Forest Ecology and Management 303 (2013) 148–159

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

The influence of ground disturbance and gap position on understory plant diversity in upland forests of southern New England

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A R T I C L E I N F O

Article history:
Received 6 December 2012
Received in revised form 8 April 2013
Accepted 15 April 2013
Available online 15 May 2013

Keywords:
Evenness
Forest harvesting
Herbaceous
Microsite
Richness
Soils

A B S T R A C T

The forest understory contains the majority of vascular plant diversity in eastern temperate forests, and its diversity, composition, and dynamics contribute directly to ecosystem function. Forest managers have traditionally viewed the understory as primarily affecting forest regeneration or wildlife habitat, but the growing recognition of goods and services the understory provides (e.g., ecosystem function, ecological resiliency, non-timber forest products) has increased concerns about the impacts of forest management on understory diversity. We monitored response of understory diversity to microsite position and degree of ground-level disturbance within experimental gaps for 10 years. We did this at four sites with distinct soil types and topographic positions of a glacial geology in southern New England that were categorized as (i) mesic, (ii) mid-slope, (iii) outwash, and (iv) sandy-skeletal. We analyzed differences in patterns of species richness, Shannon diversity, and evenness across sites and through time. Understory species richness was generally enhanced by gap formation. Gap position was the primary factor influencing species richness across all sites, but the patterns of diversity and evenness within gaps was site specific. Ground-disturbance was influential on drier sandy sites, and more pronounced earlier in the experiment. Temporal differences were also evident across sites, with richness stabilizing at all sites 10 years after gap creation. The one exception was the sandy-skeletal site, which was still increasing in richness. Resource managers interested in protecting and enhancing understory species diversity need to consider underlying site, specifically soil type when planning silvicultural treatments, as the response of the understory community to disturbance can vary greatly with site.

1. Introduction

The importance of maintaining biodiversity has been widely recognized at both national and international levels (U.S., 2000; Brooks et al., 2006; UNEP, 2010). Plant diversity is a fundamental component of ecosystem diversity, contributing to both habitat structure and ecosystem function (Srivastava and Vellend, 2005). In eastern deciduous forests, the majority of the vascular plant species diversity is found in the herbaceous layer (Whigham, 2004). Diversity within the herbaceous layer increases structural complexity, which has a beneficial effect on compositional diversity of many insects, small mammals, birds, amphibians and reptiles (Ricketts, 1999; Dauber et al., 2003). Indeed, studies have demonstrated that the richness of birds, butterflies, and certain mammals is better correlated with understory rather than overstory richness (Ricketts, 1999). The herbaceous layer plays an important role in ecosystem function, contributing organic matter, aiding in decomposition, and conserving nutrients (Muller and Bormann, 1976; Peterson and Rolfe, 1982; Zak et al., 1990; Roberts and Gilliam, 1995; Muller, 2003; Falk et al., 2008).

The structure of the forest understory has direct implications for forest succession and management. Herbaceous layer competition influences germination, establishment, and thus, spatial arrangement of regenerating tree species (Maguire and Forman, 1983; Berkowitz et al., 1995; George and Bazzaz, 2003). Structural characteristics, such as density of the forest understory, can determine forest regeneration processes. For example, vigorous monodominant clonal understories, such as hayscented fern (*Dennstaedtia punctilobula* Michx.) can severely inhibit regeneration (Beckage et al., 2000; De La Cretaz and Kelty, 2002). In managed forests biodiversity can increase economic and ecological resiliency, productivity, and community stability (Burton et al., 1992). In many regions, understory species provide opportunities for alternative revenue streams through non-timber forest products (NTFPs) (Hammett and Chamberlain, 1998). For all of these reasons forest

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http://dx.doi.org/10.1016/j.foreco.2013.04.018

management should strive to preserve and, where possible, enhance understory plant diversity (Roberts and Gilliam, 1995).

Species diversity is driven by disturbance, forest cover type, and site history (Bormann and Likens, 1979; Whitney and Foster, 1988; Singleton et al., 2001; Bellemare et al., 2002; Ellum et al., 2010). Forest harvesting can significantly alter edaphic and microclimate conditions (through increased light, soil moisture and nutrient availability), and in turn shape the diversity and composition of the herbaceous layer (Bhatti et al., 2000; Gilliam, 2002; Roberts and Gilliam, 2003; Zenner et al., 2006). Much depends on intensity of canopy removal (amount of basal area removed or gap size) and degree of ground disturbance. The amount of canopy removal may alter understory diversity and composition (Reader and Bricker, 1992; Battles et al., 2001; Jackson et al., 2006), or may have limited impacts (Hughes and Fahey, 1991; Ruben et al., 1999; Schumann et al., 2003; Kern et al., 2006). While it is apparent that ground disturbance can substantially alter understory composition (Armesto and Pickett, 1985; Peltzer et al., 2000; Roberts and Zhu, 2002; Frey et al., 2003; Aikens et al., 2007), the extent of its influence on diversity in respect to increased light availability is not well understood.

