Chapter 3
Natural Disturbances and Early Successional Habitats

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Abstract Largely a legacy of stand-replacing human disturbances, today's central hardwood forests exhibit a narrower range of stand ages and structures than those in the presettlement landscape. Although natural disturbance types and frequencies vary within the region, large stand-replacing natural disturbances have always been infrequent; typical return intervals in excess of 100 years are longer than current forests have existed. Many present-day stands are dominated by early to mid-successional species in the overstory and late successional species in the understory; natural disturbances often serve to increase dominance of the understory late successional species, unless they are severe enough to disturb the canopy, forest floor, and soil. In any case, only the most severe natural disturbances or combinations of disturbances (including human disturbance) initiate large patches of early successional vegetation. Will the amount and spatial arrangement of early successional habitats created by natural disturbances be sufficient to meet management goals? We do not have the information to answer this question at present; the answer is further complicated by the potential effects of climate change on the rates and intensities of natural disturbances.

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3.1 Today's Forests – A Legacy of Human Disturbance

Today's central hardwood forests are largely a legacy of stand-replacing human disturbances that began in the 1700s and intensified in the 1800s and early 1900s (Lorimer 2001). Many of these forests owe their origin to large scale logging that took place between 1850 and 1940, while others date from farm abandonment that has occurred, at different times in different parts of our study area, from 1880 to the present (Fralish and McArdle 2009; Hart and Grissino-Mayer 2008). Peak agricultural clearing occurred between about 1880 and 1920, and post-farming stands from that period are similar in age to the post-logging forests.

Logging and agricultural disturbance were often accompanied by soil erosion, so the significance of these disturbances was more than a simple resetting of the successional clock; productivity and successional trajectories were affected on some sites. Burning and understory livestock grazing also were widespread during the 1800s and early 1900s, and occurred over landscapes variously cleared, farmed, or burned by Native Americans (Owen 2002).

Because of their roots in historical, widespread stand-initiating human disturbances, most of today's central hardwood forests are 70–100 years old, creating a landscape with reduced structural heterogeneity and age diversity compared to the presettlement landscape (Shifley and Thompson, Chap. 6). These forests are now reaching sawtimber size over large areas. Some stand characteristics, such as leaf area and basal area, have reached levels similar to presettlement forests, but composition, maximum tree sizes, and downed woody debris remain out of presettlement norms (Flinn and Marks 2007; Trani et al. 2001).

Present day stem densities generally are greater than densities in old-growth forests for three reasons: (1) Trees are mostly only about one-quarter to one-half their maximum sizes and forest understories were more open in the past due to (2) frequent fires, and (3) understory grazing. Shade-tolerant, fire sensitive, and mesic species often dominate in these denser forest understories and the forests are slowly converting from greater dominance by oaks (*Quercus* spp.) and hickories (*Carya* spp.) (with pines (*Pinus* spp.) in some areas) to maples (*Acer* spp.) and beech (*Fagus grandifolia*) as these species regenerate after the death of overstory trees (Cowell et al. 2010; Fralish and McArdle 2009; Hart and Grissino-Mayer 2008; Hart et al. 2008). Nowacki and Abrams (1997) refer to the widespread increase in mesic fire sensitive species across the deciduous forests of eastern North America as "mesophication." Although invasive pests and diseases (e.g., chestnut blight (*Chryphonectria parasitica*), gypsy moth (*Lymantria dispar*)) became important throughout the 1900s, they also served to increase canopy turnover rates and release advanced regeneration rather than initiate early succession composition and structure.

The maturation of central hardwood forests, the roughly synchronous nature of the large scale human disturbances that produced them, and the current smaller-scale disturbance regime, mean that early successional habitats within these forests are declining. This, in turn, raises concerns about the persistence of biodiversity supported by early successional habitats. In this chapter, we address the questions: What natural disturbances are important in these forests? Will these natural disturbances recreate the heterogeneity and patchiness of the past? Do natural disturbances initiate early successional habitats, which we consider to include new stands, young forest patches, or habitat within forests for open site, early successional plants, in the present landscape? Other chapters in this volume focus more specifically on vegetation response to disturbance; for example, Elliott et al. (Chap. 7) examine disturbance effects on herbaceous vegetation composition and diversity, and Loftis et al. (Chap. 5) examine effects of silvicultural disturbances on species composition of regenerating hardwoods.

