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Monitoring the effects of gypsy moth defoliation on forest stand dynamics on Cape Cod, Massachusetts: Sampling intervals and appropriate interpretations

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ABSTRACT

Gypsy moth (*Lymantria dispar* L.) outbreaks affect stand dynamics and successional patterns in pine–oak woodlands of North America's Atlantic coastal plain. Species-poor overstories are dominated by pitch pine (*Pinus rigida*), black oak (*Quercus velutina*) and white oak (*Quercus alba*). Both oaks are preferred food for gypsy moth, and white oak is the dominant late-successional species. We documented, over a 21-year period, the effects of gypsy moth defoliation on forest stand dynamics at Cape Cod National Seashore, Massachusetts. Our goal was to better understand the influence of gypsy moth defoliation on temporal changes in stand composition. Tree species abundance and frequency were measured in 16 stands with varying abundances of pitch pine and oak. Regression of 2-dimesional rates of change calculated from principal components analysis showed that gypsy moth significantly influenced stand dynamics and successional patterns between 1981 and 1992/1993. Defoliation was virtually absent in the 1990s, and analysis of 1992/1993–2002 rates of change showed topographic slope to be the most important factor influencing stand dynamics during this time. For the period 1981–2002 rates of change analysis failed to identify either factor as influencing changes in stand dynamics. We conclude that the 1980s defoliation events had a transitory effect on upland forest composition, but that there exists the potential for significant long-term impact due to recurrent defoliation episodes. Stand composition should be monitored at intervals which roughly correspond to the time it takes for stands to recover to disturbance events, in the case of those we sampled, approximately 10 years.

1. Introduction

Vegetation of the North American Atlantic coastal plain is increasingly considered an important focus of U.S. and global conservation efforts (Neill, 2007). Sandplains are under intense development pressure, with natural plant communities being lost or replaced by landscaped vegetation. Even without development, suppression of wildfires and outbreaks of exotic insects affect successional patterns in protected areas like Cape Cod National Seashore (CCNS) in eastern Massachusetts (Patterson et al., 1983; Chokkalingam, 1995).

Wildfires have been effectively suppressed at Cape Cod National Seashore since its establishment in 1960 (NPS, 1998). Historically, 400 years of burning by Native Americans and European colonists plus forest clearing, subsequent burning, and grazing and cultivation by colonists, have profoundly influenced the landscape, acting as an evolutionary force on the biota (Cronon, 1983; Patterson et al., 1983; Patterson and Sassaman, 1988; Motzkin et al., 1996; Dunwiddie and Adams, 1995; Parshall and Foster, 2002; Eberhardt et al., 2003; Parshall et al., 2003). Historic land-use practices still affect upland forest structure, and recent studies suggest that the structure and composition of coastal forests may now be more closely tied to direct and indirect human impacts than to edaphic and climatic influences as in the past (Eberhardt et al., 2003; Parshall et al., 2003). In the last 50 years open fields and heathlands have succeeded to closed-canopy pitch pine (*Pinus rigida*) and oak forests as cultivation and burning have declined (Dunwiddie et al., 1995). At Cape Cod National Seashore there has been a recent change in management philosophy to favor increased use of prescribed fire (Clark and Crary, 2005), but fewer than 20 hectares are currently burned annually.

Along with fire suppression, gypsy moth (*Lymantria dispar* L.) defoliation has been an important disturbance factor since gypsy moth was introduced into the United States in the late 19th century. On outer Cape Cod, defoliation episodes have occurred periodically throughout the 20th century, with the most recent

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severe outbreak in the early-to-mid 1980s (Chokkalingam, 1995; Dunwiddie et al., 1995; Liebhold et al., 1995). The emergence of the fungal pathogen *Entomophaga maimaiga* has had a major effect on gypsy moth populations since approximately 1989, but it has not eradicated the moths from the New England landscape (Hajek et al., 1995). The cumulative effect of parasitoids and predators, including *Entomophaga maimaiga,* has been to slow the rate of increase in low-level populations of gypsy moth and thereby lengthen the period between outbreaks, rather than to completely prevent outbreaks from occurring (Schweitzer, 2004), making concerns about gypsy moth still relevant. The varying intensity and episodic nature of gypsy moth outbreaks make predicting their effect on upland forests difficult.

Federal and state agencies in the United States devote valuable resources to developing adaptive management plans that incorporate periodic monitoring of forest stand conditions (Smith and Zollner, 2005; Mahan et al., 2007). Monitoring protocols usually call for sampling at regularly defined intervals, but it is important to note that the scale of sampling and description affects the ability to observe individual phenomena as collections of cases that are regular enough to be described in a more generalized fashion (Levin, 1992). Care must be taken to match sampling intervals with the goals and objectives of the research; for, in the same way that a dynamic landscape can exhibit a stable mosaic at one spatial scale and not another, a disturbance regime may seem to have little effect on successional dynamics at one temporal scale and a large effect at another (Turner, 1989; Lam, 2004; Mahan et al., 2007). For the current study a sampling interval of 10 years was chosen initially based on permanent plot surveys, e.g. the continuous forest inventory method (Avery and Burkhart, 2002), which provides precise estimates of change and can be used to estimate the components of change (Scott, 1998; Woldendorp et al., 2004).

