Introduction: Disturbance and Caribbean Ecosystems

Author(s): Jess K. Zimmerman, Michael R. Willig, Lawrence R. Walker and Whendee L. Silver

Source: *Biotropica*, Dec., 1996, Vol. 28, No. 4, Part A. Special Issue: Long Term Responses of Caribbean Ecosystems to Disturbances (Dec., 1996), pp. 414-423

Published by: Association for Tropical Biology and Conservation

Stable URL: https://www.jstor.org/stable/2389085

BIOTROPICA 28(4a): 414–423 1996

Introduction: Disturbance and Caribbean Ecosystems[1]

Jess K. Zimmerman

Terrestrial Ecology Division, University of Puerto Rico, GPO Box 363682, San Juan, Puerto Rico 00936, U.S.A.

Michael R. Willig

Ecology Program, Department of Biological Sciences and The Museum, Texas Tech University, Lubbock, Texas 74909, U.S.A.

Lawrence R. Walker

Department of Biological Sciences, University of Nevada, Las Vegas, Box 454004, Las Vegas, Nevada 89154, U.S.A.

and

Whendee L. Silver

Biology Department, 5 Cummington St., Boston University, Boston, Massachusetts 02215, U.S.A.

ABSTRACT

The fifteen articles in this special issue describe long-term (≥ 5 years) responses or perspectives on disturbance in Caribbean ecosystems. Most (11) of the articles describe the responses of Caribbean forests to hurricane disturbance, particularly the effects of Hurricane Hugo on wet forest in the Luquillo Experimental Forest (LEF), Puerto Rico. Ten articles discuss, alone or in addition to hurricanes, the effects of other types of disturbance including that due to humans, treefalls, drought, and landslides. In this introductory article we summarize the post-hurricane trajectories of various ecosystem components in the LEF. We also address how responses to other types of disturbance can be brought together to obtain a more thorough understanding of the comparative responses of Caribbean ecosystems to different disturbances. Finally, we identify those areas of disturbance ecology in the Caribbean that require further investigation.

RESUMEN

Los quince artículos en esta edición especial describen respuestas o perspectivas a largo plazo (≥ 5 años) sobre perturbaciones en ecosistemas del Caribe. La mayor parte (11) de los artículos consideran las respuestas sobre bosques del Caribe a perturbaciones de huracán, particularmente los efectos de Huracán Hugo sobre el bosque húmedo en el Bosque Experimental de Luquillo (BEL), Puerto Rico. Díez artículos discuten, sólo o además de huracanes, los efectos de otros tipos de perturbaciones incluso la debido a humanos, caída de árboles, sequías, y derrumbes. En este artículo introductorio nosotros resumimos las trayectorias post-huracán de varios componentes de la ecosistema del BEL. Nosotros también consideramos respuestas a otros tipos de perturbaciones que pueden estar juntos para obtener aún más entendimiento de respuestas comparativas de ecosistemas del Caribe a las diferentes perturbaciones. Finalmente, nosotros identificamos esas áreas de la ecologia de perturbaciones en el Caribe que requieren más investigación.

Key words: *anthropogenic disturbance; communities; drought; hurricanes; landslides; long-term research; populations; Puerto Rico; treefalls.*

Fundamental issues in ecology, such as the determinants of population size in nature, the maintenance of species diversity, and the limitations to ecosystem productivity, are given a new perspective when one considers perturbations caused by natural and anthropogenic disturbance. For example, disturbance may account for much of the spatial and temporal variation we observe in the characteristics of populations, communities, and ecosystems (White 1979, Sousa 1984, Pickett & White 1985). Studies of disturbance also challenge the view that ecological systems are in equilibria with respect to counteracting processes such as competitive hierarchies (Connell 1978), species immigration and extinction (Whittacker 1996), and nutrient loss and retention (Lodge *et al.* 1994). Thus, investigations of disturbance are important because they provide insight into key ecological mechanisms and their controls. Ecological theory embodies disturbance at various levels, including evolutionary and demographic processes (MacArthur & Wilson 1967, Pianka 1970, Grime 1979, Tilman

[1] Received 20 May 1996; revision accepted 4 June 1996.

1988), community dynamics and succession (Connell 1978, Sousa 1984), and ecosystem-level processes (Bormann & Likens 1979, Vitousek *et al.* 1979). Theoretical approaches have also been developed which use disturbance to address patch dynamics and heterogeneity at the landscape level (Pickett & White 1985, Turner 1987).

Disturbance has been a central focus of ecological research since its inception (Cowles 1899, Cooper 1926, Clements 1936). Most empirical research has focused on frequent, small-scale disturbances because of their ease of study or larger-scale human disturbances because of their relevance to conservation and the ability to conduct controlled experiments (Pickett & White 1985, Jordon *et al.* 1987, Glenn-Lewin *et al.* 1992). To date, long-term studies mostly have relied on retrospective analyses (*e.g.,* Foster 1992, Horn & Sanford 1992) or on space-for-time substitution (Pickett 1989, Fastie 1995) that limit the ability of the researcher to discern or disentangle key mechanisms of change. Long-term monitoring, such as that conducted by the US Long-Term Ecological Research (LTER) Program, facilitates investigation of infrequent disturbances (Magnuson 1990, Waide & Lugo 1992). Combined with historical studies, long-term monitoring can often provide detailed descriptions of regional disturbance regimes and an understanding of the responses of key biota to various types of disturbance. This then sets the stage for testing the importance of disturbance for the fundamental issues in ecology.

