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REVIEW ARTICLE

# Synergistic effects of tropical cyclones on forest ecosystems: a global synthesis

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**Abstract** Tropical cyclones are large-scale strong wind disturbance events that occur frequently in tropical and subtropical coastal regions and often bring catastrophic physical destruction to ecosystems and economic disruption to societies along their paths. Major tropical cyclones can infrequently move into the midaltitudes and inland areas. Ecologically, tropical cyclones have profound impacts on diversity, structure, succession and function of forest ecosystems. The ecological effects are both dramatic and subtle. The dramatic effects can be visible, noticeable and to some extent predictable over the short-term and relatively well documented in the literature. However, the subtle effects are often invisible, complex and at smaller scale relatively unpredictable in the long-term. Many factors, meteorologic, topographic and biologic, simultaneously interact to influence the complexity of patterns of damage and dynamics of recovery. I present a global synthesis on the effects of tropical cyclones on forest ecosystems and the complexity of forest responses, with particular attention on the response to large hurricanes in the neotropics and the temperate North America, and strong typhoons on the subtropical and temperate forests in the East and Southeast Asia. Four major aspects provide on organizational framework for this synthesis: (1) consistent damage patterns, (2) factors that influence response patterns and predict damage risks, (3) complexity of forest responses and recovery, and (4) the long-term effects. This review reveals highly variable and complex effects of tropical cyclones on forest ecosystems. A deep understanding of the synergistic effects of tropical cyclones is essential for effective forest management and biodiversity conservation.

**Keywords** Large infrequent disturbance · Multiple-scale · Tropical cyclones · Hurricanes · Typhoons · Complexity · Tree mortality · Synergistic effects

## Introduction

As large-scale strong wind events, tropical cyclones, including hurricanes, typhoons and severe cyclonic storms, are nearly ubiquitous in tropical and subtropical coastal regions and have profound impacts on forest ecosystems in many parts of the world (Xi and Peet 2011). Many factors, meteorologic, topographic and biologic, simultaneously interact to influence the complexity of patterns of damage and dynamics of recovery. As an ecological factor (primarily as a destructive force), tropical cyclones not only cause extensive damage to trees, but also affect many aspects of the disturbed forests including individual tree growth, tree regeneration, community structure, species diversity, and ecosystem function (Coutts and Grace 1995; Ennos 1997; Xi 2005). While such large-scale strong winds are easily seen to have major visible catastrophic impacts on physical environment and forest structure, long-term effects on less conspicuous community and ecosystem attributes such as species composition, diversity and

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function are more subtle, complex, less visible and at smaller scale relatively unpredictable.

The effects of strong winds as a damage force have long been recognized and observed by foresters and ecologists (e.g., Baker 1915; Bromley 1939; Curtis 1943; Spurr 1956). Extensive researches have been conducted on the ecological impacts of catastrophic wind events in recent decades (Canham and Loucks 1984; Foster 1988a, b; Webb 1989; Boucher et al. 1990; Brokaw and Walker 1991; Walker 1991; Peterson and Pickett 1991; Merrens and Peart 1992; Bellingham et al. 1994, 1995; Boose et al. 1994; Vandermeer et al. 1995; Imbert et al. 1998; Turner et al. 1997; Sinton et al. 2000; Burslem et al. 2000; Boose et al. 2001; Platt et al. 2002; Peterson 2004; Uriarte et al. 2004; Xi and Peet 2008a, b; Xi et al. 2008a, b, 2012a, b). Most extensive studies were on the effects of tropical cyclones on forest ecosystems and subsequent ecological responses. Much progress has been made in elucidating tropical cyclone's impacts and forest recovery in specific wind-damaged forests in both tropical and subtropical regions. As a consequence of those work, the traditional view of wind as a simple damage force has evolved into the contemporary view of wind as a spatially heterogeneous, multi-scale disturbance agent that affects forest structure, diversity, dynamics, and some ecosystem processes (Reice 1994, 2001; Lugo 2008; Xi and Peet 2011).

Several reviews of windstorm impacts have provided a general framework for viewing how various windstorm disturbances might influence forest patterns and processes. Useful generalizations have emerged from early reviews (Brokaw and Walker 1991; Foster and Boose 1992; Everham and Brokaw 1996; Whigham et al. 1999; Webb 1999; Peterson 2000a, b). Recent reviews by Lugo (2008), Xi and Peet (2011) and Mitchell (2012) have all shown highly variable forest responses to windstorm disturbances in varied forest ecosystems, but there has been a continuous increase in knowledge about the complexity of the impacts of large-scale strong windstorms (Table 1). Regional reviews provided detailed information with new perspectives of the strong wind effects for specific areas or forest ecosystems (e.g., Zhu et al. 2004; Martin and Ogden 2006; Tong and Yang 2007; Xi et al. 2012a, b; Liu et al. 2012). A new global review focusing on the complex effects of tropical cyclones on forests ecosystems is necessary to incorporate new knowledge and changing perceptions.

The purpose of this review is to present a synthesis of the complex effects of large-scale tropical cyclones on forest ecosystems and forest responses to tropical cyclones and provide a framework for its interpretation and future study. The extensive literature cited in this review documents complex patterns of forest response to highly variable tropical cyclone disturbance regimes in varied forest ecosystems across the world. In this global synthesis, I particularly focus on the tropical cyclones in neotropics and temperate zone of North America and the typhoons in subtropical and temperate regions of East and Southeast Asia. I combine in one common conceptual framework several important concepts and theories pertaining to disturbance effects that have emerged in recent years. This synthesis is structured around four questions: (1) Are there consistent patterns in the damage exhibited by forest ecosystems? (2) What factors influence damage patterns and predict damage risk? (3) How do forests respond to and recover from varied tropical cyclones? (4) What are the long-term effects of tropical cyclones on species diversity, forest succession and carbon dynamics? A deep understanding of wind disturbance effects is essential for effective forest management and biodiversity conservation. This review, combined with others, should provide useful information for improving forest management that helps to minimize the timber loss under the increasing risk of catastrophic damage in the affected forest regions.

## Tropical cyclones: concepts, scales, predictability

### Concepts

Tropical cyclones are one of nature's most destructive weather phenomena that vary in their intensity and size among events and vary in their frequency among regions. In meteorology and climate science, a tropical cyclone is a non-frontal synoptic scale low-pressure system over tropical or sub-tropical waters with organized convection and definite cyclonic surface wind circulation (Holland 1993). In this review from an ecological perspective, I refer tropical cyclones as high wind events, including hurricanes, typhoons and severe cyclonic storms that may potentially result in substantial changes and catastrophic shifts in forest ecosystems. In inland cases, tropical cyclones that I focus on are a form of large, infrequent disturbance (LID) proposed by Turner et al. (1998) as natural catastrophic events that are 'large in spatial extent and infrequent in occurrence'. I also include certain information from other types of strong windstorm events, such as blowdown, tornados, downburst, and gales in the review.

Tropical cyclones can be identified from their high wind intensity and extreme maximum gusts (Foster and Boose 1992). A tropical cyclone usually originates over large bodies of relatively warm water in tropical or subtropical zones. Once it reaches speed of 17 m/s (39 mph), it is typically called a tropical storm. If winds reach 33 m/s (74 mph), then it is called 'hurricane' in the North Atlantic Ocean, the Northeast Pacific Ocean east of the dateline, or the South Pacific Ocean east of 160° E. A typical hurricane

**Table 1** List of studies of tropical cyclones on varied forests around the world by geographic locality and forest type

| Location | Forest types | Windstorm types | Reference |
|---|---|---|---|
| *Asia* | | | |
| Taiwan | Hardwoods | Typhoon | Xi et al. (2012a, b) |
| China | Subtropical forests | Typhoon | Tong and Yang (2007) |
| Japan | Subtropical forests | Typhoon | Bellingham et al. (1996), Xu et al. (2004) |
| *North America: United States* | | | |
| Florida | Mixed-hardwoods | Hurricanes | Batista and Platt (2003) |
| Florida | Slash pine savannas | Hurricanes | Platt et al. (2000, 2002) |
| New England | Hardwoods | Hurricanes | Boose et al. (2001) |
| North Carolina | Hardwoods | Hurricanes | Busing et al. (2009) |
| North Carolina | Appalachian hardwoods | Hurricanes | Elliott et al. (2002) |
| North Carolina | Xeric oak hardwoods | Hurricanes | Greenberg and McNab (1998) |
| North Carolina | Pines and hardwoods | Hurricanes | Xi (2005), Xi et al. (2008a, b, 2012a, b) |
| Texas | Mixed hardwood forest | Hurricanes | Harcombe et al. (2002) |

