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Response of herbaceous plant diversity to reduced structural diversity in maple-dominated (*Acer saccharum* Marsh.) forests managed for sap extraction

Alexandre Lenière, Gilles Houle *

Département de Biologie, Université Laval, Sainte-Foy, Qué., Canada G1K 7P4

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Abstract

High forest structural diversity is thought to be associated with high understory plant diversity, through a positive effect on environmental complexity. However, forest management may decrease structural diversity. For instance, by reducing tree species richness and variability in tree size, management of maple-dominated (*Acer saccharum* Marsh.) forests for sap extraction may decrease environmental complexity and, therefore, understory plant diversity. We tested this hypothesis by studying 30 maple-dominated forest fragments representing various levels of management, in southern Québec (Canada). The mean and spatial variability of several environmental variables (light and soil resources) were assessed, along with forest structural diversity and plant diversity. Using path analyses, we determined whether the mean of environmental variables (model 1) or the spatial variability of environmental variables (model 2) was most important for understory plant diversity. Model 1 explained 58% and model 2 explained 23% of the variance in plant diversity. The observed covariance structure (based on the data) fitted the predicted covariance structure (based on the model) perfectly (minimum fit function $\chi^2 = 5.152$, d.f. = 4, $P = 0.272$, GFI = 0.946 for model 1; minimum fit function $\chi^2 = 5.784$, d.f. = 4, $P = 0.216$, GFI = 0.940 for model 2). Forest structural diversity had no significant effect on the environmental variables (irradiance and soil resources), although it had a significant and positive influence on understory plant diversity. Soil pH also had a significant and positive effect on plant diversity in model 1; however, no other variable significantly affected species diversity in this model. In model 2, none of the environmental variables had a significant effect on understory plant diversity. An increase of the species pool with an increase of soil pH most likely accounts for the positive effect of soil pH on understory plant diversity. Assuming forest structural diversity is inversely related to management intensity, our results suggest that the traditional management of maple-dominated forests for sap extraction may have deleterious effects on understory plant diversity.

Keywords: *Acer saccharum*; Environmental variables; Forest management; Path analysis; Spatial variability; Species richness; Structural diversity; Sugar maple

1. Introduction

Natural disturbances can alter the landscape and affect ecosystem structure and functions at different spatial and temporal scales (Sousa, 1979; Tang et al., 1997; Roberts, 2004). While natural fires and insect outbreaks are frequent in the boreal forests of North America, wind, ice storms, and epidemics caused by pathogens are relatively more important for the dynamics of deciduous forests (Houston et al., 1990; Hooper et al., 2001; Frelich, 2002). However, natural disturbances are not the only factors that can alter the structure and functions of forests. Indeed, management practices have inevitable effects on ecosystem properties, including plant diversity (Bengtsson et al., 2000). Although the effects of tree harvesting practices on canopy tree species have been well studied, comparatively little work has considered understory plant species (Reader, 1987; Gilliam et al., 1995; Decocq et al., 2004). Yet, understory species contribute significantly to plant diversity and are important for a wide range of functions, including forest productivity and nutrient cycling (Muller and Bormann, 1976; Reader, 1987; Small and McCarthy, 2005). Moreover, understanding understory response to disturbances is critical to promoting species conservation (Roberts, 2004).

Maple-dominated forests are among the most managed of deciduous forests in northeastern North America. They are

* Corresponding author. Tel.: +1 418 656 3102; fax: +1 418 656 2043.
E-mail addresses: alexandre.leniere.1@ulaval.ca (A. Lenière), gilles.houle@bio.ulaval.ca (G. Houle).

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typically composed of sugar maple (*Acer saccharum* Marsh.), in association with red maple (*Acer rubrum* L.), American beech (*Fagus grandifolia* Ehrh.), and yellow birch (*Betula alleghaniensis* Britton). However, during the course of past management practices, the proportion of the associate species has been reduced in favor of sugar maple (Coons, 1992). Selective-cutting practices applied in maple-dominated forest fragments have consisted of felling older, sick, infected, and less productive maples, and all trees other than maples (Majcen, 2003). The objectives of such practices have been to increase the diameter of maple trees, encourage the expansion of maple crowns, and eliminate most of the understory trees and shrubs. After a few decades of intensive management, several maple-dominated forest fragments have been reduced to uniform, even-aged stands (Paquet, 1980). Such practices have simplified the age and vertical structure of the forests and reduced tree species diversity, sometimes to the point of a monoculture of sugar maple.

The objective of the present study is to determine the effects of maple-dominated forest management practices on understory plant species diversity and environmental factors. We propose to determine what variables most strongly influence plant species diversity in conditions altered by management in maple-dominated forest fragments, using multivariate analyses. The research hypothesis is as follows: an increase in the intensity of management results in a more homogeneous and uniform forest structure and, therefore, in reduced environmental complexity. In turn, a reduction in environmental complexity causes a decrease in understory plant diversity (Bérard and Côté, 1996; Whitney and Upmeyer, 2004). We use the Shannon diversity index, applied to tree pseudo-species, as an indirect measure of management intensity (Magurran, 1988; Staudhammer and LeMay, 2001; Tews et al., 2004).