This issue of Biotropica presents a collection of studies concerning the longer term consequences of disturbance in Caribbean ecosystems. It follows an earlier issue (Walker *et al.* 1991a) dedicated to the assessment of short-term responses by plants, animals, and ecosystems to hurricane disturbance in the Caribbean. The motivation for the current issue was to broaden the perspectives derived from the previous issue in two ways. First, we wished to provide a longer term perspective ($\geq$ 5 yr) on responses of Caribbean forests to hurricane disturbance, particularly the recovery and reorganization of wet forest in the Luquillo Experimental Forest, Puerto Rico following Hurricane Hugo in 1989. Second, we invited research on disturbances other than hurricanes (human activities, treefalls, droughts, and landslides) that may influence Caribbean ecosystems. Thus, in addition to recording and analyzing the longer term effects of hurricanes, we hoped to integrate studies of other disturbances in a way that could lead to a more thorough understanding of the degree to which biota and biogeochemical cycles return to pre-disturbance states following a disturbance, how different biotic and abiotic elements respond to the same disturbance type, and how different disturbance types affect these same elements. Most of the manuscripts (11 of 15) address longer term impacts or recovery from hurricane disturbance (Table 1), of which nine specifically consider the impacts of Hurricane Hugo on the LEF. Among these and the other articles, six consider anthropogenic disturbance, two address the effects of treefalls, three consider drought, and two examine landslides.

In the current issue, questions are addressed that could not be answered based on short-term observations made immediately after Hurricane Hugo struck the LEF (Ackerman *et al.* 1991, Walker *et al.* 1991b, Tanner *et al.* 1991). How have the components of the wet forest in the LEF, the organisms, communities, and biogeochemical cycles, responded to Hurricane Hugo after five years? Is recovery predictable based on species composition or level of damage? Did Hurricane Hugo have any long-lasting impacts on forest structure and function? Are certain species adapted to hurricane disturbance? Are patterns of community recovery based on recovery of the original fauna and flora or on successional transitions? Do hurricanes increase such ecosystem parameters as forest biomass or net primary productivity? Is the recovery from hurricanes similar to or different from that in a light gap? Do the patterns of recovery from hurricanes tell us something about the way the same ecosystems will recover from anthropogenic disturbance? How do hurricanes interact with other kinds of disturbance, for example, do anthropogenic factors (*e.g.,* land use history) modify responses to hurricanes?

The nine articles in this issue which concentrate on studies carried out in the LEF following Hurricane Hugo are rich in detail. However, the many different responses recorded (here and elsewhere) for the individual elements of the wet forest ecosystem appear, in general, to follow one or more idealized trajectories (Fig. 1). Figure 1 attempts to provide a composite account of the response of a Caribbean forest to hurricane disturbance. The immediate impact of a severe hurricane is the removal of the forest canopy causing a decline in live forest biomass, increased light levels and temperatures below the canopy, increased amounts of litter and woody debris on the forest floor and in streams, and greatly modified habitats for forest and stream animals (Tanner *et al.* 1991). Following Hurricane Hugo, short-term increases in soil nutrient pools

TABLE 1. *A summary of the contributions to the special issue, classifying the articles by disturbance type, trophic level, biological hierarchy, and conceptual approaches. Synthetic and comparative (S/C) contributions are broadly defined as those that compare effects of disturbance type, the response of different biotic elements to disturbance, or landscape-dependence of disturbance effects of responses. Modeling excludes purely statistical approaches and is restricted to analytical or conceptual models of disturbance.*

		Disturbance type					Trophic level				Biological hierarchy				Conceptual	
Contributors	Page nos.	Hurricane	Human	Treefall	Drought	Landslide	Decomposers	Primary	Secondary	Tertiary	Biogeochemistry	Population	Community	Landscape	S/C	Models
Scatena *et al.*	424–440	X						X			X					
Silver *et al.*	441–457	X	X					X			X				X	
Vogt *et al.*	458–470	X					X	X			X			X		
McDowell *et al.*	577–584	X									X			X		
Willig *et al.*	471–483	X	X				X						X	X	X	
Covich *et al.*	484–492	X			X		X		X			X		X	X	
Woolbright	493–501	X		X	X					X		X		X	X	
Secrest *et al.*	502–514	X					X		X			X		X	X	
Fu *et al.*	515–524	X	X					X				X	X		X	
Thomlinson *et al.*	525–536		X					X						X		
Aide *et al.*	537–548		X					X					X	X		
Ellison & Farnsworth	549–565		X					X					X	X	X	
Walker *et al.*	566–576					X		X			X	X	X	X	X	
Lugo & Scatena	585–599	X		X	X	X		X			X	X			X	
Vandermeer *et al.*	600–613	X						X								X