In addition to natural disturbances within forests, there are other sources of open habitats and the biodiversity they support in the Central Hardwood Region. They include rock outcrops, glades, barrens, fire-dependent prairies that develop on certain bedrocks, and floodplains and stream channels affected by flood scour and beaver populations (Anderson et al. 1999). These habitats have slow rates of succession (rock outcrops, glades, and barrens), high rates of disturbance (floodplains, prairies) or both. For example, frequent fire can expand open grasslands and savannahs beyond the immediate boundaries of the bedrock islands that underlie some of these open communities. These open sites are also early successional habitats, but in this chapter we focus only on early successional habitats within upland forests, including new stands, patches of young forest, or open patches with early successional species. Anderson et al. (1999) have described the other kinds of open and successional communities in the North American forests.

3.2 Natural Disturbances and Early Successional Habitats

Large-scale or intense disturbances above a threshold of severity (Romme et al. 1998; Frelich and Reich 1999) initiate succession or maintain early successional forest habitats and allow the periodic regeneration of shade intolerant species. Frelich and Reich (1999) concluded severe or high cumulative disturbance maintain early successional species or initiate rapid conversion from late successional species to early successional species (a compositional catastrophe). Roberts (2004, 2007) linked disturbance severity to the percent of cover or biomass removed or disrupted through canopy, understory, and forest floor layers. We have adapted the Roberts model (Fig. 3.1, *left panel*) to link natural disturbance type and severity to early successional habitats. Disturbances are likely to have different impacts through forest strata (reviewed by Roberts 2004) and the threshold of severity to initiate succession is likely to differ both among strata and disturbances. For example, fire and flooding are ‘bottom up’ disturbances, with ground layer, understory, and canopy impacts at increasing severity. In contrast, wind disturbance, ice storms, and pathogens are often ‘top down’ disturbances. As windstorm severity increases, effects move from the canopy to soil and understory disturbance through tip-ups, thereby increasing the importance of seed dispersal relative to sprouting and seed bank in recruitment of understory stems (e.g., Busing et al. 2009; Clinton and Baker 2000). In general,

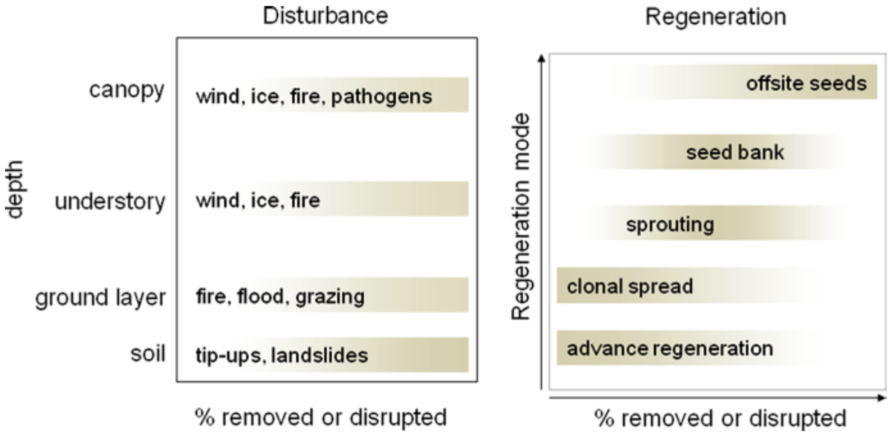


Fig. 3.1 On the *left*, a conceptual model (adapted from Roberts 2004, 2007) relates increasing severity of natural disturbance – as percent cover or biomass removed or disrupted through forest strata – to extent of early successional habitats, which is represented by the progressive shading and includes young forest and open patches with early successional plant species. Disturbance above some threshold of severity (Romme et al. 1998; Frelich and Reich 1999) may be required to initiate early successional habitats. On the *right*, the relative importance (*indicated by the shading*) of different regeneration modes changes with disturbance severity; regeneration from seed sources increases as disturbance severity increases

the establishment of shade intolerant species in the Central Hardwood Region depends on both canopy and ground layer disturbance.

