Forest Ecology and Management 347 (2015) 188–199

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Structural effects on understory attributes in second-growth forests of northern Wisconsin, USA

James E. Cook *

College of Natural Resources, University of Wisconsin-Stevens Point, 800 Reserve St., Stevens Point, WI 54481, USA

ARTICLE INFO

Article history:
Received 9 January 2015
Received in revised form 11 March 2015
Accepted 16 March 2015
Available online 31 March 2015

Keywords:
Herbaceous layer
Evenness
Shrub frequency
Maple seedling density
Conifer
Niche structure

ABSTRACT

I sampled the understory and associated structural features in forty-four second growth forests of north-central Wisconsin, USA, to assess the influence of forest structure on four understory attributes: cover, richness, composition and evenness (variant of Simpson's index). Eight structural features (overstory basal area and crown cover, percent conifer overstory, midstory basal area, shrub frequency, snag basal area, coarse woody debris volume, and maple seedling density) were measured. An additional derived variable, coefficient of variation (CV) for cover, was also tested. The objectives of the study were to determine the significance and impact (increase or decrease) of each structural feature on understory attributes. These were addressed with regression, canonical correspondence analysis, and two-sample tests. Ordination was used to assess differences in composition among forest types. The analyses indicated that structure had no effect on richness or cover, a modest influence on composition, and strong effect on evenness. An important revelation was the over-riding influence of understory structure, but a small role for the overstory. The severity and type(s) of historical disturbance interacted with species pools to strongly constrain richness in the early 20th century. Small changes related to succession have occurred since then. The amount of understory cover is still changing but appears to be succession-related. In contrast, more than 40% of the variation in evenness was explained by maple seedling density, and two interaction variables: maple density*shrub frequency and overstory*midstory basal area. Higher maple seedling density decreased evenness, probably by competitive effects. As the interaction variables increased, evenness was reduced. The regression analysis and CCA point to the shrub layer as having a direct, mechanistic effect on which species are present and their abundance; whereas the presence of shrubs is relatively benign. It is hypothesized that the abundance of upper strata resulted in varying levels of resource limitations, and influenced other environmental features to the extent that niche heterogeneity was affected. The proportion of conifer in the overstory had an important influence on understory composition, but hemlock assemblages did not differ from broadleaved forests in richness or cover. These results suggest that excess emphasis has been placed on the influence of the upper strata, but too little on the shrub and understory layers. Thus, the management of understory assemblages should carefully evaluate the sub-ordinate strata because they may be more important than upper layers.

1. Introduction

Few aspects of a forest community are more germane to function and condition than the richness and diversity of the understory layer (Gilliam, 2007). The understory accounts for the majority of plant alpha diversity (*sensu* Whittaker, 1972; Whigham, 2004; Gilliam, 2014), and is important to nutrient cycling and energy flow in early successional communities (Gilliam, 2007). Understory composition and structure, independent of diversity, are equally important because these dimensions have a major impact on insect and mammalian assemblages (Katovich et al., 1998; Mengak et al., 1989). Furthermore, the composition and abundance of the understory may partially determine future overstory composition (Gilliam and Roberts, 2014; Whigham, 2004).

There has been a large surge in the number of studies about forest understories in the past decade or more (Gilliam, 2014). These studies of undisturbed forests in the temperate and boreal zones have shown that understory richness, heterogeneity, cover and/or composition are commonly influenced by these factors: colonization capacity, environmental gradients within and among communities, understory composition and structure (especially height), overstory composition and abundance, intensity and

* Tel.: +011 01 715 346 2269.
E-mail address: jcook@uwsp.edu

http://dx.doi.org/10.1016/j.foreco.2015.03.027
0378-1127/

seasonality of browsing by large ungulates (especially white-tailed deer) [*Odocoileus virginianus* Boddaert], and abundance and composition of earthworms (glaciated regions only) (Gilbert and Lechowicz, 2004; Gilliam and Roberts, 2014; Hale et al., 2006; Waller, 2014; George and Bazzaz, 2014; Peet et al., 2014). Models proposed for understory composition and structure indicate a prominent role of forest structure (Bobiec et al., 2000; Roberts, 2004). In addition, there are numerous detailed studies of a single community or watershed that have enumerated the importance of local environmental gradients such as soil moisture, soil chemical properties and radiation (e.g., Burton et al., 2011; Chávez and Macdonald, 2010, Gazol and Ibáñez, 2009; McEwan and Muller, 2011). Almost no structural features, with exception of the overstory abundance and composition, were included in these studies or those reviewed by Gilliam and Roberts (2014). This has left a major gap in our understanding as to the full and precise influence of structural features on understory attributes in second-growth forests (Barbier et al., 2008; Bartels and Chen, 2010; McEwan and Muller, 2011; Spyreas and Matthews, 2006). In the eastern U.S., the vast majority of forests are second-growth (Frelich, 1995; Martin, 1992), and thus the effect of structure on understory richness and composition has wide applicability to forest management, ecosystem management and conservation efforts. What we know about the influence of forest structure is reviewed below.