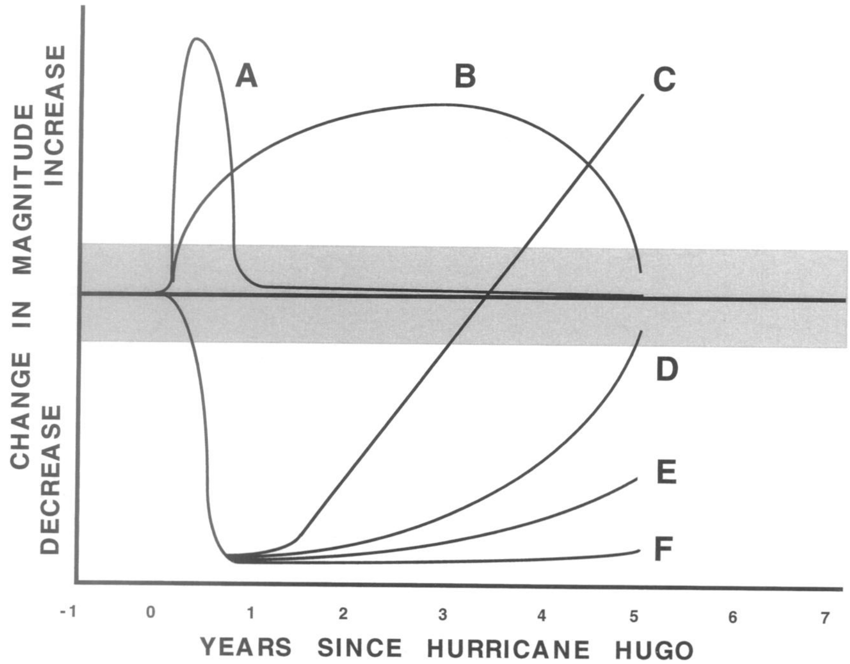

FIGURE 1. Idealized 5 yr trajectories of responses of different components of wet subtropical forest in the Luquillo Experimental Forest, Puerto Rico, to disturbance caused by Hurricane Hugo. See text for references to appropriate articles in this issue. The shaded portion of the graph represents ± 15 percent variation indistinguishable from pre-hurricane values. Curve A: transient (<1 yr) increase. Examples include forest floor biomass, some soil nutrient pools, and nitrate concentration in streams. Curve B: slow increase and return to pre-hurricane levels. Examples are net primary productivity, abundance of *Atya* shrimp in streams, adult coquí frogs, and of the terrestrial snail, *Cepolis squamosa.* Curve C: catastrophic decrease and subsequent rise above pre-hurricane levels. Examples are aboveground pools of potassium and magnesium, and the abundance of the bat *Artibeus jamaicensis* and of several species of terrestrial snails. Curve D: catastrophic decrease and return to near pre-hurricane levels. Examples are tree biomass, tree density, and the abundance of the bat *Stenoderma rufum.* Curve E: a catastrophic decline and steady increase, but not to within 15 percent of pre-hurricane levels. An example is fine total fine litterfall. Curve F: catastrophic decline and little recovery until 5 yr post-hurricane. Examples are fine root biomass and abundance of the walking stick, *Lamponius portoricensis.*

and in nutrient concentrations in groundwater and streams were identified, and may have originated from increased decomposition rates, increased leaching losses, or reduced nutrient uptake by the biota (Fig. 1, curve A; Lodge & McDowell 1991; Lodge *et al.* 1994; McDowell *et al.* 1996; Silver *et al.* 1996).

Many elements of wet forest in the LEF increased and declined slowly during the five yr post-hurricane period (Fig. 1, curve B). Aboveground net primary productivity rose and fell to pre-hurricane levels during the five yr period (Scatena *et al.* 1996) as a result of the abundant regeneration of pioneer species. Regeneration of pioneers also explained, in part, a transient increases in the concentration of macronutrients in litterfall (Scatena *et al.* 1996). In response to changes in light levels at the forest floor (Fernández & Fetcher 1991), herb and woody seedling biomass increased and then declined, but had yet to return to pre-hurricane values after five yr (Scatena *et al.* 1996).

Populations of *Atya* shrimp (Covich *et al.* 1991, 1996) and adult coquí frogs (*Eleutherodactylis coqui,* Woolbright 1991, 1996) also increased and then declined to near pre-hurricane levels during the five yr period (Fig. 1; curve B). Increases in shrimp were probably due to changes in resource levels (detritus) and increased habitat complexity caused by coarse woody debris in streams (Covich *et al.* 1996) whereas increases in frogs appeared to be related to the increased number of retreat sites caused by forest floor debris and the decline in the abundance of predators (Woolbright 1991, 1996). *Cepolis squamosa,* a terrestrial snail that was rare before the hurricane, also exhibited a period of increased abundance following the hurricane, but the causes of these changes were unclear (Willig *et al.*, in press).

Some components of wet forest in the LEF declined dramatically during the hurricane, but then rose above pre-hurricane values by the end of the five yr period (Fig. 1; curve C). At the ecosystem level, this was represented by changes in aboveground pools of potassium and magnesium that declined because of the destruction due to the hurricane (Scatena *et al.* 1993), but then accumulated rapidly in the tissue of pioneer trees and shrubs regenerating after the hurricane (Scatena *et al.* 1996). Populations of many organisms declined immediately following Hurricane Hugo in the LEF either because of direct negative impacts to their populations or because individuals migrated out of hurricane-damaged areas (Waide 1991). Numbers of terrestrial snails and walking sticks all declined precipitously because of the hurricane (Willig & Camilo 1991). Subsequently, numbers of terrestrial snails have increased to levels 2–8 times higher than pre-hurricane estimates (Fig. 1, curve C; Secrest *et al.* 1996, Willig *et al.* in press). This has resulted because of beneficial changes in habitat structure and resource availability in the forest understory. *Artibeus jamaicensis,* a wide-ranging species of bat, also declined and then increased to greater than pre-hurricane levels (Gannon & Willig 1994, Willig & Gannon, 1996), owing largely to changes in movement patterns.