Although severity of individual and multiple disturbances has been related qualitatively to forest conversion or maintenance of early successional species (e.g., Frelich and Reich 1999), few studies have quantified the severity of individual natural disturbance types needed to initiate succession or maintain early successional habitats in upland central hardwood forests. Most evidence is indirect. For example, hurricane damage that resulted, on average, in 25% basal area reduction in a mixed oak-hickory-pine forest did not shift composition toward shade-intolerant tree species (Busing et al. 2009). Natural disturbance alone also had little effect on habitat availability for early successional songbirds in a 60 year simulation study (Klaus et al. 2005). In a west-central Tennessee site that experienced moderate-severity windthrow and limited subsequent salvage logging, establishment of shade-intolerant tree species was more related to pre-disturbance forest composition than to disturbance severity (Peterson and Leach 2008). In contrast, however, Clinton and Baker (2000) found that gaps up to 4,043 m^2 could facilitate establishment of shade-intolerant species in Southern Appalachian forest. Vigorous sprouting (Clinton and Baker 2000) likely contributed to early successional forest structure, since these forests were young enough to have such species in the overstory. Elliott et al. (2002) also found that 84% reduction in basal area, through wind disturbance and subsequent salvage logging, allowed a heterogeneous mix of shade tolerant species, shade intolerant species, and opportunistic early successional understory species to establish in Southern Appalachian forests. Variation in forest composition, differences in disturbance severity over the landscape, and interaction of multiple disturbances (including interactions of natural disturbances and management) are most likely to create within-forest heterogeneity, with local patches of early successional habitats.

Differences in regeneration mechanisms among forest types and over disturbance severity gradients can contribute to the extent and, possibly, duration of early successional habitats. Figure 3.1 (*right panel*) is a conceptual model of the relationship between disturbance severity and predominant regeneration mechanism following disturbance. In general, contribution of seed sources increases with disturbance severity, although contribution from the seed bank will diminish if soil surface layers are removed (Aikens et al. 2007; Clinton and Baker 2000; Harrington and Bluhm 2001; Turner et al. 1998). Greater contribution from seed sources can increase abundance of early successional and shade-intolerant species, many of which regenerate from buried seeds or from seeds carried into the site by wind or animals. For example, regeneration after hurricane disturbance followed by salvage logging was characterized initially by many small-diameter stems and opportunistic species (*Rubus allegheniensis*) that regenerate from buried seeds (Elliott et al. 2002). Sites with a high abundance of species that resprout following disturbance are less likely to have new individuals establish, but may maintain young forest structure if early and mid-successional species dominate the canopy. Regeneration from seeds may also increase the time to canopy closure, when compared to sites with residual plants (those remaining after the disturbance) or a high abundance of species that resprout (Turner et al. 1998).

In general, only the most severe disturbances, such as catastrophic windstorms, fire, or landslides, create extensive early successional habitats. However, repeated natural disturbances, management following a disturbance event, or disturbance following management action could effectively increase disturbance severity or increase the duration of early successional species or structure (Elliott et al. 2002; Gandhi and Herms 2010; Kupfer and Runkle 1996). Frelich and Reich (1999) pointed out the importance of cumulative disturbance severity in maintaining early successional species or initiating catastrophic conversion of late successional to early successional species. Cumulative disturbances also are likely to maintain early successional habitats by preventing establishment of late successional species.

3.3 Disturbance Patterns Within the Central Hardwood Region

Some parts of the Central Hardwood Region are more susceptible than others to particular disturbance types. Understanding the variation in disturbance types and frequencies within the region can guide management actions to promote or sustain early successional habitats (see Shifley and Thompson, Chap. 6).

We used spatial information to examine the patterns of natural disturbances within the Central Hardwood Region. A Geographic Information System (GIS) coverage for ice storm potential (freezing rain) was derived by geo-referencing Fig. 3.1 (a map of the annual number of days with freezing rain as defined by 988 weather stations from 1948 to 2000) from Changnon and Bigley (2005). Line coverage of historical North Atlantic tropical cyclone tracks, 1851–2000 (NOAA 2009) was used to generate a density map of tropical storm occurrence within the region. Tornado density was calculated in ArcGIS (v. 9.3) using United States tornado touchdown points 1950–2004 (NWS 2005). A landslide coverage was based on a spatial index of landslide susceptibility and occurrence (Godt 1997). Raster digital data for mean fire return interval were obtained from LANDFIRE (US Forest Service 2006). The base maps for these disturbances are shown in Appendix I.

