, ecosystem regime shifts are infrequent compared to the number of medical patients, but have the potential to cause extensive damage to a considerable number of people, as do economic depressions. It would be difficult to study regime shifts in ecosystems in repeatable, statistically significant ways. However, there is a need for extensive research on ecosystem regime shifts using any sort of approach such as theory, observation, and experiments in order to prevent damage to human well-being at the society scale, trying not to make the same mistakes as human health at the individual scale. As humans continue to impact nature, regime shifts in ecosystems are not just ecological, but economic problems that are at the crossroads of ecology and public management (Carpenter 2003). In general, ecosystems subject to regime shifts are best managed by institutions that invest in new research while flexibly instituting solutions; furthermore, stakeholders must understand that regime shifts are a collective problem and not an individual one (Berkes et al. 2002).

Acknowledgments I am deeply indebted to three groups of colleagues. For their contributions to arouse my interest in ecology, I thank Kentaro Nozaki, Hiromune Mitsuhashi, and Hitoshi Miyasaka. I thank Norio Yamamura, Masami Nakanishi, and Masahiko Higashi at the Center for Ecological Research, Kyoto University, for their generous guidance and critical attitude to science. I thank Stephen R. Carpenter at University of Wisconsin–Madison for providing me the chance to apply theory to ecological applications. I also appreciate Steve Carpenter and Matt Helmus for reading and their comments on the manuscript. I am currently supported by the 21st century COE Program at Ehime University. This work was also sponsored by the Ministry of Education, Culture, Sports, Science and Technology of Japan, the Japan Society for the Promotion of Science, the US National Science Foundation, and the Andrew W. Mellon Foundation.

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