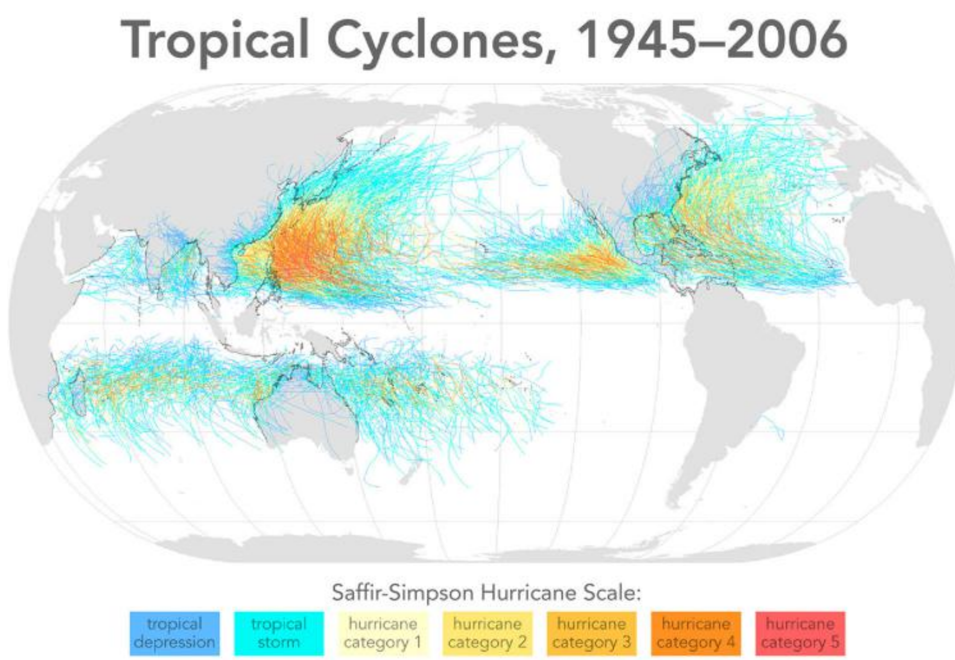


**Fig. 1** Recorded tracks of tropical cyclones for the period 1945–2006. Data from the Joint Typhoon Warning Center and the U.S. National Oceanographic and Atmospheric Administration. From Wikipedia.org: http://www.en.wikipedia.org/wiki/File:Tropical_cyclones_1945_2006_wikicolor.png

has an average wind speed of 70 m/s (157 mph). Tropical cyclone is called 'typhoon' in the Northwest Pacific Ocean west of the dateline, or 'severe tropical cyclone' in the Southwest Pacific Ocean west of 160° E or Southeast Indian Ocean east of 90° E.

Occurrences of tropical cyclones vary greatly in frequency and return times among cyclone types and localities (Fig. 1). Tropical cyclones originate over tropical or subtropical warm waters and therefore can be very common in near-coast tropical and subtropical regions, but are less frequent in inland tropics and subtropics and temperate zone. Tropical coastal areas can experience multiple hurricanes a year. Major catastrophic hurricanes (defined as Saffir-Simpson category 4 or 5) reoccur for a particular area of the coastal tropics on average every 20–60 years (Brokaw and Walker 1991). Frequency of tropical cyclones decreases from tropical and subtropical coasts to inland regions.

Major catastrophic hurricanes occasionally achieve landfall in temperate coastal areas, and reach the inland temperate areas (Webb 1999). In the United States, the reoccurrence intervals of major hurricanes in temperate forests vary greatly from less than 20 years in the Southeastern coastal regions (Gresham et al. 1991; Doyle 1997; Platt et al. 2000), to about 50 years in the temperate Piedmont of the Southeastern United States (Xi 2005; Xi et al. 2008a, b), to about 70–100 years in the Northeastern United States (Foster and Boose 1992). Major catastrophic hurricanes like the Great New England Hurricane of 1938 (Category 5) that caused disastrous forest damage in the last century in the Northeastern United States typically occur in the region only once a century (Spurr 1956).

The reoccurrence rates of major catastrophic hurricanes on a geological time scale for a specific location in a temperate region might be even longer. A sediment core study used to quantify hurricane activity in the Lake Shelby region of coastal Alabama (USA) showed a recurrence interval of about 300 years for major catastrophic hurricanes during the last 5,000 years, and about 600 years during the last 10,000 years (Liu and Fearn 2000). Compared to hurricanes, the occurrences of other types of catastrophic wind events (e.g., tornado, gales, downburst and severe storms) are more frequent but highly variable (Xi and Peet 2011).

## Scales

Tropical cyclones' impacts on forest ecosystems and subsequent forest dynamics are scale-dependent phenomena. Therefore both spatial and temporal scales are particularly important in understanding the effects of tropical cyclones on forest ecosystems. Consequently, it is essential to clarify the spatial and temporal scales over which the damage and ecological effects and the recovery patterns are examined.

### *Spatial scales*

Tropical cyclones often distribute over a broad range of spatial scales. The spatial extent or magnitude of tropical cyclones, which can be expressed as mean affected area per disturbance event, varies significantly. For example, size of a hurricane is generally huge (normally have a 300-340 km diameter) and wind damage could extend 50-100 km in width along its path. One example to illustrate the large size of a hurricane was the Great New England Hurricane of 1938, one of the most catastrophic windstorms in United States history, which blew down more than 2,400 km$^2$ of forestland in central New England (Spurr 1956).

Certain damage effects and recovery patterns can only be observed at a specific spatial scale in the context of specific processes. In their studies on the impacts of major hurricane in Northeastern temperate forests, Foster and Boose (1992) demonstrated that certain processes are dominant only for a specific spatial scale. For example, geographic and meteorological factors that control the formation and movement of hurricanes can only be understood on a continental scale ($\sim$5000 km), whereas wind velocity, local topography (variation in site exposure), and individual stand attributes are the controlling factors of hurricane damage at the landscape scale ($\sim$10 km).

### *Temporal scale*

It is critically important to clarify the temporal scales across which the studies are conducted and ecological patterns are compared. Forest recovery from a major tropical cyclone varies tremendously from a few years to several 100 years, depending on wind intensity, damage severity, regeneration capability and forest growth of the damaged forest ecosystems. Moreover, major forest processes also vary with time. During a hurricane, mortality processes dominate, whereas recruitment process becomes important in the years immediately after the hurricane damage (1–3 years). Consequently, the timing of surveys of hurricane-disturbed forests is critical for understanding the impacts, mortality and recovery. Ecologists often divide windstorm impacts and post-disturbance forest responses into three temporal categories: immediate (a few months to one year, e.g., Walker et al. 1992), short-term (few months to several years, e.g., Vandermeer et al. 2000; Pascarella et al. 2004) and long-term (few decades to over centuries, e.g., Hibbs 1983; Foster 1988a, b; Burslem et al. 2000). Lugo (2008) organized the effects of hurricanes on forest ecosystems based on a heuristic time framework that distinguishes between immediate effects (0–3 years), immediate responses (0–20 years), trajectories of responses (0–100 years) and long-term legacies (>100 years) (Lugo 2008).

## Predictability

The predictability of tropical cyclone's effects on forest ecosystems and recovery patterns is also scale-dependent. Although wind conditions are highly variable in all aspects during a tropical cyclone, wind gusts are more random at smaller scales. At small scales, biotic factors become more significant. The predictability of forest damage at the stand scale ($\sim$1 km) is, therefore, relatively low due to the random effects of wind gusts and the complex interactions among their neighbor individual trees. Regional scale damage patterns and recovery processes can be predicted reasonably well. Large-scale damage patterns are more predictable based on wind speeds, topography (site exposure), stand structure, disturbance, and land-use history (Foster 1988a, b; Foster and Boose 1992; DeCoster 1996; Xi et al. 2008a, b).

At the landscape scale, the predictability of tree mortality risk is more complex and often correlated with site exposure and tree size. Much of the tree damage is concentrated at the topographic extremes, particularly near stream bottom as where the wettest soils are located (e.g., Xi 2005; Xi et al. 2008a, b) and on ridges where the exposure to wind is greatest. Tree morality risks at the stand scale are often related to tree size and resistance to wind and less predictable. Our previous study in the Piedmont forests of the southeastern United States revealed that the risk factors that best explain variation in damage vary with scale of observation. Tree size (i.e., its vertical stratum) and species resistance to wind are the most important indicators of mortality probability during a major hurricane and explain damage variation at the stand scale; while topographic, site and stand factors explain damage variation at the landscape scale and wind speed and precipitation explain damage variation at the regional scale (Xi 2005; Xi et al. 2008a, b; Xi and Peet 2011).

The occurrence of windstorms may also interact with other disturbance forces such as subsequent wildfires, insect outbreaks, and fungal infections in complex ways to increase the degree and unpredictability of damage in temperate forest (Webb 1999).

## The influencing factors and their interactions

Severity of forest damage and tree mortality is related to both abiotic factors (wind speed, topography and soil) and biotic factors (individual tree characteristics, tree species, and stand attributes). Although wind speeds are the primary determinant of forest damage and tree mortality, topographic exposure, soil moisture and community attributes are the most important factors under similar wind conditions across landscapes (Xi et al. 2008a, b; Xi and Peet 2011). Exposure to winds, saturated soil, and high stand density are all associated with high tree damage and mortality risks. Tree species mixtures are important for predicting landscape and stand-level damage severity, but evidence of species-specific damage and mortality can be less clear as species effects often interact with tree size (Mitchell 2012).