1.1. Abundance

An extensive review of the relation between overstory abundance (basal area or density) and understory characteristics found evidence ranging from a strong effect to very-limited-to-no effects (Gilliam and Roberts, 2014). I reviewed additional literature and most outcomes were neutral, though four negative effects were noted for richness, evenness or diversity and one parabolic pattern was found (Appendix A). Furthermore, different attributes may respond in an opposite manner within the same forest. In the mixedwood, boreal region of Canada overstory abundance had no effect on understory richness or diversity, but negatively affected evenness (Chipman and Johnson, 2002). Contradictory results have been reported for mesic northern hardwood and Douglas-fir forests. Thus, no strong, consistent trend for the role of overstory abundance has been established (Appendix A).

1.2. Composition

Gilliam and Roberts (2014) proposed a mechanism for the linkage between the overstory and understory based on similar responses to environmental gradients in forests that are past the "thinning phase" of succession. Within this framework, they reviewed in detail two studies that exhibited a high level of correlation between overstory and understory composition. In other literature, six of ten studies documented a significant correlation between overstory and understory composition (Appendix A). Gilliam and Roberts (2014) found, as i did, a wide range of conclusions. For example, in British Columbia, there was a very strong and significant correlation between the tree and herbaceous layer in the western red cedar (*Thuja plicata* Donn ex D. Don) forests, but not in the Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) type (Gagnon and Bradfield, 1986). A study of 42 forests in the northern Rocky Mountains examined five layers (tree, shrub, herb, bryoid and epiphyte) and the maximum coefficient of determination involving the herb layer was 0.09 (McCune and Antos, 1981). In the Carpathian Mountains, diversity and evenness of the tree and herb layer were significantly correlated, but richness was not (Durak, 2012). Gilliam and Roberts (2014) suggest that this conflicting evidence is a function of spatial scale of the investigation. I do not see how this resolves the disparity of results.

The most common effect is for some understory species to show an *affiliation* for one overstory species or group (e.g., conifers). Eastern hemlock (*Tsuga canadensis* (L.) Carr.) is the most commonly cited species, but the effect is variable. Other understory attributes affected include cover, diversity and richness (Beatty, 1984; Ellum et al., 2010; Hicks, 1980; Rankin and Tramer, 2002). In a mixed mesophytic forest, five of seven species had no notable effect, beech (*Fagus grandifolia* Ehrh.) had a minor effect and white oak (*Quercus alba* L.) had a strong effect on the understory assemblage (Crozier and Boerner, 1984). In the Carpathian Mts., mountain beech had a strong negative effect on herb layer structure (Durak, 2012).

An extensive literature review found that conifer dominated forests have lower understory richness than forests in which broad-leaved species are more common (Barbier et al., 2008). A broad-leaved genus (*Prunus* L.) and *T. canadensis* had opposite effects on herb cover and richness, respectively (Maguire and Forman, 1983). Differences have been found among angiosperms also. In northern Minnesota, aspen (*Populus* spp. L.) had an opposite effect on understory diversity as did the other broad-leaved species (Berger and Puettmann, 2000). In summary, overstory composition often has a noticeable impact on understory attributes; however the effect varies from forest to forest, may vary within a forest, and is not universal.

1.3. Intermediate strata

Vertical structure has been proposed as an important determinant of understory attributes (Bobiec et al., 2000; Roberts, 2004). The intermediate strata (shrub to midstory) contribute to the amount of [potential] competition, affect radiation quantity and quality, and alter forest floor environmental conditions (Barbier et al., 2008). Positive, neutral and negative effects have been reported on diversity, cover and plant density; composition may be affected but the outcomes differed among studies (Appendix A). A repressive effect is common as intermediate abundance (in one or more layers) increases. Subtle effects can manifest as two layers within two forest types had opposite effects on cover (Gagnon and Bradfield, 1986; McKenzie et al., 2000). The shrub and sapling layers can affect composition, cover and richness, though no effect and a very weak effect were found in two studies. In summary, shrub and sapling strata typically have an inverse relationship with understory abundance; however, these structural components have not been extensively studied. Furthermore, the role of the midstory is completely unknown.

1.4. Coarse woody debris

The evidence is roughly equally split on the importance of coarse woody debris (CWD), and the decay state may be more important than amount (Burton et al., 2009; Hicks, 1980; Scheller and Mladenoff, 2002). In old-growth northern hardwood forests, diversity and heterogeneity are related to decayed CWD, but among common species there were equal numbers of positive, negative and neutral relations (Miller et al., 2002). No common species were restricted to CWD in northern hardwood forests of the Adirondack Mountains, New York; an equal number of species had greater densities on logs and on the forest floor (McGee, 2001). Coarse woody debris was not found to have a significant influence in boreal mixed woods (Chávez and Macdonald, 2010). Thus, the evidence suggests that uncommon species are most likely to respond to CWD volume and/or state of decay, but for some forest types, or at certain stages of development, there may not be any influence.