Forest Ecology and Management 271 (2012) 19–26

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

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

# Partitioning vascular understory diversity in mixedwood boreal forests: The importance of mixed canopies for diversity conservation

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ARTICLE INFO

*Article history:*
Received 14 September 2011
Received in revised form 6 December 2011
Accepted 26 December 2011
Available online 25 February 2012

*Keywords:*
Understory communities
Additive partitioning
Alpha and beta diversity
Dominant species
Relative abundance
Mixedwood forests

ABSTRACT

Progress in understanding the patterns of plant diversity requires a conceptualization and quantification of the hierarchy of patch configuration that exists in plant communities across levels of observation. In order to identify the scales at which vascular plant diversity is maximized, we investigated the hierarchical organization of understory vascular plant diversity in relation to canopy patch types in mature boreal mixedwood forests in western Canada. In each of two study areas within a 30 km$^2$ landscape (55° N, 112° E) we sampled four canopy patch types: conifer, mixed conifer-broadleaf, broadleaf and canopy gaps. Understory diversity (richness and Shannon's ($H'$) index) was additively partitioned in relation to these four canopy patch types across a hierarchy of four scales; $\alpha_{\text{-individual patch}} + \beta_{\text{1-among patches within canopy patch type}} + \beta_{\text{2-among canopy patch types within area}} + \beta_{\text{3-between areas}}$. We also examined understory species abundance patterns by means of rank-abundance plots fitted to relative abundance models. The largest partition of species richness was among patches within canopy patch type ($\beta_1$). For Shannon diversity index, the largest partition was at the within-individual patch level ($\alpha_1$) indicating that evenness was high at the patch level but that dominance increased at higher levels in the hierarchy. The assessment of relative abundance by means of rank abundance plots suggested that the canopy patch types differed in terms of the ecological mechanisms influencing diversity patterns. Considering plant diversity within a hierarchical framework is critical for the understanding and management of biodiversity as maximum levels of plant richness and evenness do not necessarily occur at the same observational scales. Management practices which retain the natural hierarchies of vegetation patches will help conserve plant community richness and diversity.


## 1. Introduction

The patterns of plant species richness and evenness – the two components of diversity – vary across different scales of observation but not necessarily in the same way, nor are these two affected by the same ecological processes (Wagner et al., 2000; Chandy et al., 2006). Unraveling their patterning across different scales of observation can provide insight into the most influential ecological processes structuring plant communities, an aspect that is critical for management and conservation measures (Wagner et al., 2000; Chandy et al., 2006).

Understory plant communities hold a large proportion of plant diversity in forest ecosystems and fulfill important ecological roles such as providing habitat and food for faunal communities and playing key roles in nutrient cycling, forest succession, and long-term stand productivity (Gentry and Emmons, 1987; Halpern and Spies, 1995; Nilsson and Wardle, 2005; Hart and Chen, 2006, 2008; Gilliam, 2007). The boreal mixedwood forest, which exists as a landscape mosaic of stands with varying dominance by broadleaf or coniferous trees, hosts the most diverse understory communities of the North American boreal forests (Hart and Chen, 2006, 2008). Within this mosaic, stands with a mixed conifer-broadleaf canopy host the greatest diversity for understory plants (Hart and Chen, 2006; Macdonald and Fenniak, 2007) and other biotic groups such as birds (Hobson and Bayne, 2000) and arthropods (Hammond et al., 2001; Work et al., 2004; Buddle et al., 2006). Understory plant community composition and diversity are strongly influenced by canopy composition (Hart and Chen, 2006; Macdonald and Fenniak, 2007) and, while it is widely accepted that plant diversity is higher when resource heterogeneity is high (Huston, 1979), the patterns underlying biotic diversity within forest stands of mixed canopy composition remain largely unexplored.

An understanding of the hierarchical organization of understory species richness and evenness in relation to canopy patches is important for managing vascular plant diversity in mixedwood forests, which in recent decades have become highly desirable for commercial harvesting. Current silvicultural and regeneration regulations in some regions of Canada favor the establishment and growth of relatively pure stands of conifers, separate from

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doi:10.1016/j.foreco.2011.12.038

stands of broadleaf trees (Man and Lieffers, 1999; Chen and Popadiouk, 2002; Haeussler et al., 2004). Such modifications of canopy structure can potentially change the ecological structure and function from what is observed in unmanaged mixedwood forests, in turn modifying the patterning of understory plant diversity. Additive partitioning of species diversity provides a framework within which to assess diversity patterns at different levels of organization, providing an estimation of the relative contribution of within ($\alpha$) and between ($\beta$) community diversity to total diversity ($\gamma$) (Allan, 1975; Lande, 1996; Loreau, 2000; Crist et al., 2003; Gering et al., 2003). From a management and conservation perspective, additive partitioning allows the characterization of the heterogeneity of a region at different levels of observation and the identification of the scale at which maximum diversity occurs (Allan, 1975; Lande, 1996; Loreau, 2000; Crist et al., 2003; Gering et al., 2003).

We used additive partitioning of diversity to investigate the hierarchical organization of understory vascular plant diversity in relation to the heterogeneous mosaic of canopy patch types within mature, unmanaged boreal forest stands that had a mixed canopy composition. Although non-vascular plants constitute a great proportion of understory diversity (Hart and Chen, 2006), they were out of the scope of this project.