We used a data set compiled over a 21-year period to examine the short and long-term effects of gypsy moth defoliation during a period of complete fire suppression (Dunwiddie and Adams, 1995). The study period incorporates an 11-year period with intense defoliation and a second 10-year period with almost no defoliation. The change in disturbance dynamics led to two questions which formed the basis of this study: (1) was the level of defoliation in the 1980s severe enough to influence stand dynamics through the 1990s? and (2) If not, what other environmental factors influenced stand dynamics during this time period? Answering these questions led us to examine the question of appropriate monitoring intervals for forests subjected to frequent disturbances occurring at irregular intervals.

2. Methods

2.1. Study area

Outer Cape Cod was formed 15,000–20,000 years ago from glacial outwash material deposited from the late Wisconsin south channel ice lobe to the east on what is now the continental shelf (USGS, 2003). Level outwash plains and rolling knob and kettle topography formed when ice blocks buried in outwash melted. As a result, the elevation on the outer Cape ranges from sea level to 48 m. Coarse, sandy, upland soils are highly podzolized and droughty with low decomposition rates which promote fuel accumulation and increase wildfire hazard. The modern climate is influenced by the Cape's proximity to the Atlantic Ocean, which moderates seasonal temperatures. Distinct winter and summer seasons are characterized by adequate precipitation (averaging about 103 cm/year) and high humidity (Strahler, 1966).

CCNS is comprised of 17,660 ha on the lower (outer) arm of Cape Cod. Included are portions of the towns of Wellfleet, Truro, Provincetown, Eastham, Orleans, and Chatham; study sites were located in the first three of these towns (Fig. 1). Pitch pine forest is the most abundant forest type at the Seashore (3080 ha, 17.4% of area), followed by pine–oak (1936 ha, 11.0%) and oak woodland (1280 ha, 7.2%) (Cape Cod National Seashore, 1991).

2.2. Forest stand dynamics

Research conducted at Cape Cod National Seashore and elsewhere in coastal plain vegetation provides a basic understanding of the pine–oak ecosystem (Little, 1979; Olsvig, 1980; Patterson et al., 1983; Patterson and Sassaman, 1988; Chokkalingam, 1995; Motzkin et al., 2002). A conceptual model (Fig. 2) describes succession from heathlands to oak forests, focusing on potential long-term impacts of gypsy moth defoliation in the absence of fire due to suppression. The model assumes that once pitch pine seedlings establish on open ground they grow more rapidly than oak seedlings, leading to pitch pine dominance (Patterson et al., 1983). Because pine seedlings cannot survive more than 30–40% shade (Burns and Honkala, 1990) and pitch pines are shorter-lived than oaks, black oak (*Quercus velutina*) and white oak (*Quercus alba*) establish and grow into the canopy; and stands transition to pitch pine–oak forests. As the canopy and understory become increasingly dominated by oaks, stands transition to oak-pitch pine. Without fire, pitch pines fail to regenerate, and as mature trees die the overstory is increasingly dominated by oaks. Alternate successional pathways are based on available seed sources for pitch pine and gypsy moth outbreaks. Due to the susceptibility of oak to gypsy moth defoliation (Campbell and Sloan, 1977; Davidson et al., 2001) and the lack of pitch pine regeneration without fire, oak-pine stands could eventually revert to heathlands under severe, chronic defoliation (Chokkalingam, 1995). Depending upon the pre-defoliation condition of the forest, stands reverting to shrublands could have an intermediate woodland phase defined by an open canopy and generally smaller trees, with openings occupied by sedges and ericaceous shrubs. Incorporating fire into a conceptual model of pine–oak forest development has been considered elsewhere (Jordan et al., 2003; Lilly et al., 2004).

2.3. Sample design

Twenty-one sites broadly representative of the Seashore's upland vegetation were identified in 1981. Overstory trees were sampled on approximately 20 variable radius plots (Mueller-Dombois, 1974) per site, as were shrubs in the understory on adjacent quadrats. Data were collected at each site to determine 20th century occurrence of fire, which was found to be uncommon (Patterson et al., 1983). Pitch pine and/or oak-dominated sites, excluding any burned within the previous 20 years, were re-sampled in 1992/1993 and categorized into four stand types using cluster analysis: pitch pine (PP, $N = 8$), pine–oak (PPO, $N = 3$), oak-pine (OP, $N = 4$), and mesic hardwoods (MH, $N = 1$) (Chokkalingam, 1995). These 16 sites were re-sampled in 2002; no evidence of recent fires was observed.

Permanent sampling points were not established in 1981, but field observations showed the 2–5 ha stands to be homogeneous throughout. This was verified by subsequent analysis of the 1981 data (W.A. Patterson, unpublished). The boundaries of these stands were relocateable in 1992/1993, so permanent sampling points were established at 30–40 m intervals along parallel transects (Chokkalingam, 1995). The number of sampling points at each site ranged from 12 to 49, with most sites having between 20 and 26. Trees were considered to be woody stems greater than 1.4 m tall and 2.5 cm diameter-at-breast height.