### Abiotic factors

#### *Wind speed*

The force exerted by a hurricane increases as a function of wind velocity and storm duration, and decreases with distance from the eye of the hurricane. Various studies have examined the relationship between wind speed and tree damage and found that forest damage severity can be considered to be a function of wind speed. Fraser (1964) found that tree damage increases linearly with wind speed. Peltola (1996) found that the wind speed required to uproot a tree was much smaller than that required to cause the stem to break, and wind speeds of 12–14 m/s can be strong enough to uproot slender individual Scots pines located along a stand edge. Local variation in wind speeds must be taken into account in examining landscape- and regional level wind damage since even in flat terrain wind speeds can vary substantially at scales of less than a kilometer (Foster and Boose 1992; DeCoster 1996; Peterson 2000a, b).

#### *Topography*

Topographic exposure has major effects on tree damage at the landscape scale. In a Jamaican forest, Bellingham et al. (1995) found that higher damage on southern slopes and ridge crests that were exposed to the hurricane-face winds, while lower damage occurred on protected northern slopes. Boose et al. (2001) found a similar pattern of hurricane damage in New England, USA: major damage occurred on southwestern slopes exposed to the hurricane winds, whereas minor damage occurred in a protected deep valley. Boose and others concluded that topographic exposure, combined with wind intensity and forest stand attributes could largely explain damage patterns at landscape scale.

#### *Rainfall and soil features*

Rainfall is also a critical factor influencing both damage severity and tree damage type. Pre-hurricane soil moisture has been found to be a major controlling factor in dominant damage type (uprooting vs. stem breakage). Where soil was dry, uprooting was more difficult, trees more commonly experienced stem breakage (DeCoster 1996). When the soil is wet, uprooting is more common (Xi 2005; Xi et al. 2008a, b; Xi and Peet 2011). In the cold temperate forest zone such as in Finland, soil frost can reduce uprooting, and a decrease in the period or depth of frost can make trees more vulnerable to windthrow (Peltola 1996).

### Biotic factors

#### *Individual tree architecture*

Largest canopy trees often experience the most severe damage. In general, damage severity tends to increase approximately linearly with increasing tree height (e.g., Putz et al. 1983; Walker et al. 1992; Xi and Peet 2011). Peltola (1996) found that the wind speeds required to blow down a tree or break the stem of a tree located along a stand edge decreased as the height-to-diameter ratio or the crown-to-stem weight ratio of the trees increased (as well as more generally when the tree size increased). Consequently, pine trees with tall, slim stems are usually extremely vulnerable (Barry et al. 1993).

#### *Species susceptibility*

Tree species vary in their ability to withstand wind damage, their resistance depended on the interaction of several factors such as strength of wood, shape and size of the crown, extent and depth of root systems, shape of the bole, canopy characteristics, leaf features, and characters of root systems (Barry et al. 1998). Species with weaker wood (Webb 1989), low leaf reconfiguration ability (Vogel 1996), and shallower root systems (Gresham et al. 1991; Putz and Sharitz 1991) generally suffer greater damage and mortality, although it is difficult to distinguish the effects of species from effects of tree size. In the Duke Forest on the Carolina Piedmont, the 1996 Hurricane Fran (Fig. 2) caused a higher incidence of damage in canopy layer hardwoods than pines. This was because hardwood trees usually have broad spreading canopies and flat leaves that can catch the force of the wind much more readily than the smaller canopies and the needle leaves of pine trees. Moreover, hardwood trees often have shallow, spreading root systems that increase their susceptibility to uprooting during the hurricane (Xi 2005; Xi et al. 2008a, b).

Tree species can be classified into different groups based on their susceptibility to wind disturbance. Bellingham et al. (1995) studied tree damage and responsiveness in a Jamaican montane forest following Hurricane Gilbert. Based on indices of hurricane-caused damage (including short-term change in morality and percent of stem that lost crown) and species response following the hurricane (including change in recruitment rate, change in growth rate, and frequency of sprouting), they classified 20 tree species into four groups: resistant (low damage, low response), susceptible (high damage, low response), resilient (high damage, high response), and usurpers (low damage, high response). Bellingham and Tanner further predicted that species classified as usurpers would increase their relative abundance in the forest in the next decades, while the susceptible tree species would decrease in relative abundance of adults (Bellingham and Tanner 1995).

**Fig. 2** Satellite image of Hurricane Fran on September 4, 1996. Fran was a category three hurricane when it made landfall near Cape Fear on the southeast coast of North Carolina on September 5, 1996. After making landfall, Fran moved from southeast to the northwest across North Carolina's Coastal Plain and Piedmont, its eye passing about 24 km east of the Duke Forest. Although wind intensity had begun to decrease, Fran caused substantial forest damage in central North Carolina Piedmont forests. (Image from the Laboratory for Atmospheres, NASA Goddard Space Flight Center; http://www.rsd.gsfc.nasa.gov/images/Fran.html)

Barry et al. (1993) have provided a rank of resistance of tree species to hurricane-related damage for the major tree species in the southern United States. Similarly, in an old-growth forest damaged by hurricanes in southeastern USA, Batista and Platt (2003) classified ten tree species into four similar syndromes of response to high wind disturbance according to observed mortality, recruitment, and growth patterns: resilient, usurper, resistant and susceptible. Although a more complete classification is needed, these classifications provide helpful information for forest managers.

*Community attributes*

Community attributes such as stand height and age, stand density, and stand edge inevitably influence tree damage risk. Taller forests are generally subject to greater damage and mortality risk than shorter ones. This pattern is thought to be primarily a result of greater exposure to wind in the canopy and the increased leverage achieved with canopy movement. Because wind speeds are much higher at and above the crown level than within the stand, the larger trees are subject to higher damage risk than shorter ones (Fraser 1964). Another reason for increasing damage with increasing stand height is that smaller, younger trees are generally more flexible to wind flows (Vogel 1996). Foster and Boose (1992) found where severe windthrow of more than 75 % of the trees was reached, it mostly occurred in stands of $\geq$25 m height. Similarly, DeCoster (1996) reported a positive relationship between stand height and tree damage for the 1989 Hurricane Hugo in South Carolina Piedmont forests.

Literature reports on the effect of stand density on damage risk as have been variable. Most studies have shown a trend of increasing damage with decreasing stand density (Foster 1988a, b; Hook et al. 1991), but there were contrasting results, in part because denser stands often consist of younger and more flexible trees. Fraser (1964) found that a dense stand would decrease the lateral spread of roots and therefore increase tree damage (Fraser 1964). Overall, comprehensive and complex effects of stand density on tree damage is unclear because confounding effects of stand density, tree size, tree species, and tree architectural characteristics have generally not been adequately separated. These relationships need to be examined through comprehensive field experiments (e.g., Vogel 1996; Xi 2005; Xi et al. 2008a, b; Xi and Peet 2011).

### Interactions of the influencing factors

Much of the complexity of forest damage and tree mortality is a result of simultaneously interacting among meteorologic, topographic, and biologic factors and all influencing factors simultaneously interact to contribute the observed complexity. Consequently, the interactions among influencing factors must to be taken into account to better understand complex wind-damage relationships. DeCoster (1996) found the interactions between species and sizes were significant in predicting tree morality risk in a temperate deciduous forest of South Carolina, USA. Canham et al. (2001) examined the specific variation in susceptibility to windthrow as a function of tree size and storm severity for northern temperate tree species. Smaller trees sustain wounds caused by the falling tops of adjacent uprooted trees and the major branch breakages during the windstorm are often attacked by insects or affected by diseases. Trees with damaged root systems are often invaded by root rot organisms and subjected to higher risk to subsequent windstorms.

The features of a tropical cyclone, forest location relative to the windstorm, pre-disturbance community attributes, disturbance history, species susceptibility to wind all play a role in generating the complex and subtle patterns of damage. The influence of site factors on the extent of forest damage decreases as the magnitude of the hurricane increases. Moreover, Wind-induced effects and their interactions (insect breakouts, subsequent fires) need to be considered in evaluating indirect damage. In temperate forests, large wild fires often interact with hurricanes to cause greater forest damage (Platt et al. 2002). Myers and Lear (1998) in a literature review found that conditions after exceptionally strong hurricanes promote the occurrence of fires of higher than normal intensity (Myers and Lear 1998). Paleotempestological records support this hurricane-fire interaction in the Holocene maritime pine-oak forests of the Gulf coast region. Conversely, Kulakowski and Veblen (2002), working in montane forests of Colorado, USA, found fire history and topography can influence severity of wind blowdown and susceptibility of forest stands to wind damage (Kulakowski and Veblen 2002).

## The synergistic effects, forest response, ecological consequences

### Effects on forest physical environment

Tropical cyclones often cause substantial changes in forest physical environmental conditions at both small and large spatial scales: from changes in the microenvironment of a forest stand to changes in the environment of whole affected region. The primary effect of tropical cyclones on forest ecosystems largely is to shift the previous forest environment and re-set the ecological space and resources available to organisms, both plants and animals. Forest damage severity increases with intensity of a hurricane, but the amplitude of the relationship depends on the physical and biotic factors of a given site (e.g., topography, geomorphology, soil moisture, species composition, vegetation structure, state of recovery since last disturbance, plant architecture, size, age, and anatomy). The intensity and magnitude of the winds determines the speed and direction of response by individual tree, tree populations and whole forest ecosystems. By changing environmental conditions, tropical cyclones create a set of biotic responses that range temporally from seconds to centuries. The variability of biotic response to tropical cyclones is due in part to the variability of environmental conditions that develop after the passage of the hurricane (Lugo 2008). The range of effects can be first illustrated with the effects of increasing light.