To evaluate the patterns of the combined disturbances, we first scaled each disturbance (0–100 scale) among 17 ecoregions (US Environmental Protection Agency 2009) contained within the larger Central Hardwood Region and calculated the mean value of each scaled disturbance weighted by the number of pixels that represented the disturbance within the ecoregion. We used principal components analysis (PCA) to identify linear combinations of the five disturbance types over the ecoregions. It is important to note here that base disturbance intensity differs among the disturbance types. For example, the landslide coverage includes both susceptibility and occurrence; ice storm potential is assessed through data on the days of freezing rain rather than ice storm damage; tropical storms vary in intensity; and mean fire return interval includes a range of severity from understory to stand-replacing fires.

The predominant disturbance type varies among ecoregions within the larger Central Hardwood Region (Figs. 3.2, 3.3). The first two principal components explained 77% of the variance in disturbances among the ecoregions. Axis 1 correlated positively with tornados (0.90) and negatively with landslides (−0.88) and tropical storms (−0.80). This axis represents an east–west gradient (Fig. 3.3) from tropical storms, the predominant disturbance in the east, to tornados in the west (Table 3.1, Fig. 3.2). The frequency of tropical storms decreases from the Piedmont (ecoregion 45, Table 3.1) and adjacent Blue Ridge (ecoregion 66) westward to the Ridge and Valley (67), Central Appalachians (69) and Western Allegheny Plateau (70), which are more susceptible to landslides (Figs. 3.2, 3.3; Table 3.1).

Principal component Axis 2 correlated positively with fire return interval (0.82) and negatively with freezing rain (ice storm potential) (−0.81). Not surprisingly, northern extensions of the region, including the Huron and Erie Lake Plains (57), Southern Michigan and Northern Indiana Drift Plains (56), and Eastern Corn Belt Plains (55) have the highest occurrence of freezing rain (Table 3.1; Figs. 3.2, 3.3). Western regions, from the Central Corn Belt Plains (56) south to the Ouachita Mountains (36), have the highest occurrence of tornados, but areas farther north (56) also experience freezing rain and more southern regions (36, 37, 38) experience frequent fire (5–15 year fire return intervals, Appendix I). The Appalachians and adjacent Plateau regions are an exception to the north – south gradient from freezing rain to high fire return intervals (Fig. 3.3); relatively high rainfall results in