Species dominance is high in mature boreal forests (Hart and Chen, 2006); thus, we also explored the patterns of species abundance among canopy patch types paying special attention to the identity of common and dominant understory species. The functional relevance of dominant plant species has received considerable attention recently (Smith and Knapp, 2003; Emery and Gross, 2007; Hillebrand et al., 2008; Mokany et al., 2008; Sasaki and Lauenroth, 2011 but see Lyons et al., 2005). As such, we anticipated that dominant species may strongly influence understory diversity patterns through effects on species evenness.

We hypothesized that (i) the additive partition of understory richness and diversity (expressed as an index that incorporates species abundance and evenness) across the hierarchy of canopy patches would follow different trends which reflect patterns of dominant and common species and, (ii) the natural intermix of canopy patch types within mixedwood forest stands is crucial for the maintenance of understory diversity because it creates heterogeneity in environmental conditions and ecological mechanisms that shape diversity patterns.

## 2. Methods

### 2.1. Study site and field procedures

The study was conducted in the Boreal Mixedwood Ecoregion in forest stands near Lac La Biche, Alberta, Canada (55° N, 112° E ~610 m above sea level) (Strong, 1992). Mesic sites in this region host boreal mixedwood forests with canopy co-dominance by broadleaf trees (primarily *Populus tremuloides* Michx. (trembling aspen)) and conifers (mainly *Picea glauca* (Moench) Voss (white spruce)). The region has a boreal climate with a mean summer temperature of 13.5 °C (May through August) and a mean winter temperature of −13.2 °C (November through February). The mean annual precipitation is 397 mm which occurs mostly during the summer (Strong, 1992).

Within a ~30 $km^2$ landscape, we sampled within the portion of the forest land base that had been classified as 'mixed' (having between 40% and 60% canopy cover of both coniferous and broadleaf trees) at the stand (polygon) scale by the most recent forest vegetation inventory in the region. All sampled forests were of fire origin, approximately 100 years old and previously unmanaged. Sampling was concentrated in either the northern or southern portion of the total study area; the two areas were approximately 30 km from one another. We established a total of 98 sampled points distributed as evenly as possible between these two areas. We used a stratified random approach to select sample points in four different canopy patch types: (1) conifer patches (a total of 26 plots): composed of at least 70% (by canopy cover and tree density) conifer (mainly *P. glauca*); (2) broadleaf patches (25 plots): at least 70% broadleaf trees (mainly *P. tremuloides*); (3) mixed patches (23 plots): at least 40% and no more than 60% conifer (mainly *P. glauca*); (4) gap patches (24 plots): canopy openings where a 50 $m^2$ circular plot could be located without any canopy cover above the understory strata. Each sample point was at least 50 m away from forest edges, cut lines or trails, and points were at least 30 m apart from each other.

Because the patchiness of canopy composition in mixedwood forests likely gives rise to high micro-site heterogeneity, it was necessary to define the appropriate 'observation window' (Niemela et al., 1996) that ensured the detection of such heterogeneity and avoided the obscuring of habitat heterogeneity behind averages. Based on tree size and density and crown structure in these forests, we sampled within 50 $m^2$ circular (4-m radius) plots at each sample point in order to detect non-random micro-habitat variation within mixedwood stands caused by the spatial variation of canopy composition. To ensure we were sampling the understory plant community that was being influenced by the canopy composition of the sample patch, we established one vegetation sample point at the center of each 50 $m^2$ plot. At each sample point, visual estimates of plant cover were made for each vascular plant species within a 2 × 2 m quadrat centered within the larger plot; this was divided into four 1 × 1 m sub-plots to increase accuracy of visual cover estimates. Three species were identified only to the genus level (one *Salix* and two *Carex* spp.). Nomenclature followed Moss (1983). Prior to calculation of the diversity index, cover estimates for each understory species were averaged over the four 1 × 1 m sub-plots to give a single cover value per species for each understory vegetation quadrat.

### 2.2. Data analysis

#### 2.2.1. Species diversity and observed and estimated richness

In each plot, we measured species richness and calculated Shannon's index ($H'$) to quantify diversity. In order to assess whether our sample size captured variation in species presence, we estimated total species richness for each canopy patch type using several non-parametric richness estimators: Jackknife 1, Jackknife 2, Chao 1, Chao 2, Incident-based Coverage Estimator (ICE), and Abundance Coverage Estimator (ACE). For this we used the EstimateS program with 1000 randomizations for each data set (Colwell, 2005).

#### 2.2.2. Additive partitioning

The additive partitioning of diversity ($\gamma = \beta + \overline{\alpha}$) was originally suggested by Allan (1975) and re-considered by Lande (1996). It differs from Whittaker's (1960, 1972) multiplicative model ($\gamma = \beta\overline{\alpha}$) in that alpha and beta diversity have the same units which makes possible the calculation of their relative contribution to gamma diversity over a range of scales (Lande, 1996; Loreau, 2000; Crist et al., 2003; Gering et al., 2003). We partitioned understory plant diversity (quantified as species richness and Shannon's index ($H'$)) across the four canopy patch types in mature mixedwood forests based on the following model: $\gamma_{\text{-mixedwood landscape}} = \alpha_{\text{-individual patch}} + \beta_{\text{1-among patches within canopy patch type}} + \beta_{\text{2-among canopy patch types within area}} + \beta_{\text{3-between areas}}$ (Fig. 1). Subsequently, understory plant diversity was partitioned for each canopy patch type separately using the following model: $\gamma_{\text{-canopy patch type}} = \alpha_{\text{-individual patch}} + \beta_{\text{1-among patches within canopy patch type}}$. We used the software program