#### *Increasing light*

Tropical cyclones can substantially alter forest physical environment as a result of a substantially increase in gap size and a dramatic rise in understory light. Among studies of forest physical environmental changes, canopy damage varies greatly from slight defoliation to about 90 % increases in understory light (Turton 1992; Veblen et al. 1989; Bellingham et al. 1996). In addition, catastrophic cyclones can increase within-stand spatial heterogeneity by simultaneously increasing understory light heterogeneity, decreasing overall canopy height, and increasing canopy patchiness. As a result of the uneven uprooting and stem snapping among different species and tree size classes, distribution of hurricane-induced tree mortality as well surviving trees within wind-damaged forest stands showed clumped patterns (McDonald et al. 2003; Xi and Peet 2011).

Lugo's study showed that forest microenvironment changed dramatically owing to the loss of canopy after hurricanes pass the Puerto Rico Island (Lugo 2008). Changes included increased light intensity and increased temperature inside the forest and decreased relative humidity. Fernández and Fetcher (1991) found dramatic changes in the light environment over a period of 1 year following the Hurricane Hugo in Puerto Rico forests. The changes of light are complex owing to spatial and temporal variability and the photosynthetic photon flux density (PPFD) showed a highly skewed distribution. Understory light heterogeneity measured by the mean daily total values peaked at 10 months after the hurricane. Another example in tropical Puerto Rico forests was done by Bellingham and his colleagues. They (1996) measured photosynthetic active radiation (PAR) during the first 33 months after the passage of Hurricane Gilbert over Jamaica and found significant increases in the hurricane -damaged Puerto Rico forests. The PAR levels were much higher in defoliated areas than in sites where not all the trees were defoliated (Bellingham et al. 1996). Snitzer and others found that Hurricane Isabel significantly increased the light on the forest floor in the Piedmont of Maryland, USA (Snitzer et al. 2005). Mature forest was largely dark. After Hurricane Isabel, light increased almost an order of magnitude in heavily damaged areas. Mean light levels in the high-light quadrats in the damaged area were 24.7 %.

*Ground features: mounds and pits, leaf litter, woody debris*

In addition to increased light, tropical cyclones generate a highly diverse substrate with treefall pits and mounds, stumps, leaf litter and rotting logs (Fig. 3). With increased light, ground features (microsites) play important roles, influencing forest understory species composition, biodiversity, growth, and dynamics (Webb 1999). These newly formed microsites often differ from intact forests in their greater soil moisture and nutrient availability, thereby allowing rapid establishment of plant species that require not only increased light, but also abundant soil water and nutrients than typically found in an intact stand.

**Fig. 3** Uprooting was the major form of damage for the medium and large trees during Hurricane Fran. This 2001 photograph shows two large uprooted oak trees (*Quercus* sp.) in the Duke Forest. The explanation for uprooting being the major damage type was that heavy rainfall occurred before and during the storm, saturating the soil. Hurricane Fran brought about 224 mm of rainfall to Duke Forest and adjacent areas during the two-day hurricane period. Perhaps equally important was a heavy rainfall (ca. 76 mm) 2 days before Hurricane Fran, causing the surface soil to be saturated prior to the arrival of the major windstorm. Photograph by Weimin Xi

Although several studies have examined the roles of pits and mounds following tropical cyclones, the results varied greatly between forests and wind disturbance events. Walker (2000) examined seedling and saplings dynamics in treefall pits in a Puerto Rican rain forest and found that treefall pits significantly altered recruitment and mortality of many understory species, but not species richness. In some cases, tree fall mounds supported more species than pits or un-damaged forests. However, Peterson and others found lower species richness on the mounds than in the treefall pits in a temperate forest.

Increased leaf litter can be an important factor influencing seed germination and seedling establishment after major tropical cyclone disturbances. Woody debris can provide important sites for seed germination and seedling establishment (Webb 1999). Guzman-Grajales and Walker (1991) examined the effects of three litter treatments on seedling emergence, growth, density, and mortality during the year following Hurricane Hugo in a Puerto Rican tropical forest and concluded that leaf litter is a major constraint to seedling recruitment. The role of leaf litter in temperate forests is still less known.

## Effects on forest structure

In addition to the visible effects on forest physical environment, the most conspicuous forest changes caused by catastrophic tropical cyclones are structural changes, which are often measured in terms of the changes in tree size distributions (or age distributions), basal area or biomass, stem density, or canopy heterogeneity. Forest structure can be defined by the complexities of vertical vegetation layers as well as horizontal patch distributions. Three consistent patterns in forest structural change that have been reported in both tropical cyclone-damaged tropical and temperate forests are: (1) immediate increase in canopy heterogeneity, (2) immediate decrease in tree density of all sizes followed by a dramatic increase in understory density a few years after wind damage, and (3) short-term decrease in biomass followed by a varied mid-term or long-term recovery in biomass. In temperate forests, the degrees of the structural change vary greatly depending on many abiotic and biotic factors including wind intensities, rainfall associated with the storm, community attributes, site conditions, and susceptibility to windstorm damage.

Studies of forest damage have reported loss of stand biomass following tropical cyclone disturbances to be highly variable and to depend on wind intensity, forest type, site exposure to wind, pre-disturbance species composition, and interactions of these major factors with subsequent risk factors such as fires and insect inflections. Reported losses of stand biomass vary greatly from 2 to 94 % among forests and wind events. In most reported cases, temperate forests have experienced extreme biomass loss due to the extreme intensities of windstorms and the high vulnerability of temperate forests to windstorm disturbances. The largest basal area loss reported thus far was in the northeastern temperate forests of the United States during the 1938 hurricane that resulted in about 94 % basal area loss in a 2,000-ha survey area (Spurr 1956; Foster 1988a, b).

Tropical cyclones have profound impacts on the size distribution of trees and can induce substantially increases in the relative abundance of small size-class trees in the damaged forests during the subsequent years. Although catastrophic cyclones usually cause immediate reduction in tree densities of all sizes, especially for large canopy trees, they often result in a dramatic increase in the density of understory seedlings and saplings several years after the windstorms due to subsequent release of suppressed understory stems and widespread sprouting. Sprouting is undoubtedly an important mechanism of tree recovery following windstorms in temperate forests. Studies have shown sprouting rates in the 20–80 % percent range to be typical for temperate forests (Peterson and Pickett 1991; DeCoster 1996).

Our study on the effects of the 1996 Hurricane Fran on the Duke Forest in North Carolina has shown that hurricanes significantly diversify the live-tree size distribution in damaged forest stands (Xi et al. 2008a, b; Xi et al. 2012a, b). Overall, the predominant tree species of the upper canopy layer in both pine and hardwood forests decreased substantially due to the higher mortality of large-size trees. In the damaged pine stands, the mean size of the most dominant tree species (*Pinus taeda*) was increased and the density of pines decreased in all size classes. The hurricane also greatly affected pine stands by decreasing the relative abundance of small sized oaks (*Quercus* spp.) and hickories (*Carya* spp.). Several light-demanding and shade-intolerant hardwood species, such as tuliptree (*Liriodendron tulipifera*) *and* sweetgum (*Liquidambar styraciflua*) increased dramatically in density in the smallest size class (1–3 cm) during the 5 years following the hurricane, whereas dogwood (*Cornus florida*), the most damaged tree in the pine stands, decreased in stem density in all tree sizes (Xi 2005; Xi et al. 2008a, b). These general patterns should be broadly applicable to Piedmont forests and more generally to adjacent areas of the southeastern United States.

## Complex patterns of tree mortality

One of the most obvious effects of tropical cyclones on forests is to increase tree mortality. Tree morality in general appears to be positively related to wind intensity (i.e., wind speed) and inversely related to frequency. However, wind-induced mortality can be subtle, complex, and delayed, depending on several contributing factors such as the wind intensity, species of interest, individual size, and life form. In the literature, wind-induced tree mortality rates in temperate forests vary greatly among forest types and wind events ranging up to around 80 %. Nonetheless, there was no clear relationship between forest type and damage or tree mortality (Everham and Brokaw 1996).

In the tropics, tree mortality rates after a severe hurricane tend to be low. Walker (1991), for example, only recorded 7 % mortality 1 year followed Hurricane Hugo (a category 3 hurricane) in Puerto Rica. Bellingham et al. (1994) found 8 % tree mortality 23 months after Hurricane Gilbert in Jamaica. Whigham and others reported 11.2 % in a Mexican forest 17 months after Hurricane Gilbert. These forests experience high hurricane return rates and the tree species that occupy them appear well adapted to these frequent disturbances.

Wind-induced tree mortality in temperate forests varies from low to extremely high. For example, Batista and Platt (2003) reported 7 % mortality for the overstory trees after the relatively modest 1985 Hurricane Kate in an old-growth forest. However, high tree mortality by catastrophic winds has been reported for a number of temperate forests. Foster (1988a, b) reported about 30 % tree mortality for the 1938 hurricane in central New England, USA. Similarly, Hook et al. (1991) found that Hurricane Hugo caused over 80 % tree mortality in the Santee Experimental forest, South Carolina. In Piedmont forests, I found tree mortality of large-size trees to double in the period that spanned the hurricane event, in comparison to the pre-hurricane, although this increased mortality was not uniformly distributed across species. In addition, there was widespread delayed mortality of hardwood tree species following the hurricane. These significant structural and dynamic changes appear likely to have a great and continuing influence on stand regeneration and forest development.