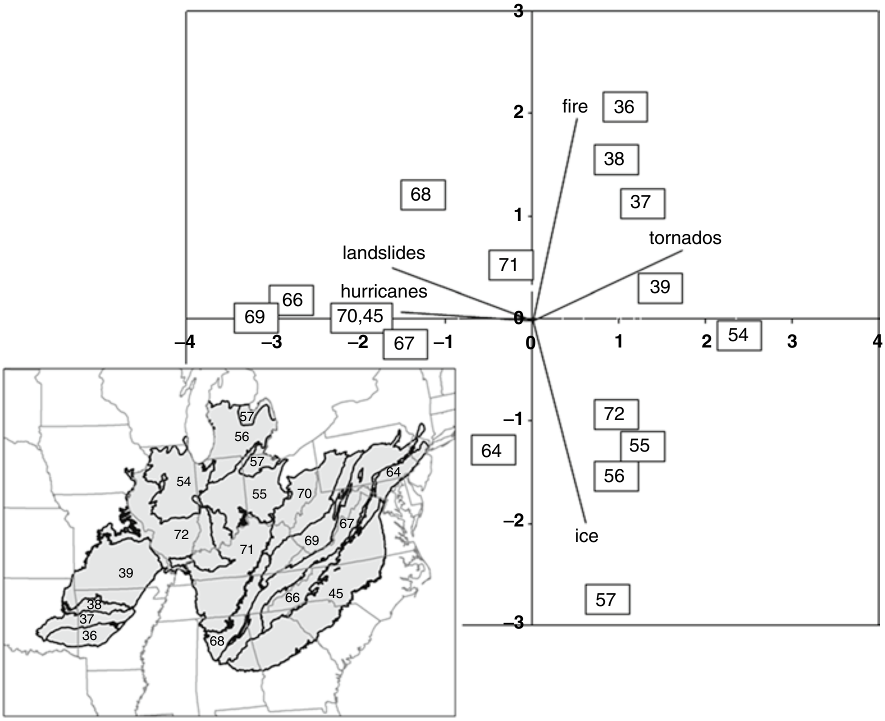


Fig. 3.2 Ecoregions of the Central Hardwood Region and five disturbance eigenvectors (*scaled to unit length*) plotted on the first and second principal component axes. Names of the numbered ecoregions are given in the text

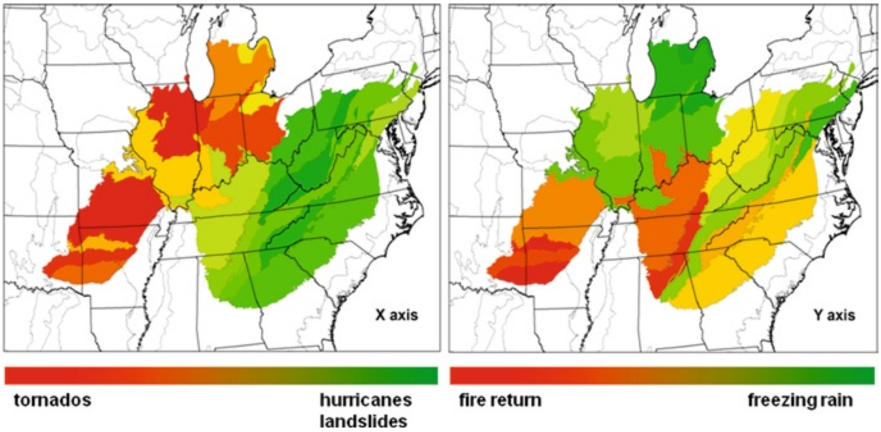


Fig. 3.3 Ecoregions of the Central Hardwood Region color-coded by their PCA scores (*first (X) and second (Y) axes*). First axis scores were positively correlated with tornados and negatively correlated with landslides and hurricanes. Second axis scores were positively correlated with fire return interval and negatively correlated with freezing rain

Table 3.1 The likelihood of experiencing disturbances within each ecoregion

Ecoregion	Freezing rain days/year	Tornados #/ km^2/10 year ($\times 10^{-3}$)	Trop. storms #/ km^2/10 year ($\times 10^{-5}$)	Fire return interval (years)
56	3.8	1.8	2.4	14.6
67	2.9	0.9	8.9	9.2
57	3.9	1.6	6.2	23.4
54	4.3	2.6	2.5	3.9
64	3.8	1.9	11.9	8.9
55	4.1	2.0	3.8	14.9
70	2.7	0.6	3.6	8.6
69	2.1	0.3	5.1	12.7
72	3.4	1.7	4.0	12.9
45	2.4	1.2	12.8	7.3
71	1.8	1.5	5.9	9.1
39	3.4	1.5	3.7	4.5
66	3.0	0.4	12.0	7.8
68	1.0	1.5	12.0	8.0
38	2.3	1.0	11.8	3.4
37	2.0	2.7	8.5	7.8
36	1.3	1.2	9.7	5.0

Information about the temporal scale and data sources for each disturbance is included in the text. Qualitative data for landslide incidence and susceptibility could not be averaged and thus were not included in the table. Averages for freezing rain (days/year) and fire return interval (years) were derived from area-based spatial data (Appendix 1) and were weighted by the proportion of area representing different values within the ecoregion. Tornados are the number of touchdowns points per km^2 per decade within the ecoregion. Tropical storm values were derived from storm tracks (line data, Appendix 1), and are reported as the number per km^2 per decade within the ecoregion

longer fire return intervals and higher elevations likely experience more frequent freezing rain or ice (Table 3.1).