There has been significant work in temperate forests examining understory response to clearcuts with inconsistent results (see reviews by Roberts and Gilliam (2003) and Moola and Vasseur (2008)). Many studies examining group selection treatments have found increases in understory diversity (Jenkins and Parker, 1999; Falk et al., 2008), although the temporal component must also be considered. Additionally, the mechanisms driving these patterns may shift with succession (Gilliam et al., 1995), and it is unclear what the permanent effects of forest harvesting are on understory diversity (Duffy and Meier, 1992; Meier et al., 1995). Many studies only look at a moment in successional time, but examining longer time frames is necessary to isolate treatment effects (Falk et al., 2008). Further, understory cover and compositional change may be more influenced by gap dynamics than diversity (Moore and Vankat, 1986). Few studies have been able to carefully assess the impacts of ground-disturbance intensity and gap position, using both pre- and post-disturbance data, controlled and compared across varying soil types over successional time.

To truly understand the biological diversity of a community species abundance measures must be incorporated; evenness may represent a different suite of ecological functions than species richness (Magurran, 2004). Our objective was to examine patterns in understory plant species diversity in response to microsite position and two levels of ground-disturbance intensity. The disturbance levels included "lethal" treatments (all vegetation removed and mineral soil exposed), and "release" (only the overstory removed). We conducted the study at four distinct sites in southern New England (different soils and canopy compositions) to examine whether patterns are similar across the region's common forest types. We examined data over a multi-year time period to capture successional changes in diversity. We hypothesize that both ground layer disturbance and gap position influence understory diversity, but expect gap position will be more influential. We predict that diversity will be highest in gap positions that offer the greatest levels of resources (light) and the least competition (from edge trees), and that these trends will be parallel across the four soil types studied. Across all sites we predict diversity to increase initially before stabilizing and then eventually decrease with resource limitations due to canopy development and shading effects.

2. Methods

2.1. Study sites

We conducted this study at four sites in southern New England selected to represent the variety of soils found in the region. Three are glacial till soils and one is of glacial–fluvial origin (Table 1). The climate throughout the region is cool-temperate and humid; approximately 110 cm of precipitation is evenly distributed throughout the year.

The first two sites are located at Yale-Myers Forest (41°56′N, 72°7′W), a 3213-hectare research and demonstration forest in northeastern, Connecticut. The forest belongs to the region classified as Central Hardwood–Hemlock–Pine (Westveld, 1956). The forest consists primarily of mixed-deciduous second-growth developing on abandoned agricultural land from the mid 19th century (Meyer and Plusnin, 1945). The topography is ridge-valley with an elevation range between 170 m and 300 m above sea level. The soils are glacial tills composed of moderate to well-drained stony loams overlying bedrock. Average temperatures at Yale-Myers Forest in July and January are 21.2 °C and −4.1 °C, respectively (Ashton and Larson, 1996; McKenna, 2007).

The first site, labeled "Mesic", has a gentle slope (<10% slope) with an easterly aspect. Soils are well-drained coarse-loamy tills. The canopy is composed primarily of *Quercus rubra* L., with components of *Acer rubrum* L., *Acer saccharum* Marsh., *Betula alleghaniensis* Britton., *Betula lenta* L., *Betula papyrifera* Marsh., *Carya ovata* (Mill.) K. Koch, *Fraxinus americana* L., *Liriodendron tulipifera* L., and *Tsuga canadensis* L. The midstory–woody species that will never grow into canopy trees – includes *Carpinus caroliniana* Walter, and *Hamamelis virginiana* L. The understory is fairly diverse, with *Carex* spp., *Aralia nudicaulis* L., and a variety of ferns (*Thelypteris noveboracensis* (L.) Nieuwl., *Polystichum acrostichoides* (Michx.) Schott, *D. punctilobula*, *Athyrium filix-femina* (L.) Roth) as the dominant species. The mesic site had the highest levels of pre-treatment understory richness.

The second site, labeled "Mid-slope", has a slight northwest aspect (<10% slope). Soils are well-drained coarse-loamy till with coarse unsorted rocks of varying sizes. Overstory composition is primarily *Q. rubra*, the midstory consists of *A.rubrum*, *and B. lenta* with an intermittent shrub layer of *Kalmia latifolia* L. The dominant herbaceous understory species are *Carex* spp., *D. punctilobula*, and *Trientalis borealis* Raf.

Table 1
Summary of the four study sites in southern New England.

Site	Location	Coordinates	Elevation (m)	Soil series	Drainage class	Richness[a]	Canopy composition
Mesic	Yale-Myers Forest, Eastford, CT	41°56′N, 72°07′W	200	Charlton and Leicester	Well-drained to poorly drained	39 (49)	Mixed mesic hardwoods
Mid-slope	Yale-Myers Forest, Eastford, CT	41°57′W, 72°07′W	265	Brookfield/Brimfield and Paxton/Montauk	Well drained to excessively well-drained	14 (20)	Red oak, with mixed hardwoods and pine
Sandy-skeletal	Cadwell Forest, Pelham, MA	42°22′N, 72°24′W	325	Gloucester	Excessively well-drained, heterogenous	14 (14)	Upland oak with pine
Outwash	Adam's Brook, Amherst, MA	42°23′N, 72°29′W	90	Merrimac	Excessively well-drained	16 (22)	White pine with oak

[a] Total pre-harvest understory plant species richness sampled values are followed by a first-order jackknife estimator in parentheses.