Tree mortality may vary among species. Several studies have assessed species-specific mortality caused by hurricanes in temperate forests (Foster 1988a, b; Foster and Boose 1992; Bellingham et al. 1995, 1996; Batista and Platt 2003). In a comprehensive study of response of trees to the 1938 hurricane in central New England, Foster (1988a, b, 1992) found large differences among tree species in their susceptibility to windstorm damage. However, species-specific mortality may not always be clearly distinguished since other mortality risk factors may interact to contribute to the complex patters of tree mortality. For example, in a study of the impact of a typhoon on Japanese warm temperate forests, Bellingham et al. (1996) found that there was no consistent mortality pattern for most common species, but they found a few species, such as *Symplocos prunifolia,* sustained a high level of basal area loss, while others, such as *Podocarpus nagi*, had low mortality.

Understory morality patterns are less documented than those of the overstory, both in tropical and temperate forests. In some cases understory mortality may be low due to the shielding effects from high canopy trees, but these effects vary among forests. Other factors such as leaf litter, woody debris, and light may also contribute to the mortality patterns of seedlings and saplings. In temperate Piedmont forests, the most rapid changes following catastrophic winds were seen in the understory seedling layer (Xi 2005). Seedling density and species richness experienced an immediate drop. This was followed by a rapid rebound in seedling density and more gradual recovery and enhancement in richness and diversity. Seedling recruitment did not increase continuously over time and overall seedling density was relatively low compared to pre-hurricane level. These disturbance-induced changes in the understory must be viewed in the context of variation in pre-disturbance tree species composition resulting from differences in habitat and stand history.

Cross-site comparisons of tree mortality between forests are needed for a number of reasons. One is the need to correct for variable background mortality rates among tree species, forest types, and successional phases. Another one is that mortality following large catastrophic windstorms is often delayed (Walker 1991, 1995; Sharitz et al. 1992). Temperate forest researchers have noticed that most damaged deciduous hardwood trees can remain alive for many years while still suffering enhanced mortality, plus a certain portion of the damaged trees might grow back through sprouting (e.g. Peterson and Pickett 1991; DeCoster 1996). Consequently, tree mortality must be examined over a long time period and in the context of background mortality of the specific species and successional phases. An immediately survey after a catastrophic wind event could significantly underestimate wind-induced tree death rates. I concur with the suggestion of Everham and Brokaw (1996) that "Mortality should be tracked for several years after catastrophic wind events to determine the extent of elevated mortality." I further suggest that the 5-10 years of observation of the damaged plots is critical for a better understanding of long-term recovery process, particularly the underlying mechanisms of forest recovery from large tropical cyclone disturbances.

## Change in species composition and diversity

Changes in species composition and diversity following wind damage in temperate forests are often gradual and complex. The effects of high winds on tree composition and diversity vary greatly and depend on many contributing factors such as specific windstorm characteristics, site conditions, pre-disturbance community attributes, forest disturbance history, and the temporal and spatial scales at which the changes are observed. Such subtle compositional changes can only be understood through longer-term observation, and in the context of baseline data at specific spatial and temporal scales. To a large extent, these changes are difficult to detect without baseline data, which are rarely available.

A variety of patterns of change in species composition and diversity following large wind events have been reported in the literature. Relatively large changes in species composition and diversity are often, though not always, reported in temperate forests following catastrophic winds. With respect to tree species diversity, studies in temperate zone to date have shown three alternative outcomes: diversity enrichment, compositional maintenance, and loss of diversity. Species diversity enrichment may occur during long periods of recovery in places where a canopy species has been heavily damaged, thereby releasing species present in the understory and perhaps allowing establish of new species in the less competitive environment (Spurr 1956; Abrams and Scott 1989). Severe wind intensities are needed to create large patches and to reconfigure the limited resources such as light and soil nutrients. In these cases species diversity is enriched at the scales of the multiple-patch mosaic, and succession is set back (Webb 1999).

Changes in species composition in temperate forests following wind disturbance can be modest if the same species that regenerate in disturbed patches are most heavily damaged. For example, after examining changes in two Minnesota forests during 14 years following a catastrophic windthrow, Palmer et al. (2000) concluded that the windstorm affected understory species composition, and forests increased in understory species richness, but the magnitude of the changes was modest. There is also the case for positive neighborhood effects. This model links the fate of a disturbed forest patch to the nature and strength of the overstory and understory relationship. Where the positive neighborhood effect is strong, little compositional change will occur because wind-thrown trees are often replaced by the same species (Webb 1999).

The third possible outcome of wind disturbance commonly seen in temperate forests is loss of species diversity following large wind disturbance. This outcome results when shade-intolerant species sustain heavy mortality and are unable to colonize disturbed patches because of a pre-established understory of shade-tolerant species. Sharitz et al. (1992), for example, found that Hurricane Hugo reduced the tree diversity in the slough forest communities in a South Carolina riparian area by having disproportionably larger negative effects on shade-intolerant and transition species of the canopy than on the shade-tolerant species that dominated the subcanopy.

In the Piedmont temperate forests, changes in sapling diversity following the 1996 Hurricane Fran were varied.

Mostly, sapling diversity increased slightly following the hurricane. However, a decrease of sapling diversity was also observed where canopy damage was extreme high, though this may ultimately prove to be compensated for by increased establishment of new seedlings of shade-intolerant species. The density of saplings initially decreased in most damaged plots, but sapling recruitment subsequently increased due to release of previously established seedlings. This observation is consistent not only with the hypothesized relaxation of competition, but also the hypothesis that windthrow contributes greatly to tree diversity in the Piedmont temperate forests (Xi 2005).

In temperate-zone forests, the most conspicuous changes caused by catastrophic winds are structural changes, and the degree of the structural change varies greatly. Relative to tropical forests, large but varied changes in species composition are reported in temperate forests following catastrophic winds (Table 2). With respect to tree diversity, previous studies in temperate forests have shown three possible outcomes: diversity enrichment, compositional maintenance, and loss of species diversity. Clearly, forests exhibit a wide range of responses to windstorms. Consequently, the effects must to be examined at relevant spatial and temporal scales and in the context of specific site conditions and stand history.

## Forest responses

The distinct feature of tropical cyclones-damaged forests, as compared with forests that have experienced other large, infrequent disturbances such as wild fires and volcano eruption, is that the damaged forests often have relatively rapid recovery through multiple recovery pathways.

Foster (1988a, b) identify two major regeneration pathways: (1) from surviving vegetation through advanced regeneration (advanced growth) and vegetative reproduction (sprouting), and (2) from seedling dispersal, recruitment and establishment. The rapid recovery of wind-damaged forests largely results from stem sprouting and the advanced growth of the surviving trees in the new environment of increased light, soil moisture, and nutrient resources. In addition, windthrow creates more diverse soil substrates and allows active seedling and sapling regeneration. Here I further review studies of surviving trees and the understory response to canopy tree gaps and newly available soil.

### *Regrowth of surviving trees by sprouting*

Regrowth plays an important role in tree recovery from catastrophic wind disturbances, especially in temperate hardwood deciduous forests. After damage by intensive winds, a high portion of hardwood trees can regrow from sprouts. Although several researchers have reported differences among species in sprouting ability in both tropical (Walker et al. 1992; Zimmerman et al. 1995; Bellingham et al. 1994) and temperate forests (Peterson and Pickett 1991; DeCoster 1996), this capability appears common. In Piedmont forests of North Carolina, resprouting of damaged individuals and vegetative production of additional shoots were common for most hardwoods (Xi 2005).

### *Understory response*

The understory of damaged forests plays a major part in forest response to windstorms in temperate forests (Webb 1999). Three mechanisms have been often reported in the wind disturbance literature include release of understory plants, recruitment, and repression. “Release” refers to the rapid growth of suppressed understory plants following catastrophic disturbances. Strong winds often cause an increased growth of established seedlings and saplings of primarily shade-tolerant species that were present in the understory at the time of disturbance. Most work on plant “release” after catastrophic winds has been done for saplings and small trees, though the release of established seedlings could also be expected. Piedmont forests have remarkable resilience to hurricane damage because of widespread advanced regenerations. In Piedmont North Carolina, most tree seedlings and saplings approximately doubled their relative growth rates after the 1996 Hurricane Fran, although not uniformly across tree species (Xi 2005; Xi et al. 2012a, b; Fig. 4).

Recruitment is the addition of new individuals into a community. Previous post-disturbance observations on seedling establishment have shown an increase in seedling density following hurricanes, due probably to increased light and soil nutrient availability (Guzman-Grajales and Walker 1991). In Puerto Rican forests, recruitment from seeds was promoted by the large increase in area of gaps and the increased understory light following Hurricane Hugo.

Repression refers to suppression of secondary succession by the establishment or growth of plants that restrict regrowth or recruitment of canopy trees; it also refers to forest succession suppressed by heavy litter. For example, in a New England deciduous forest, George and Bazzaz (1999) found that a fern understory could serve as an ecological filter that decreased establishment, growth, and survivals of canopy-tree seedlings.