Variation in natural disturbances over the Central Hardwood Region is likely to result in different patterns and probabilities of early successional habitats being created or maintained. Catastrophic windstorms, associated with tropical storms and hurricanes in the east and with tornados in the west, can create patchy and sporadic early successional habitats, although research suggests these storms generally are below the threshold needed for the initiation of extensive early successional stands unless followed by management (e.g., salvage logging) or a subsequent natural disturbance (Elliott et al. 2002; Gandhi and Herms 2010; Kupfer and Runkle 1996; Peterson and Leach 2008) that increases disturbance severity. In the Piedmont (eastern) and Ouachita (southwestern) ecoregions, fire is the most likely natural disturbance to act in concert with wind (Fig. 3.3). Historically, these fires were initiated by Native Americans, settlers, or lightning; today they are most likely to be initiated by land managers (see Spetich et al., Chap. 4).

In northern ecoregions, as well as on slopes and ridges of the Appalachians, ice storms are most likely to cause damage to the canopy. Susceptibility to ice storms may be greatest on steep slopes (Mou and Warrilou 2000) and damage can be more intense on edges (Millward and Kraft 2004). However, ice storms often do not lead to change in forest composition, although growth of understory species can slow recovery, especially in larger gaps (Mou and Warrilou 2000). Slopes of the Appalachians and adjacent Plateaus also are susceptible to, and have a high incidence of, landslides. These localized disturbances have high heterogeneity, with patches of unstable exposed soil, erosional and depositional zones, and an initial mix of surviving vegetation and early colonists (Myster and Fernandez 1995; Francescato et al. 2001; Walker et al. 2009). Rates and trajectories of succession can be highly variable on landslides (Francescato et al. 2001; Walker et al. 2009); early successional herbs and patches of shrubs can persist for decades or be replaced more rapidly by forest species (Francescato et al. 2001; Walker et al. 2009).

The presettlement forest landscape, except of course on sites of Native American cultivation, was largely forests whose dominant trees often survived to reach ages of 300–500 years. The mortality of canopy trees therefore occurred at low rates, probably varying from about 0.05% to 2% of canopy trees per year (Runkle 1982; Busing 2005). Large stand-replacing natural disturbances were always infrequent relative to tree lifespans, with return intervals in the 100s of years. Thus, return intervals are longer than the current forests have existed (Hart and Grissino-Mayer 2008; Lorimer 2001; Schulte and Mladenoff 2005). For example, Hart and Grissino-Meyer (2008) found evidence of only one stand release, in the 1980s, in an oak-hickory forest that established in the 1920s. Less severe disturbances, those that do not lead to stand replacement are, of course, more frequent.

Return intervals of particular disturbances at small scales are affected by local factors, such as topography, as well as regional factors such as climate. There are several challenges in predicting natural disturbance return intervals at a local scale. First, they are scale dependent. For instance, the return interval for tropical storms over the last 100 years in the state of North Carolina as a whole (139,396 km^2) is about 1.3 years (www.nc-climate.ncsu.edu). The return interval for Orange County, North Carolina, an inland county of 1,040 km^2 is about 50 years, while the return interval for a particular stand of trees within Orange County is in excess of 100 years (see also Busing et al. 2009). A second challenge is that disturbance rate and severity are contingent, proximately, on current structure and composition and, ultimately, on successional history. Thus, the disturbance rates in the homogeneous forests of the present, with their high densities and uniform canopy of trees that are smaller than old growth forests, are themselves a result of the synchronous origin of these stands some 70–100 years ago. A third challenge is that cumulative effects of repeat or multiple disturbances are more likely to produce early successional habitats than single events (Frelich and Reich 1999). A fourth is that invasive pest species are still spreading in this region. Finally, disturbance rates and severities are likely to change with changing climate and socioeconomic factors. Wear and Greis (Chap. 16) forecast how forest type and age class distribution might change over the next 50 years in response to biophysical and socioeconomic dynamics. Below, we discuss the linkage between natural disturbance and early successional habitats at the landscape scale.