2. Methods

2.1. Study site description

This research was conducted in 30 forest fragments of the Bois-Francs region, in central Québec, between 46°04′–46°32′N and 71°56′–72°43′ W (Table 1, Fig. 1). The study area is part of the Great Lakes—St. Lawrence forest region of Rowe (1972), sub-sections mid (L-2) and high (L-3) St. Lawrence. The dominant tree species are sugar maple, American beech, American linden (*Tilia americana* L.), and yellow birch. The regional climate is wet and continental, with an annual precipitation of ca. 1100 mm (24% falls as snow) and an annual daily mean temperature of 4.9 °C (at the nearby

Table 1
General characteristics, number of species (in parentheses, herbaceous plant species), proportion of herbaceous species (vs. total species number), and parameter and statistics of the species–area curve for the 30 study sites (Bois-Francs region, Québec, Canada)

Study sites	Symbols	Latitude (N)	Longitude (W)	Number of species	Proportion of herbaceous species	z_{herb}[a]	r^2	P
Baie-du-Febvre 1	BF1	46°18.005′	72°32.011′	59 (41)	69.5	0.599	0.995	0.0001
Baie-du-Febvre 2	BF2	46°08.668′	72°35.230′	56 (44)	78.6	0.662	0.963	0.0091
Baie-du-Febvre 3	BF3	46°06.468′	72°43.990′	42 (29)	69.0	0.591	0.965	0.0029
La Visitation	LaVi	46°06.615′	72°36.626′	68 (53)	77.9	0.707	0.947	0.0063
Léon Provancher Reserve 1	LP1	46°17.820′	72°30.740′	62 (44)	71.0	0.655	0.957	0.0038
Léon Provancher Reserve 2	LP2	46°17.896′	72°30.911′	50 (33)	66.0	0.553	0.997	0.0001
Léon Provancher Reserve 3	LP3	46°17.525′	72°31.076′	45 (30)	66.7	0.543	0.971	0.0021
Parisville 1	P1	46°06.616′	72°36.630′	43 (24)	55.8	0.553	0.973	0.0019
Parisville 2	P2	46°32.161′	72°02.520′	43 (27)	62.8	0.544	0.982	0.0011
Parisville 3	P3	46°31.460′	72°01.460′	55 (35)	63.6	0.562	0.983	0.0009
Saint-Célestin	StCe	46°08.385′	72°24.670′	36 (22)	61.1	0.538	0.974	0.0018
Saint-Grégoire 1	StGr1	46°16.760′	72°26.586′	76 (56)	73.7	0.691	0.970	0.0022
Saint-Grégoire 2	StGr2	46°16.455′	72°27.351′	66 (45)	68.2	0.673	0.952	0.0046
Saint-Grégoire 3	StGr3	46°16.426′	72°32.398′	48 (27)	56.3	0.544	0.990	0.0004
Saint-Léonard d'Aston 1	StL1	46°08.798′	72°22.105′	43 (29)	67.4	0.563	0.986	0.0007
Saint-Léonard d'Aston 2	StL2	46°05.090′	72°22.161′	42 (25)	59.5	0.479	0.982	0.0010
Saint-Léonard d'Aston 3	StL3	46°04.600′	72°22.340′	46 (29)	63.0	0.591	0.963	0.0031
Saint-Léonard d'Aston 4	StL4	46°05.893′	72°18.181′	58 (37)	63.8	0.635	0.960	0.0034
Saint-Sylvère 1	StSy1	46°16.036′	72°11.370′	51 (34)	66.7	0.593	0.978	0.0014
Saint-Sylvère 2	StSy2	46°12.123′	72°17.076′	34 (19)	55.9	0.529	0.954	0.0042
Saint-Wenceslas 1	StW1	46°09.270′	72°16.971′	28 (16)	57.1	0.495	0.967	0.0026
Saint-Wenceslas 2	StW2	46°10.206′	72°17.450′	33 (22)	66.7	0.495	0.994	0.0002
Saint-Zéphirin	StZe	46°05.888′	72°37.001′	75 (59)	78.7	0.689	0.966	0.0027
Sainte-Angèle-de-Laval	StAn	46°18.135′	72°32.063′	57 (36)	63.2	0.629	0.964	0.0029
Sainte-Gertrude 1	StGe1	46°16.050′	72°19.078′	20 (12)	60.0	0.401	0.995	0.0002
Sainte-Gertrude 2	StGe2	46°16.053′	72°18.905′	42 (28)	66.7	0.519	0.988	0.0006
Sainte-Sophie-de-Lévrard 1	StS1	46°27.198′	72°04.805′	47 (30)	63.8	0.562	0.990	0.0004
Sainte-Sophie-de-Lévrard 2	StS2	46°27.125′	72°04.691′	39 (20)	51.3	0.498	0.987	0.0006
Sainte-Françoise 1	StF1	46°29.341′	71°56.156′	61 (43)	70.5	0.670	0.959	0.0036
Sainte-Françoise 2	StF2	46°29.658′	71°56.343′	39 (22)	56.4	0.501	0.991	0.0004

[a] z_{herb} represents the slope of the species–area relationship calculated for herbaceous species in a serial nested-quadrat system (see Section 2.2.1).