Aboveground biomass and tree density declined dramatically during the hurricane but recovered to near pre-hurricane levels after five yr (Fig. 1, curve D; Scatena *et al.* 1996, Fu *et al.* 1996) reflecting the abundant regeneration of pioneer species and the growth of surviving nonpioneer trees (Yih *et al.* 1991, Zimmerman *et al.* 1994). Aboveground nitrogen and phosphorus pools exhibited parallel changes (Scatena *et al.* 1996). Numbers of the less vagil, endemic bat, *Stenodurma rufum,* have recovered slowly to pre-hurricane levels (Gannon & Willig 1994, Willig & Gannon, 1996) as has the abundance of the amblypygid *Phrynus longipes,* an important predator of coquí (Woolbright 1996).

Litterfall in the LEF had not returned to pre-hurricane levels after five yr (Fig. 1, curve E; Scatena *et al.* 1996, Vogt *et al.* 1996). Some estimates indicated that after five yr leaf fall had returned to within 15% of pre-hurricane values (arbitrarily defined by us to be "near normal"), but other litterfall components, particularly wood fall, remained well below pre-hurricane levels. Trajectories of recovery of litterfall varied with topographic position; litterfall into streams was lower than riparian or upslope areas (Vogt *et al.* 1996).

Biomass of live fine roots was one component of the forest vegetation that was slow to recover from hurricane disturbance (Silver *et al.* 1996; Fig. 1, curve F). One walking stick, *Lamponius portoricensis,* essentially disappeared after the hurricane and has only recently been recorded in appreciable numbers (M. Willig, pers. obs.). The causes of the severe decline in walking sticks and their slow recovery are unclear.

Not all components of the wet forest ecosystem in the LEF responded to disturbance caused by Hurricane Hugo. For example, soil organic matter in forest soils did not increase during the first five yr following the hurricane (Silver *et al.* 1996), contrary to expectations. Species richness of tree communities did not change significantly (Fu *et al.* 1996) in part because hurricanes only affect the relative abundance of tree species (Brokaw & Walker 1991, Zimmerman *et al.* 1994). Some species of shrimp (*Macrobrachium, Xiphocaris*) did not change in abundance because of the hurricane (Covich *et al.* 1996). Any declines in components of the wet forest ecosystem because of the hurricane were sudden rather than gradual. Despite the wide variety of responses, with rapid increases and decreases in population size of different species as a result of the hurricane, no species extinctions were recorded.

The overall view of the five yr of response of wet forest in the LEF to the destructive effects of hurricane disturbance is one of remarkable resilience. In part, this is explained by nutrient retention mechanisms in soils that ameliorate the impacts of hurricane disturbance (McDowell *et al.* 1996, Silver *et al.* 1996). The destruction is a boon to pioneer shrubs and trees whose high nutrient content also serves as a significant nutrient retention mechanism (Scatena *et al.* 1996). While the abundance of some organisms declines dramatically following a hurricane, some organisms respond positively to changes in resource availability and habitat structure caused by the increase in decaying litter and coarse woody debris (Waide 1991). The rapid turn-over of leaf litter from pioneer species provides additional habitat structure and high quality detritus to consumers and decomposers (Secrest *et al.* 1996, Woolbright 1996). Many trees survive the hurricane and regenerate the forest canopy directly (Yih *et al.* 1991), which, together with pioneer species, rapidly alleviate the extreme conditions that exist in the understory immediately after a hurricane. Thus, despite widespread habitat alteration by the hurricane, preferred habitats were quickly regenerated, although perhaps not in their previous locations or abundance (Secrest *et al.* 1996). After five yr of recovery, the forest appears in many ways to be similar to the way it appeared the day before Hurricane Hugo. Together with data on changes in forest structure and composition recorded by the USDA Forest Service beginning 11 years after a severe hurricane struck the LEF in 1932 (Crow 1980, Weaver 1986), a complete picture of the entire interhurricane cycle is emerging (Lugo *et al.,* in press).