3.4 Natural Disturbance and Early Successional Habitats on the Landscape

At landscape and regional scales, we can ask: how do natural disturbances affect the amount and distribution of early succesional habitats and is this pattern dynamically stable (i.e., in equilibrium and likely to be maintained) over time? A strict definition of equilibrium is "quantitative" equilibrium or "shifting mosaic steady state" in which disturbance rate is constant and the percentage of various patch types and stand ages, including early successional vegetation, is constant through time at large spatial scales. Given all the historic and present disturbances that impact forests of the Central Hardwoods Region, quantitative equilibrium is unlikely. A less stringent form of dynamic stability is "qualitative" or "persistence" equilibrium (see discussion in White et al. 1999) in which the rate of disturbance and size of disturbance patches vary, but within boundaries such that patch types, stand ages, and the species associated with these conditions fluctuate from year to year but do not disappear at large spatial scales. Qualitative equilibrium is more likely, and given that it suggests persistence of species dependent on all patch types, may be a reasonable standard for conservationists and managers.

Given (1) the narrow age range of current forests, (2) observations in the literature which suggest later successional species in understories increase after disturbance, and (3) the low probability of stand-replacing natural disturbances, large patches of early successional habitats may be declining on the landscape. However, disturbances do create edges. Light, nutrient, and seed dispersal gradients across edges allow open-site and early successional species to establish and persist in edge zones. For example, edges between forests and agricultural fields had a greater number of light-demanding species than forests interiors, and south-facing edges were as wide as 23 m (Honnay et al. 2002). In forest edges younger than 6 years, most edge-oriented species were close to the edge, with distributions related to light and light-related variables, but some species had peak density up to 40 m into the forest (Matlack 1994). Species composition and distribution patterns characteristic of edges persisted up to 55 years after edges were closed by succession (Matlack 1994).

Canopy gaps and similar disturbance patches also contain light, nutrient, and seed dispersal gradients that promote early successional forest composition and young forest structure. For example, canopy openness in 3-year-old experimental gaps greater than 20 m radius in bottomland hardwood forest declined linearly from the open center (>20% canopy openness) across the edge (>10% canopy openness) to more than 60 m (<5% canopy openness) into the surrounding forest (Collins and Battaglia 2002). Ten years after the gaps were created, the centers had a young forest canopy; species composition differed from gap centers into the surrounding forest, with wind-dispersed species more common in gap centers (Holladay et al. 2006). In a high-latitude Scots Pine (*P. sylvestris*) and Norway Spruce (*Picea abies*) forest, cumulative photosynthetically active radiation (PAR) was asymmetrically distributed around a canopy gap (deChantal et al. 2003). PAR decreased from 1,100 MJ m^{-2} in the gap to 300 MJ m^{-2} beneath surrounding forest over 20 m on the north side and over 36 m on the south side of the gap. After only two growing seasons, there was evidence that the asymmetric distribution of light and resources could contribute to Scots Pine and Norway Spruce becoming dominant in different parts of the gap.