## Long-term effects

Tropical cyclones have various long-term effects on dynamics and successional development of forest ecosystems. Those effects vary greatly from setting back forest

**Table 2** Comparison of temperate forests and tropical forests in their responses to tropical cyclone disturbance events

| | Damage patterns and forest responses |
|---|---|
| Tropical forests | Geographically variable, but in general more frequent catastrophic hurricanes. Trees are more wind-resistant. Less composition and diversity change; high and relatively stable tree species diversity. Regrowth and sprouting are common |
| Temperate forests | Although geographically variable, generally a low frequency of hurricane damage, but less intense. Windstorms are frequent. Trees are more susceptible to windthrows. In some cases damage severity can be extremely high. Release of advanced regeneration is common. Greater portion of uprooting than in other types |

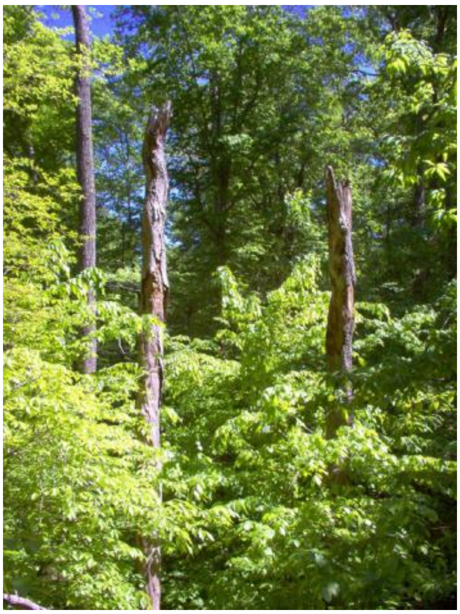

**Fig. 4** Piedmont forests are remarkable resilience to hurricane damage because of widespread advanced regeneration. This 2004 photograph, taken 8 years after Hurricane Fran illustrates the rapid regrowth (advanced regeneration) of established understory hardwood trees in a forest gap in the Duke Forest. Photograph by Weimin Xi

succession to speeding up forest succession. For example, in the Piedmont region I found that historical windstorms appear to have reduced the predictability of stand composition and to have accelerated the existing trend of late successional oak and hickory replacement by more light-demanding red maple. In addition, windstorms in these forests appear to be responsible for increased variance in regeneration, which contributes to a diverse but temporally relatively stable canopy layer. The occurrence of past hurricanes has served to further document and clarify the variable and non-equilibrium nature of late-successional, mixed-aged temperate hardwood forests (Xi 2005; Xi and Peet 2011).

Despite the fact that much has been learned about immediate damage patterns and short-term impacts of catastrophic winds, less is known regarding long-term effects on forest composition, diversity, and succession. Study of long-term effects of historical wind events is difficult because rarely have ecologists been able to combine long-term pre-event and long-term post-event data. Moreover, the few long-term datasets that are available for this purpose were generally not designed or initiated with disturbance events in mind. Nonetheless, sufficient information is available to indicate that hurricanes can have long lasting effects on tree growth, species composition, diversity, and succession, and that these effects can vary greatly with wind intensities, pre-disturbance community attributes, and the timing of the winds.

*Effects on species composition and diversity*

A widely accepted view among forest ecologists is that severe hurricanes have relatively minor long-term effects on species composition and diversity in tropical forest regions and coastal temperate regions where hurricanes are common. Many case studies in the tropics, including studies in Puerto Rico, Nicaragua, Jamaica, and Kolombangara, support this general conclusion. Burslem et al. (2000) found that historical hurricanes only had limited effects on species composition after 60 years of forest recovery.

In contrast with results from most tropical studies, significant but highly variable results regarding long-term change in community composition and species diversity have been reported in temperate forests (Table 2). Large, infrequent wind disturbance events have played an important role in shaping regional vegetation and influencing dynamics in many temperate forests (Webb 1999). Change in species diversity following catastrophic wind disturbance ranges from increasing to decreasing to no change, depending on many factors such as damage intensity as well as the scale of the investigation. However, large temperate-zone hurricanes generally have had a stronger impact on species richness in heavily damaged stands (Boose et al. 2001). For example, Peet and Christensen (1980) reported increased species richness in a comparison study of two hardwood plots in the Duke Forest, North Carolina Piedmont, 23 years after the 1954 Hurricane Hazel. The permanent plots that were severely damaged had twice as many as tree species saplings as compared with the number before Hurricane Hazel. This post-disturbance increase in regeneration of multiple species following an intense windstorm is consistent with a general pattern of dynamic, patch-driven regeneration and diversity maintenance in temperate forests (Peet and Christensen 1980).

Species dominance may shift substantially after wind disturbance because early successional species thrive in the hurricane-created gaps but as long-term term effects are less evident. Nonetheless, the addition of early succession species in those successional patches may lead to short-term increases in landscape diversity. Moreover, the results may be scale dependent. For example, following the 1989 Hurricane Hugo, the number of plant species increased in some sites when observed at an intermediate spatial scale (i.e. hectares), but was essentially constant at both larger and smaller scales. Over the several decades following a hurricane, the short life span of the early successional species, coupled with the self-thinning process may again result in reduced dominance and landscape diversity. Thus, overall, tropical cyclone disturbance may have a limited small-scale effect on species diversity over time, while enhancing diversity at a landscape scale.

### *The lasting effects on forest succession*

The long-term effects of tropical cyclones on forest composition, diversity, and succession are still less known, but available evidence indicates that hurricane-induced changes in tree species composition and diversity can be long lasting. Extreme windstorms tend to differentially remove the oldest and largest trees in a stand. As a consequence, large, catastrophic wind events has been concluded to significantly change forest structure and alter the rates of various processes in the temperate forests, even though their long-term effects on forest succession is uncertain (Waring and Schlesinger 1985). Studies of the long-term wind effects on temperate forest succession to date have shown that windstorms can have all possible effects from setting succession back to advancing successional stages, to initiating multiple-stages of succession depending on wind intensity, frequency, forest types and their pre-disturbance successional stages.

The traditional idea that wind disturbance sets back succession to some earlier seral stage may apply in temperate forests where extreme high winds create large forest openings and initiate secondary succession. The mechanism for this change is that severe windstorms substantially damage the late-successional, canopy-dominant tree species and lead to establishment of early successional species. Therefore, ‘setting back of succession’ often occurs in the later successional hardwood forests exposed to extreme wind intensity. The New England hurricane of 1938, for example, leveled many thousands of acres of mature and semi-mature hardwood forests and initiated new forest associations over a large area with the long-lasting effects.

Wind disturbance can accelerate succession when early successional canopy tree species are heavily disturbed (White and Jentsch 2004). In temperate forests where pines and oaks are dominants, instantaneous death of the even-aged canopy by intensive winds tends to advance forest succession and differentially favor the shade-tolerant understory species. Abrams and Scott (1989) in particular showed that windstorms, among other disturbances, can accelerate forest succession in some North American forest communities. The 1938 hurricane that caused in excess 30 % tree mortality and large areas of windthrow in New England heavily damaged the earlier successional *Pinus strobus* forests, accelerating successional turnover to hardwood forests that were in some cases already present in the understory (Foster and Boose 1992). Arevalo et al. (2000) examined the changes in both pine forest and hardwood stands 14 years following a catastrophic windstorm in Minnesota and concluded that the wind disturbance acted to accelerate the successional process in both forest types by increasing the rate of compositional change from early successional pines and hardwoods to late-successional hardwoods. Although this pattern may be somewhat simplistic, the patterns they found appear common in temperate forests, especially in old-field forests.

When the dominants in temperate forests are damaged by windstorms but are replaced by same type of species, succession can be held at the same stage. Biotic factors such as propagule supply may strongly influence long-term forest recovery and succession following a large disturbance. In the case of intensive wind, the interactions of survivors and the pre-disturbance understory small trees and saplings may determine the initial state in which the forest develops and the recovery pathways from the catastrophic wind event. Turner et al. (1998) argued that the abundance and spatial arrangement of the survivors and the arrival pattern of propagules may be the pivotal factors determining how succession differs between catastrophic disturbances. However, few studies actually examine this effect and the role of propagule in influencing forest regeneration and succession largely remains a matter of conjecture (Webb 1999).

## Effects on fire regimes

Fire prevalence and intensity can be increased in hurricane-damaged ecosystems. Myers and van Lear (1998) found substantially higher fire intensity in hurricane-affected broadleaf forests as compared to unaffected broadleaf forests in Central America after controlling for various factors, including rainfall. The increase in downed wood caused by hurricanes coupled with the proximity to agricultural lands (a source of fire) was found to pose serious risk to hurricane-affected forests. They also found that the effect was not constant in all post-hurricane years and that the variation in annual fire activity in hurricane-affected forests was closely related to dry season rainfall patterns. More importantly, dry season rainfall had no effect on fire activity in unaffected forests, suggesting that hurricane damage does increase fire activity in broadleaf forest but only when dry seasons were unusually dry (Myers and van Lear 1998).