Ten articles in this issue consider solely, or as part of a larger perspective, disturbances other than hurricanes (Table 1). Several articles consider the impacts of humans on Caribbean ecosystems. Population densities in the Caribbean are some of the highest in the world—5 of the 25 most densely populated countries occur in the Caribbean Basin (Anonymous 1995, Ellison & Farnsworth 1996). Primary forests in Puerto Rico had been decimated by the late 1940s, leaving intact only the least productive, high elevation forests (Birdsey & Weaver 1987). Deforestation continues in many mainland areas of the Caribbean basin (*e.g.,* Sader & Joyce 1988). Thomlinson *et al.* (1996) and Aide *et al.* (1996) describe the establishment of secondary forests on abandoned agricultural land that has taken place in Puerto Rico over the past 40–60 yr. The economic changes and subsequent increases in secondary forests in Puerto Rico provide the opportunity to predict increases in forest cover in other areas of the Caribbean should similar economic and land use changes occur. Prior history of human disturbance can lead to changes in tree species composition that predispose these secondary forests to high levels of hurricane damage (Zimmerman *et al.* 1994). Thus, the consequences of a history of human disturbance and more recent hurricane damage may be confounded with regard to spatial patterns (Everham *et al.,* pers. comm.) as revealed by the functional diversity of soil bacteria in wet forest in the LEF (Willig *et al.* 1996). Fu *et al.* (1996) describe the effect of an aspect of land use history by comparing the relative impact of Hurricane Hugo on natural secondary forest and a nearby forest plantation. Silver *et al.* (1996) describe the impact of an experimental removal of aboveground forest biomass on soil nutrient pools and vegetation recovery prior to Hurricane Hugo. The effects of extraction, pollution, reclamation, and changing climate on mangroves are thoroughly reviewed (Ellison & Farnsworth 1996) and suggest a bleak outlook for this important forest type in the Caribbean Basin. These examples of human disturbance emphasize the diverse ways in which humans affect natural ecosystems. This makes it difficult to use patterns of recovery from hurricanes or any natural disturbance to make predictions about the recovery of these same ecosystems from anthropogenic disturbance.

Four articles in this special issue consider natural disturbances other than hurricanes. Treefalls are viewed from the perspective of tree mortality and coquí frogs (Table 1). The question persists as to whether a severe hurricane represents a qualitatively different disturbance than an isolated treefall and associated light gap. With respect to the impact of hurricanes on vegetation damage and recovery time, Ackerman *et al.* (1991) suggested there is a gradient in hurricane damage over which, at intermediate levels of damage, the impact of hurricanes are similar to treefall gaps. The impact of a hurricane appears to depart from that of treefalls when the "Swiss cheese" pattern of damage caused by isolated treefalls coalesces to form a pattern of damage that is something of the reverse—patches of shade in sunlight (Fernández and Fetcher 1991). Lugo and Scatena (1996) summarize the many qualitative differences in community and ecosystem responses caused by the isolated death of a tree versus a severe hurricane. However, the increase in retreat sites caused by forest floor debris makes treefalls and hurricanes similar disturbances to coquís (Woolbright 1996). Responses to treefalls do not so clearly predict the responses of terrestrial snails to hurricane disturbance (Alvarez & Willig 1993, Secrest *et al.* 1996) and the slow recovery of walking stick populations (Willig & Camilo 1991) contradicts its preference for light gaps (Willig *et al.* 1986).

A three-month drought after Hurricane Hugo was a significant component of the hurricane's impact on the LEF (Scatena & Larsen 1991, Waide 1991). The long-term studies reported here include 1994, a year in which rainfall was the lowest in 20 yr of monitoring in the LEF (Luquillo LTER, unpublished data). The 1994 drought had little impact on the abundance of *Atya* and *Macrobrachium* shrimp in streams but altered the elevational distribution of *Xiphocaris,* probably because of disruptions to seasonal dynamics of migration and reproduction (Covich *et al.* 1996). Impacts of drought on the abundance of coquí frogs are undoubtedly important because of the effects on breeding and juvenile survivorship, but were difficult to detect against the background of other changes (Woolbright 1996).

This issue also includes a review of the current knowledge of landslide disturbance in the Caribbean, primarily from ongoing studies in the LEF (Walker *et al.* 1996). The disturbance regime of landslides is defined and retrospective studies of changes in soil nutrient pools, soil organic matter, and vegetation are reviewed and indicate a relatively slow rate of recovery. Estimates of aboveground biomass suggest a recovery time of 55–500 years, depending on forest type. The long recovery is primarily explained by the loss of surface soils, the low nutrient content of the exposed mineral soils, and continued soil instability. The spatial heterogeneity of landslides, mechanisms of nutrient accumulation and succession, and the role of landslides as refugia for pioneer species are identified as important areas for future research.

The articles in this special issue, together with past efforts, have shown that the effects of disturbance on ecological systems are complex and are dependent on dimensions of size, severity, and frequency of disturbance (Sousa 1984, Pickett & White 1985, Waide & Lugo 1992). In this issue, one common consequence of disturbance, tree mortality, is viewed in the context of the different dimensions of disturbance (Lugo & Scatena 1996). Focusing on this single element of a forested ecosystem, it is shown that background tree mortality is often the most important source of tree death, even in forests frequently subject to hurricane and landslide disturbance. They also point out that hurricanes should select for characteristics of trees that make them resistant or resilient to hurricane disturbance when the interval between hurricanes is short relative to tree life span.

Finally, Vandermeer *et al.* (1996) provide a contribution to the role of disturbance in community theory. The community model they develop shows that periodic disturbance can prevent competitive exclusion of species, but that the results depend on the nature of the changes in species' abundance caused by disturbance. If during a disturbance the abundance of each species is reduced by a constant proportion, then competitive exclusion is not prevented. However, if the abundances of species before and after a disturbance are uncorrelated, as occurred in forest communities in Nicaragua during Hurricane Joan, then disturbance can promote species diversity by preventing competitive exclusion. Thus, despite the previously unappreciated distinction between the kinds of impacts that disturbance can have on communities, hurricanes should promote tree species diversity in Caribbean forests.