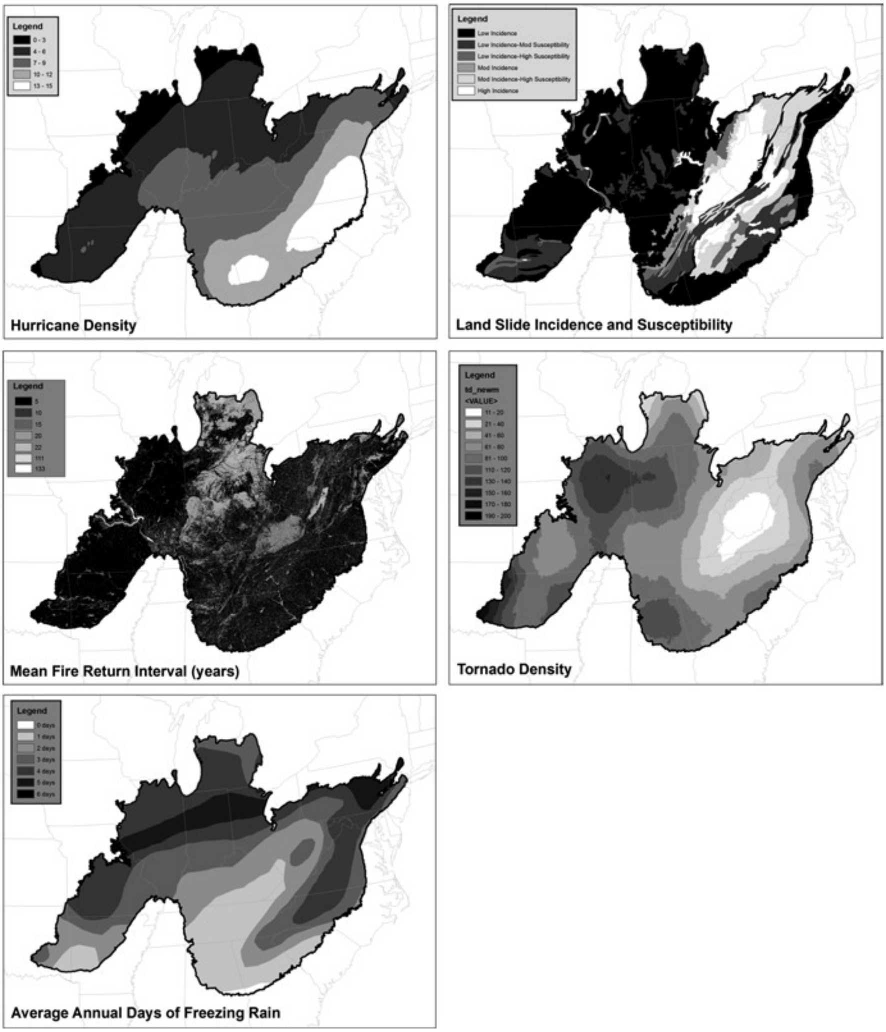
Other mechanisms will also create refuges for early successional species at landscape and regional scales. Habitat fragmentation with urbanization and second home construction will increase edge habitat. Alien pests and pathogens that affect central hardwood forests, such as the emerald ash borer (*Agrilus planipennis*) and hemlock woolly adelgid (*Adelges tsugae*), will continue to create canopy openings. However, the relative homogeneity of stands ages in the Central Hardwood Region and current regeneration patterns in these forests suggest that early successional habitats will decline as these forests age. There are therefore concerns for particular management units, in terms of loss of heterogeneity and early successional habitats. Nonetheless, there are many processes that support the local regeneration of early successional species across this region. Unfortunately, data are not often collected at relevant scales to evaluate the net balance of these sets of processes.

3.5 Conclusion

The synchronous origin and narrow range of stand ages in the Central Hardwood Region will have implications for decades to come (see Shifley and Thompson, Chap. 6). Variation in the types and frequencies of natural disturbances creates a range of early succession and young forest species composition and structure; thus, scattered to connected patches of early successional habitats generated by natural disturbance are likely to be represented in the central hardwood forests of tomorrow. However, the narrow range of stand ages, reduced structural heterogeneity, current successional processes, and low frequency of disturbance at the local scale suggest loss of abundant early successional habitats, at least that generated by natural disturbance alone, at a scale relevant to conservation and management. We do not know if the frequency, patch size, and spatial distribution of natural disturbance-generated early successional habitats will be sufficient to sustain biological diversity (or for any other management goal). Additional research is needed on the scale-dependence of natural disturbance return intervals, the interactions among specific disturbance types, the impact of new invasive pests, and the potential influence of climate change on the frequency and intensity of natural disturbance events.

Appendix I: Base Maps of Natural Disturbances Within the Central Hardwood Region

The map of Hurricane Density within the Central Hardwood Region was derived from line coverage of historical North Atlantic tropical cyclone tracks, 1851–2000 (NOAA 2009). The Landslide map was based on a spatial index of landslide



susceptibility and occurrence (Godt 1997). Raster digital data for Mean Fire Return Interval were obtained from LANDFIRE (US Forest Service 2006). Tornado density was calculated in ArcGIS using United States tornado touchdown points 1950–2004 (NWS 2005). The map of ice storm potential (Freezing Rain) was derived by geo-referencing Fig. 3.1 (a map of the annual number of days with freezing rain as defined by 988 weather stations from 1948 to 2000) from Changnon and Bigley (2005).

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