It is hypothesized that the combination of hurricane and fire in synergy could lead to significant compositional and structural changes in coastal forest ecosystems (Myers and van Lear 1998). This hypothesis assumed that hurricanes increase fire activity and intensity in affected forest ecosystems and it was supported in fire-adapted ecosystems of the Gulf and southeastern coast of the US (Liu et al. 2008). Beckage and Ellingwood (2008) found that hurricane disturbances could mediate the frequency of fire that leads to ecological thresholds. They used a cellular automaton model of fire-vegetation dynamics based on pine savanna communities to explore the potential for fire-vegetation feedbacks to lead to ecological thresholds and abrupt transitions between alternate ecosystem states (Beckage and Ellingwood 2008).

## Impacts on wildlife

Some interesting phenomena of wildlife communities, which were related to hurricanes and typhoons, have been observed and investigated. The initial effect of Hurricane Hugo on the animal community of a subtropical wet forest was a reduction in primary consumers such as avian frugivores, bats, some herbivorous insects and a spatial redistribution of secondary consumers. Some invertebrate primary consumers (snails and walking sticks) had greatly reduced populations after the hurricane and were slow to recover. Other invertebrates (blackflies, moths, aquatic insects) had population surges.

Tropical cyclones are an important factor to affect bird population as distribution and assemblage of bird population is usually influenced by the vegetation physiognomy and composition of forest ecosystems. Winds from the 1989 Hurricane Hugo were so strong on the Francis Marion National Forest that 87 % of the red-cockaded woodpecker cavity trees were lost in a single night. Hurricanes significantly altered the bird nesting habitats in the affected areas in the Fushan forest, Taiwan. A study of a dominant bird species, forest-gray-checked fulvetta (*Alcippe morrisonia*) revealed that population of juveniles decreased significantly by typhoon but its adult population was not affected (Xi et al. 2012a, b). In a tropical forest, researchers documented decreases in abundance of birds within 6 months of a hurricane. However, recovery of bird populations after a hurricane was rapid. In Puerto Rico, Mexico, and Nicaragua, both species richness and bird abundance returned to pre-hurricane levels within 9, 17 and 17 months after their respective hurricane. Michener et al. (1997) summarized the hurricane effects, both short- and long-term on birds and their implications for trophic structure. They observed that 35 % of endemic birds live in hurricane-prone regions and that this figure could increase with a small change in the geographic distribution of hurricanes (Michener et al. 1997).

King and others found that different species of fresh water fish decreased dramatically but restored about 2 weeks after storms when streams remained wild and was not disturbed by humans. Another interesting finding was a troop of Formosan macaques (*Macaca cyclopis*), which inhabited the forests and lived mainly on leaves of hardwood forest, disappeared from the forest after typhoons struck in 1994, and then returned after 1 year (King et al. 2000).

Esselstyn et al. (2006) examined the abundance of Mariana fruit bats (*Pteropus mariannus*) on the Pacific islands of Rota and Guam in the Mariana archipelago before and after a severe typhoon in December 2002. They found that after the typhoon, bat abundance declined by 70 % on Rota. On Guam, bat abundance initially increased by ca. 100 individuals (103 %), perhaps due to immigration from Rota, but then declined an average of 32 % from pre-typhoon levels for the remainder of 2003. The decrease of the bat population may lead forest ecosystems suffer because *P. mariannus* is almost certainly an important seed disperser and pollinator on these islands.

Spiller and others censused lizard and spider population immediately before and after Hurricane Lili on 19 islands near Great Exuma, Bahamas that differently affected by the storm surge and found that on the protected side, a moderate of individual lizards and spiders survived. The mean number of lizard individuals per island was 34 % lower than before the hurricane, whereas the mean number of web-spider individuals per island was 79 % lower. On the exposed side, all lizards and spiders population were exterminated (Spiller et al. 1998). In a controlled experiment to simulate hurricane damage effects, Spiller and Agrawal found that hurricane could enhance plant susceptibility to herbivory on islands near Great Exuma, Bahamas. The experimental results indicated that enhanced herbivory on exposed islands following Hurricane Lili was caused, at least in part, by increased susceptibility of the sprouted foliage to herbivorous arthropods (Spiller and Agrawal 2003).

## Effects on invasive species

Research showed that tropical cyclones may result in conditions conducive to invasive plant establishment.

Conner et al. (2002), for example, found that Chinese tallow (*Triadica sebifera*) became the dominant tree species on plots measured in the Atchafalaya Basin, LA, USA, following the removal of large portions of the forest canopy by Hurricane Andrew. While hurricanes are a natural phenomenon that generally contributes to increased species richness and diversity in coastal forests, the increasing occurrence of Chinese tallow tree along the Gulf Coast is a particular concern.

Bellingham et al. (2005) found that Hurricane Gilbert accelerated the invasion of the alien tree Victorian Box (*Pittosporum undulatum*) in montane forests of Jamaica. Twenty years after the hurricane, the species was still gaining in density and basal area. In the Duke Forest of North Carolina Piedmont region, I found that Hurricane Fran created forest gaps that facilitated establishment of invasive tree species and allowed increased growth of previously established individuals. The disturbed forests experienced an increase in certain exotic trees such as princess tree (*Paulownia tomentosa*) and tree-of-heaven (*Ailanthus altissima*). Both increased significantly as a result of the hurricane (Xi 2005; Xi and Peet 2008a, b; Fig. 5).

In the Luquillo Experimental Forest of Puerto Rico, Hurricane Hugo was followed by the germination of invasive herbaceous plants in places with an open canopy and non-native trees in a mature tabonuco forest. Lugo (2008) described the formation of new forests in Puerto Rico as a result of the invasion of abandoned agricultural lands by non-native species. One of these species was *Spathodea campanulata*, currently the most common tree species in Puerto Rico. The species sprouts profusely and grows so fast, that after hurricane passage and regardless of hurricane effects on its canopy and stems, it maintains dominance over sites and only yields to native species by the inability of its seedlings to grow in the shade of a closed canopy (Lugo 2008).

Hurricanes often accelerate growth the existing invasive tree species in the damaged forests. Snitzer and others (2005) found that invasive plant species responded strongly to the increased light levels in patches of forest damaged by Hurricane Isabel in the Piedmont Maryland area. Collectively, the mean increase in percentage cover of exotic plants was 47.8 % in high-light canopy gaps versus only 4.8 % in low-light non-gaps and 4.2 % in the less-damaged forest. Several individual exotic species—*Polygonum perfoliatum, Polygonum caespitosum, and Lonicera japonica* had significant positive responses to higher light levels (Snitzer et al. 2005).

After the passage of Hurricane Andrew, Horvitz et al. (1998) found 28 % of the flora was introduced, including 34 % of the vines and 24 % of other species in south Florida, USA. Both native and non-native species contributed to increases in stem density 2 years post hurricane and non-native species generally exceeded native species in either cover or frequency and did so by germination and growth. Hurricanes did not introduce any new non-native species to their sites, but allowed for changes in the relative importance of natives and non-native species, thus accelerating any process of invasion in progress before the hurricane.

**Fig. 5** Hurricane Fran created forest gaps that facilitated establishment of invasive tree species and allowed increased growth of previously established individuals. The exotic princess tree (*Paulownia tomentosa)* and tree-of-heaven (*Ailanthus altissima)* both increased significantly as a result of the Hurricane Fran. This photograph shows invasion of a princess tree into a pit in the Duke Forest after Fran. However, overall, invasive species have not yet widely spread in the permanent plots across the Duke Forest, NC, USA. Photograph by Weimin Xi

In addition, typhoon was also identified as a possible pathway for invasive pest species (Ruiz and Carlton 2003). In Japan from 1917 to 1999, among 98 invasive pest species, four of them were likely introduced by air current or typhoons. Snitzer and others (2005) found that passing viable seeds from invasive plants by white-tailed deer (*Odocoileus virginianus*) and lacking of the co-evolved herbivores influenced the spread of invasive plants and regeneration of the forests after Hurricane Isabel in the Piedmont of Maryland, USA.

## Effects on carbon flux, sequestration and nutrient cycling

Tropical cyclones can have significant effects on the carbon flux, sequestration and nutrient cycling in a region.

Hurricanes can reduce the amount of current amount of live stand carbon through tree uprooting and stem breakage. On average, a single major hurricane can covert the equivalent of about 10 % of the total annual US forest carbon sequestration from living to dead wood (McNulty 2002). It was estimated that the total amount of detritus from Hurricane Hugo to be 20 Tg.; hurricanes are a significant factor in reducing short-term term carbon storage in US forests and negatively impact the ability of US forests to sequester atmospheric carbon (McNulty 2002). Pacala et al. (2001) estimated that forest trees in United States sequestered 110–150 Tg of carbon per year over the period 1980–1990 (Pacala et al. 2001). Zeng et al. (2009) found an average of 97 million trees affected each year over the entire United States, with a 53-Tg annual biomass loss, and an average carbon release of 25 Tg/y. Over the period 1980–1990, released $CO_2$ potentially offset the carbon sink in forest trees by 9–18 % over the entire United States. Fisk et al. (2013) estimated the net impacts of tropical cyclones on the carbon balance of US forests over the period 1851–2000. To track both disturbance and recovery and to isolate the effects of storms, a modeling framework is used combining gridded historical estimates of mortality and damage with a mechanistic model using an ensemble approach. The net effect of tropical cyclones on the carbon balance is shown to depend strongly on the spatial and temporal scales of analysis. On average, tropical cyclones contribute a net carbon source over latter half of the 19th century. However, throughout much of the 20th century a regional carbon sink is estimated resulting from periods of forest recovery exceeding damage. The large-scale net annual flux resulting from tropical cyclones varies by up to 50 Tg C $yr^1$, an amount equivalent to 17–36 % of the US forest carbon sink.