Viewed together, we can begin to compare and contrast the severity of differing disturbances in the Caribbean as reflected in the timing of recovery and reorganization. Lacking a full understanding of the impacts of all important disturbances on Caribbean ecosystems prevents anything but a cursory analysis. However, one important point that emerges is that the timing of recovery and reorganization depends a great deal on the component of the ecosystem one considers. For example, in the wet forests of the LEF, nitrate in soils and streams return quickly (1–2 yr) to pre-disturbance levels (McDowell *et al.* 1996, Silver *et al.* 1996). Most other components of forest ecosystems—biomass, nutrient content, and nutrient cycling—appear to return to pre-hurricane levels in 5–10 yr (Scatena *et al.* 1996, Vogt *et al.* 1996). Recovery from treefalls may be much shorter, depending on the size of the disturbance (Lugo & Scatena 1996). Focusing on forest biomass alone, it appears to require 40 or more years for forest biomass to recover in an abandoned pasture (Aide *et al.* 1996) and 50–500 yr for a similar level of recovery following a landslide (Walker *et al.* 1996). However, considering hurricanes and abandoned pastures, forest composition continues to change over much longer periods of time. Forest composition may continue to change throughout the inter-hurricane interval in the LEF (Lugo *et al.* in press) such that the forest never attains a stable community composition. Zimmerman *et al.* (1995b) suggested that land use history may cause long lasting (>60 yr) if not permanent differences in forest composition in the LEF.

Many topics that would fill the lacunae in our knowledge of disturbance effects on Caribbean ecosystems (Table 1) have yet to be studied. Here we list some of the more critical ones. The coarse woody debris produced by hurricane disturbance is likely to have important effects on long-term biogeochemical cycling, but the mechanisms are poorly understood (Sanford *et al.* 1991, Zimmerman *et al.* 1995a). More long-term studies on the impacts of hurricanes and other disturbances on invertebrates, particularly insects, are needed (Willig & Camilo 1991, Torres 1992). Impacts of disturbance on plant-animal interactions are poorly understood as well (Schowalter 1994). Indeed, although food webs have been described in detail in the Caribbean (Goldwasser & Roughgarden 1993, Reagan & Waide 1996), we currently have only a basic understanding of how disturbance influences food web dynamics. Interactions among disturbances, although touched on by many contributions to this issue, have not been considered thoroughly. For example, are the effects of different disturbances additive or synergistic? This should be a major focus as we continue to investigate the effects of disturbance on Caribbean ecosystems. Finally, wider comparisons to other parts of the Caribbean and other areas of the tropics outside the hurricane belt are needed to provide a comprehensive understanding of how disturbance regimes determine tropical ecosystem dynamics.

ACKNOWLEDGMENTS

We thank David Foster, Jean Lodge, and Jill Thompson for providing comments on this introductory article. We are indebted to E. Raymond Heithaus for his encouragement and assistance in the preparation of this special feature. We give special thanks to 62 colleagues who agreed to review manuscripts. Jordi Altimiras translated and edited many Spanish versions of the abstracts and Rachel Lawrence helped with correspondence. Financial support from the International Institute of Tropical Forestry, as part of the Luquillo Long-Term Ecological Research Program (supported by NSF grant DEB-9411973 to the University of Puerto Rico), made this project possible. Additional support was provided by the University of Puerto Rico and University of Nevada, Las Vegas.

LITERATURE CITED

Ackerman, J. D., L. R. Walker, F. N. Scatena, and J. Wunderle. 1991. Ecological effects of hurricanes. Bull. Ecol. Soc. Am. 72: 178–180.

Aide, T. M., J. K. Zimmerman, M. Rosario, and H. Marcano. 1996. Forest recovery in abandoned cattle pastures along an elevation gradient in northeastern Puerto Rico. Biotropica 28: 537–548.

Alvarez, J., and M. R. Willig. 1993. Effects of treefall gaps on the density of land snails in the Luquillo Experimental Forest of Puerto Rico. Biotropica 25: 100–110.

Anonymous. 1995. Demographic yearbook, 45th issue. United Nations, New York.

Birdsey, R. A., and P. L. Weaver. 1987. Forest area trends in Puerto Rico. Research Note SO-331. U.S. For. Serv. Gen. Tech. Rep., So. Exp. Sta., New Orleans , Louisiana.

Bormann, B. T., and G. E. Likens. 1979. Pattern and process in a forested ecosystem. Springer-Verlag, New York.

Brokaw, N. V. L., and L. R. Walker. 1991. Summary of hurricane effects on vegetation. Biotropica 23: 442–447.

Clements, F. E. 1936. Nature and structure of the climax. J. Ecol. 24: 252–284.

Cooper, W. S. 1926. The fundamentals of vegetation change. Ecology 7: 391–413.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302–1310.

Covich, A. P., T. A. Crowl, S. L. Johnson, D. Varza, and D. L. Certain. 1991. Post-hurricane increases in Atyid shrimp abundances in a Puerto Rican montane stream. Biotropica 23: 448–454.

———, ———, ———, and M. Pyron. 1996. Distribution and abundance of tropical freshwater shrimp along a stream corridor: response to disturbance. Biotropica 28: 484–492.

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

Crow, T. R. 1980. A rainforest chronicle: a 30 year record of change in structure and composition at El Verde, Puerto Rico. Biotropica 12: 42–55.

Ellison, A. M., and E. J. Farnsworth. 1996. Anthropogenic disturbance of Caribbean mangrove ecosystems: past impacts, present trends, and future predictions. Biotropica 28: 549–565.

Fastie, C. L. 1995. Causes and ecosystem consequences of multiple pathways of primary succession at Glacier Bay, Alaska. Ecology 76: 1899–1916.

Fernández, D. S., and N. Fetcher. 1991. Changes in light availability following Hurricane Hugo in a subtropical wet forest in Puerto Rico. Biotropica 23: 393–399.

Foster, D. 1992. Land-use history (1730–1990) and vegetation dynamics in central New England, USA. J. Ecol. 80: 753–772.

Fu, S., C. Rodríguez Pedraza, and A. E. Lugo. 1996. A twelve-year comparison of stand changes in a mahogany plantation and a paired natural forest of similar age. Biotropica 28: 515–524.

Gannon, M. R., and M. R. Willig. 1994. The effects of Hurricane Hugo on the bats of the Luquillo Experimental Forest of Puerto Rico. Biotropica 26: 320–333.

Glenn-Lewin, D. C., R. K. Peet, and T. T. Veblen (eds.). 1992. Plant succession: theory and prediction. Chapman and Hall, London.

Goldwasser, L., and J. Roughgarden. 1993. Construction and analysis of a large Caribbean food web. Ecology 74: 1216–1233.

Grime, J. P. 1979. Plant strategies and vegetation processes. John Wiley and Sons, Chichester, England.

Horn, S. P., and R. L. Sanford. 1992. Holocene fires in Costa Rica. Biotropica 24: 354–361.

Jordon, W. R., III, M. E. Gilpin, and J. D. Aber. 1987. Restoration ecology. Cambridge University Press, Cambridge, England.

Lodge, D. J., and W. H. McDowell. 1991. Summary of ecosystem-level effects of Caribbean hurricanes. Biotropica 23: 373–378.

———, ———, and C. McSwiney. 1994. The importance of nutrient pulses in tropical forests. Trends Ecol. Evol. 10: 384–387.

Lugo, A. E., and F. N. Scatena. 1996. Background and catastrophic tree mortality in tropical moist, wet, and rain forests. Biotropica 28: 585–599.

———, J. Figueroa Colon, and F. N. Scatena. In press. The Caribbean. *In* M. Barbour, and H. Mooney. Vegetation of North America. Cambridge University Press, Cambridge, England.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey.

Magnuson, J. J. 1990. Long-term ecological research and the invisible present. BioScience 40: 495–501.

McDowell, W. H., C. P. McSwiney, and W. B. Bowden. 1996. Effects of hurricane disturbance on groundwater chemistry and riparian function in a tropical rain forest. Biotropica 28: 577–584.

Pianka, E. R. 1970. On r and K selection. Am. Nat. 102: 592–597.

Pickett, S. T. A. 1989. Space-for-time substitution as an alternative to long-term studies. *In* G. E. Likens (Ed.). Long-term studies in ecology: approaches and alternatives, pp. 110–135. Springer-Verlag, New York.

———, and P. S. White, Editors. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, San Diego, California.

Reagan, D. P., and R. B. Waide, Editors. 1996. The food web of a tropical rain forest. University of Chicago Press, Chicago, Illinois.

Sader, S. A., and A. T. Joyce. 1988. Deforestation rates and trends in Costa Rica, 1940–1983. Biotropica 20: 11–19.

Sanford, R. L., W. J. Parton, D. S. Ojima, and D. J. Lodge. 1991. Hurricane effects on soil organic matter dynamics and forest production in the Luquillo Experimental Forest, Puerto Rico: results of simulation modeling. Biotropica 23: 364–372.

Scatena, F. N., and M. C. Larsen. 1991. Physical aspects of Hurricane Hugo in Puerto Rico. Biotropica 23: 317–323.

———, W. Silver, T. Siccama, A. Johnson, and M. J. Sanchez. 1993. Biomass and nutrient content of the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico, before and after Hurricane Hugo, 1989. Biotropica 25: 15–27.

———, S. Moya, C. Estrada, and J. D. Chinea. 1996. The first five years in the reorganization of aboveground biomass and nutrient use following Hurricane Hugo in the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico. Biotropica 28: 424–440.

Schowalter, T. D. 1994. Invertebrate community structure and herbivory in a tropical rain forest canopy in Puerto Rico following Hurricane Hugo. Biotropica 26: 312–319.

Secrest, M F., M. R. Willig, and L. L. Peppers. 1996. The legacy of disturbance on habitat associations of terrestrial snails in the Luquillo Experimental Forest, Puerto Rico. Biotropica 28: 502–514.

Silver, W. L., F. N. Scatena, A. H. Johnson, T. G. Siccama, and F. Watt. 1996. At what temporal scales does disturbance affect belowground nutrient pools? Biotropica 28: 441–457.

Sousa, W. P. 1984. The role of disturbance in natural communities. Annu. Rev. Ecol. Syst. 15: 353–391.

Tanner, E. V. J., V. Kapos, and J. R. Healey. 1991. Hurricane effects on forest ecosystems in the Caribbean. Biotropica 23: 513–521.

Thomlinson, J. R, M. I. Serrano, T. del M. López, T. M. Aide, and J. K. Zimmerman. 1996. Land-use dynamics in a post-agricultural Puerto Rican landscape (1936–1988). Biotropica 28: 525–536.

Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, New Jersey.

Torres. J. A. 1992. Lepidoptera outbreaks in response to successional changes after the passage of Hurricane Hugo in Puerto Rico. J. Trop. Ecol. 8: 285–298.

Turner, M. G., Editor. 1987. Landscape heterogeneity and disturbance. Springer-Verlag, New York.

Vandermeer, J., D. Boucher, I. Perfecto, and I. Granzow De La Cerda. 1996. A theory of disturbance and species diversity: evidence from Nicaragua after Hurricane Joan. Biotropica 28: 600–613.

Vitousek, P. M., J. R. Gosz, C. C. Grier, J. M. Melillo, W. A. Reiners, and R. L. Todd. 1979. Nitrate losses from disturbed ecosystems. Science 204: 469–474.

Vogt, K. A., D. J. Vogt, P. Boon, A. Covich, F. N. Scatena, H. Asbjornsen, J. L. O'Hara, J. Pérez, T. G. Siccama, J. Bloomfield, and J. F. Ranciato. 1996. Litter dynamics along stream, riparian, and upslope areas following Hurricane Hugo, Luquillo Experimental Forest, Puerto Rico. Biotropica 28: 458–470.

Waide, R. B. 1991. Summary of responses of animal populations to hurricanes in the Caribbean. Biotropica 23: 475–480.

———, and A. E. Lugo. 1992. A research perspective on disturbance and recovery of a tropical montane forest. *In* J. G. Goldammer (Ed.). Tropical forests in transition: ecology of natural and anthropogenic disturbance processes, pp. 173–190. Berkhauser-Verlag, Basel, Switzerland.

Walker, L. R., N. V. L. Brokaw, D. J. Lodge, and R. B. Waide Editors. 1991a. Special issue: Ecosystem, plant, and animal responses to hurricanes in the Caribbean. Biotropica 23: 313–521.

———, D. J. Lodge, N. V. L. Brokaw, and R. B. Waide. 1991b. Introduction to hurricanes in the Caribbean. Biotropica 23: 313–316.

———, D. J. Zarin, N. Fetcher, R. W. Myster, and A. H. Johnson. 1996. Ecosystem development and plant succession on landslides in the Caribbean. Biotropica 28: 566–576.

Weaver, P. L. 1986. Hurricane damage and recovery in the montane forests of the Luquillo Mountains of Puerto Rico. Caribb. J. Sci. 22: 53–70.

White, P. S. 1979. Pattern, process, and natural disturbance in vegetation. Bot. Rev. 45: 229–299.

Whittacker, R. J. 1996. Disturbed island ecology. Trends Ecol. Evol. 10: 421–425.
Willig, M. R., and G. R. Camilo. 1991. The effect of Hurricane Hugo on six invertebrate species in the Luquillo Experimental Forest of Puerto Rico. Biotropica 23: 445–461.
———, and M. R. Gannon. 1996. Mammals. *In* D. P. Reagan and R. B. Waide (Eds.). The food web of a tropical rain forest, pp. 399–431 University of Chicago Press, Chicago.
———, R. Garrison, and A. J. Bauman. 1993. Population dynamics and natural history of a neotropical walking stick, *Lamponius portoricensis* Rehn (Phasmatodea: Phasmatidae). Tex. J. Sci. 38: 121–137.
———, D. L. Moorehead, S. B. Cox, and J. C. Zak. 1986. Functional diversity of soil bacterial communities in the tabonuco forest: Interaction of anthropogenic and natural disturbance. Biotropica 28: 471–483.
———, M. F. Secrest, J. F. Cary, S. B. Cox, G. R. Camilo, and M. R. Gannon. In press. Long-term ecological studies of invertebrates in the Luquillo Experimental Forest. *In* F. Dallmier and J. Comisky (Eds.). Measuring and monitoring forest biodiversity. Smithsonian Press, Washington, D. C.
Woolbright, L. L. 1991. The impact of Hurricane Hugo on forest frogs in Puerto Rico. Biotropica 23: 462–467.
———. 1996. Disturbance influences long-term population patterns in the Puerto Rican frog, *Eleutherodactylus coqui* (Anura: Leptodactylidae). Biotropica 28: 493–501.
Yih, K., D. H. Boucher, J. H. Vandermeer, and N. Zamora. 1991. Recovery of the rain forest of Southeastern Nicaragua after destruction by Hurricane Joan. Biotropica 23: 106–113.
Zimmerman, J. K., E. M. Everham, JR., R. B. Waide, D. J. Lodge, C. M. Taylor, and N. V. L. Brokaw. 1994. Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico: implications for tropical tree life histories. J. Ecol. 82: 911–922.
———, W. Pulliam, D. J. Lodge, V. Quiñones, N. Fetcher, S. Guzmán-Grajales, J. A. Parrotta, C. E. Asbury, L. R. Walker, and R. B. Waide. 1995a. Nitrogen immobilization by decomposing woody debris and the recovery of tropical wet forest from hurricane damage. Oikos 72: 316–322.
———, T. M. Aide, L. J. Herrera, M. A. Rosario, and M. I. Serrano. 1995b. Effects of land management and a recent hurricane on forest structure and composition in the Luquillo Experimental Forest, Puerto Rico. For. Ecol. Manage. 77: 65–76.