Research showed various changes in post-hurricane productivity. While some model simulations suggested that Hurricane Hugo could reduce ANPP and biomass accumulation after a hurricane, field study showed that ANPP is high and biomass accumulation rate is fast, likely reaching prehurricane values in less than 15 years. In most cases, hurricanes remove large canopy trees and thus allow the potential more productive forest understory to replace the overstory. The nutrients from leaf tissue and the increased surface aeration from uprooted trees could increase overall soil productivity (McNulty 2002).

Overall, the most immediate impact of a hurricane on a forest is a massive increase in the amount of dead wood that is converted from living wood. Shortly after, the dead wood begins to decompose. While there were hurricane-related timber salvages, the majority (>90 %) of the wood is left to decompose within the forest after a major hurricane. At the same time, risks of fire, insect and disease to carbon storage in living trees increase. Massive wood fall of low nutritional quality after a hurricane has the capacity of immobilizing nutrients, particularly N, and thus reducing nutrient availability (Zimmerman et al. 1995). Beard et al. (2005) suggested that adding woody debris to a forest increased the turnover of organic matter by litter fall and increased fine root biomass. Land use legacies, such as presence of N-fixing trees, could have also contributed to overcoming N immobilization by woody debris (Beard et al. 2005; Lugo 2008). Rice and others studied woody debris decomposition in Louisianan (USA) and found that woody debris displayed strong sources activities for P, but a greater tendency toward sink behavior for N. Woody debris might act as a phosphate source but could provide short-term retention of inorganic N (Rice et al. 1997; Lugo 2008).

## Synthesis, research needs and management implications in a changing climate

### Synthesis

In this review, I combine illustrative examples to present current knowledge then link them to several important themes that have emerged in recent years for understanding the complexity of tropical cyclone effects on forest ecosystems and subsequent forest response. Two relatively separated lines of investigation are apparent in the literature review, one focused on the complexity of forest damage patterns and their risk factors, and the other focused on the high degree of variation among forests in their structural and compositional responses to windstorm disturbances.

The variation among tropical cyclone regimes and forest responses makes generalization a challenge. The literature here reviewed shows the complexity of pattern in forest damage and tree mortality following tropical cyclones, as well as the significant variation among forests in structural and composition responses. Many factors interact to influence the patterns of damage and dynamics of recovery. Therefore, evaluating the relative importance of multiple factors and various recovery patterns across the full spectrum of disturbance severity levels will help elucidate these factors and their interactions. Nonetheless, there remains a clear need for additional studies that quantify wind disturbance severity and complexity of impact in high-wind damaged forests.

Tropical cyclones-induced dynamics may vary at the different spatial and temporal scales. The ecological consequences of catastrophic winds are complex, subtle, and at smaller scale relatively unpredictable. Consequently, wind-induced changes must be viewed in the context of interaction and variations among multiple factors, especially species composition resulting from differences in habitat and stand history. Remarkably few studies have actually examined multiple factors and multiple-scale wind damage and forest recovery. Windstorm-induced effects should be examined across a gradient of spatial and temporal scales.

Such studies are needed to explore these complicated and scale-dependent processes and patterns. Long-term studies of forest response to different combinations of the wind disturbance severity are needed. The variable effects of windstorms on temperate forests largely depend on the wind intensity, size, specificity, frequency of individual windstorms in a given location, pre-disturbance species composition, and successional stage. The complex impacts of winds and variable forest recovery are more readily discerned when detailed, long-term pre-disturbance and long-term post-disturbance data are available. Certainly, more extensive long-term studies on permanent research sites will be very important for understanding the long-term impacts of tropical cyclones.

## Climate change and tropical cyclones

A changing climate can affect the distribution of species, the geography of forests, and the rates of all ecosystem processes. All these changes have an effect on how the resulting forests respond to the forces of tropical cyclones. The role of climate change on hurricanes is still unclear. Michener et al. (1997) explored the consequences of climate change on hurricanes and sea level change in relation to coastal ecosystems and the possibility of shifts in the geography of hurricanes raise important research questions for future. The intensification of tropical cyclones in warming climate is still an open question. Emanuel suggested that hurricanes would intensify with climate change. Goldenberg et al. (2001) and Emanuel (2005) found a doubling of overall hurricane activity and a 2.5-fold increase in major hurricanes in the Atlantic between 1995 and 2000, compared with the period of 1971 and 1994.

More recent research by Altman and others provided new evidence about dramatic increase in occurrence of strong typhoons since the end of 19th century (~1880) for eastern Asia by the mean of analysis more than 30,000 tree-rings and climatic data about typhoon frequency and intensity (Altman et al. 2013). Knutson et al. (2010) suggested that future projections based on theory and high-resolution dynamical models consistently indicate that greenhouse warming will cause the globally averaged intensity of tropical cyclones to shift towards stronger storms, with intensity increases of 2–11 % by 2100. Existing modelling studies also consistently project decreases in the globally averaged frequency of tropical cyclones, by 6–34 %.

Future tropical cyclones are likely to become more intense, with larger peak wind speeds and increased heavy precipitation. Extra-tropical storm tracks are projected to move poleward, with consequent shifts in wind, precipitation, and temperature patterns. Increases in the amount of precipitation are very likely in high latitudes and decreases are likely in most subtropical land regions, continuing observed patterns. Increases in the frequency of heavy precipitation events in the coming century are very likely, resulting in potential damage to crops and property, soil erosion, surface and groundwater contamination, and increased risk of human death and injury.

## Research needs

Researchers need continue to examine the synergistic effects of tropical cyclones on forest ecosystems in as many forest types and over the longest time possible. More long-term, multiple-scale comparative analyses and a worldwide observatory network are needed to fully understand these scale-dependent processes, to accurately predict the consequences, and to effectively manage the impacts. Overall, hurricane strength and spatial allocation needs to be measured in real-time and be more accurate. Continuous instantaneous measurements of storm characteristics (wind speed, direction and barometric pressure) over the whole path of hurricanes are needed to advance the hurricane impact research. In future studies, research should address the interplay of multiple factors pre- and post- wind disturbance events through experiments, modeling, and cross-site comparison to separate the confound effects.

Better and more generally applicable simulation models are needed for predicting the impacts of future catastrophic tropical cyclones on forest ecosystems. Both population-based gap models and spatially explicit landscape models provide powerful tools for predicting forest disturbance and dynamics. Recent progress has been made in constructing such models applicable to temperate forests (Doyle 1997; Schumacher et al. 2004), but parameterization of these models for species-rich systems presents considerable challenges. Direct estimates of colonization and mortality rates from long-term studies in tropical and temperate forests could be highly valuable for improving these models. Predictive models will ultimately provide the knowledge essential for better understanding the role of tropical cyclone disturbances in forest ecosystems, in guiding conservation efforts, and in informing forest management decisions.

## Management implications

The knowledge concerning the effects of tropical cyclones and forest response is critical and should be incorporated in preparing strategic management and ecological restoration plans in tropical cyclone impact forest regions. Previous tropical cyclones provided opportunities to examine regional forest management objectives toward incorporating both large and fine-scale disturbance effects such as more complex stand structure into ongoing forest management in order to reduce vulnerability to damage from future tropical cyclones. A better understanding of risk to natural response may induce management changes to reduce vulnerability and natural system could be used to reduce vulnerability of urban or managed forest ecosystems.

In the tropical cyclone impact regions, forest management practices of reducing risk prior to wind damage events are important. Reducing the potential damage largely depends on forest managers and land owners making appreciate silvicultural decisions to minimize the risk. Forest managers and land owners need to understand the long-term implications of their actions. Reduce short-term impact following the tropical cyclone impact is also important. Lessons learned from previous major tropical cyclones make it clear that rapid assessment of damage extent, severity and significance are critical to successfully mitigating immediate effects. Management response following tropical cyclones can include salvage to recover value, mitigation of wildfire hazard and restoration. Values, services and benefits from resource other than timber (such as wildlife) should be considered in the decision process. Maintaining wildlife habitats and aiding in recovery efforts should be include in the overall response plan.

Beyond the short-term management, managing the long-term recovery needs to be put into consideration in the context of climate change. As the recovery will take many years and require investment of time and resources, the long-term risks need to be examined and mitigation strategic plan needs to put in place to reduce the vulnerability. Vulnerability can be lessened by converting to trees that are less susceptible to wind damage. Other strategies to reduce vulnerability include limiting exposure of individual stands by spatially distributing management treatments that could increase vulnerability to wind damage. By staggering thinning, a manager can limit the amount of thinned stands in an area. Balancing age classes also reduces the overall risk of catastrophic loss within an area or on an ownership (Stanturf et al. 2007). Decreasing vulnerability of forests to tropical cyclones requires that we understand risks under changing climate. This information is particularly important as ongoing climate change is likely to sustain the recent increased incidence of major tropical cyclones for the foreseeable decades (Goldenberg et al. 2001; Emanuel 2005; Xi 2005; Xi and Peet 2011).

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