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Author(s): Isabelle AUBIN, Sophie GACHET, Christian MESSIER, and André BOUCHARD

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# How resilient are northern hardwood forests to human disturbance? An evaluation using a plant functional group approach<sup>1</sup>

Isabelle AUBIN<sup>2</sup>, Institut de recherche en biologie végétale, Université de Montréal, 4101 rue Sherbrooke Est, Montréal, Québec H1X 2B2, Canada, e-mail: [iaubin@sympatico.ca](mailto:iaubin@sympatico.ca)

Sophie GACHET, Muséum National d'Histoire Naturelle - CNRS UMR 7179, 4 rue du Petit Château, 91800 Brunoy, France.

Christian MESSIER, Centre d'étude de la forêt (CEF), Département des sciences biologiques, Université du Québec à Montréal, C.P. 8888, Succ. Centre-Ville, Montréal, Québec H3C 3P8, Canada.

André BOUCHARD, Institut de recherche en biologie végétale, Université de Montréal, 4101 rue Sherbrooke Est, Montréal, Québec H1X 2B2, Canada.

**Abstract:** Evaluating forest ecological integrity remains a major challenge for ecologists. We analyzed understory vegetation using an approach that combined plant functional types and vertical stratification to evaluate the effects of human disturbances on the ecological integrity of sugar maple-dominated stands in southern Québec. Ecological integrity was evaluated by analyzing the divergence of understory species assemblages from those observed in comparable unmanaged forest. Multivariate analyses of biological traits revealed 13 emergent groups that share common traits associated with a similar life history strategy. Responses of these groups, of specific traits, and of understory structure to different human disturbances were tested. Nine of the 13 emergent groups varied in occurrence or diversity among disturbance types. Analyses also revealed a set of traits specifically associated with unmanaged old growth forest, indicating that species possessing these traits may be sensitive to human disturbance. Overall, the understory vegetation assemblage was found to be relatively stable among all human disturbances investigated. However, our results suggest some issues of possible long-term conservation concern given a continuation of human disturbances: (i) an increase of species associated with open environment, including exotic species; (ii) a decrease of spring geophytes; (iii) a decrease of certain shade-tolerant forbs; and (iv) a modification of understory structure by the development of a dense sapling stratum.

**Keywords:** old growth, plant biological traits, second growth, single-tree selection harvest, understory flora, vertical structure.

**Résumé :** Évaluer l'intégrité écologique des forêts représente un défi majeur pour les écologistes. Nous avons analysé la végétation de sous-bois à l'aide d'une approche qui combinait les types fonctionnels et la stratification verticale afin d'évaluer les effets des perturbations anthropiques sur l'intégrité écologique d'érablières à sucre dans le sud du Québec. L'intégrité écologique a été évaluée en comparant les assemblages d'espèces de sous-bois de ces forêts avec ceux de forêts comparables mais non aménagées. Les analyses multivariées des caractéristiques biologiques ont fait ressortir 13 groupes possédant des traits communs associés à des stratégies similaires. La réponse de ces groupes de traits spécifiques ainsi que de la structure du sous-bois ont été testées pour différentes perturbations anthropiques. L'occurrence et la redondance de 9 des 13 groupes variaient en fonction des types de perturbations. Les analyses ont aussi révélé une combinaison de traits spécifiques aux forêts anciennes non aménagées, indiquant que les espèces possédant ces caractéristiques peuvent être sensibles aux perturbations anthropiques. Dans l'ensemble, les assemblages de la flore de sous-bois étaient relativement stables quelque soit la perturbation anthropique évaluée. Cependant, nos résultats laissent entrevoir certains risques de modifications au niveau de la conservation à long terme dans le cas où les perturbations se poursuivent : (i) une augmentation des espèces de milieu ouvert, incluant des espèces exotiques; (ii) une diminution des géophytes printanières; (iii) une diminution de certaines herbacées tolérantes à l'ombre; et (iv) une modification de la structure du sous-bois par le développement d'une strate dense de gaulis.

**Mots-clés :** coupe de jardinage par arbre, flore de sous-bois, forêt ancienne, forêt de seconde venue, structure verticale, traits biologiques.

**Nomenclature:** Gleason & Cronquist, 1991.

## Introduction

Despite the increasing human-induced transformation of forests all around the world, evaluating forest ecological integrity, defined broadly as the capability of a system to maintain a community comparable to that of a natural

habitat of the region (Karr & Dudley, 1981), remains a challenge for ecologists. In essence, the challenge centres on quantifying ecological structures and processes that define the "natural" functioning of a forest at different spatial and temporal scales (De Leo & Levin, 1997). Often, we assume a forest has lost its ecological integrity when the disappearance of key structural elements or species can be identified. This identification requires an adequate control or reference

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<sup>2</sup>Author for correspondence.

point of the natural state as well as the determination of what constitute key elements to monitor.

In this study, we used understory functional and structural attributes to evaluate ecological integrity. Understory flora may be a suitable key element with which to monitor ecological integrity because of its great diversity as well as its important role in ecosystem functioning (George & Bazzaz, 2003; Gilliam & Roberts, 2003; Nilsson & Wardle, 2005). Moreover, because of life history characteristics of its component species, the understory stratum is likely more sensitive to disturbances or to changes in environmental conditions than the overstory (Bratton, 1994; Moffatt & McLachlan, 2004; Flinn & Vellend, 2005).

Numerous studies in northern hardwood forests have addressed the impact of human disturbances on understory species composition (see Roberts & Gilliam, 2003) and diversity (see Battles *et al.*, 2001). However, the substantial variation in their conclusions illustrates the site-specific nature of floristic responses to disturbance (Gilliam & Roberts, 2003; Moffatt & McLachlan, 2004). This highlights the difficulties in evaluating ecological integrity across a vast region or range of stand conditions that arise from the great diversity of forest understories, regional differences in species distributions, and strong correlations between physical or regional characteristics and land use history. Therefore, to allow generalization, several authors have suggested emphasizing functional traits rather than taxonomic differences when analyzing plant community responses to disturbance (McCarthy, 2003; Moffatt & McLachlan, 2004). Over the last decade, classifications based on plant functional types (PFT) have been widely used to study vegetation processes (Smith, Shugart & Woodward, 1997). More recently, PFT have been used for understanding ecosystem responses to land-use change (Verheyen *et al.*, 2003; Kolb & Diekmann, 2005). While the definition of PFT depends on the authors, generally PFT are species groups that have evolved convergent life history strategies by developing similar processes of resource allocation among their various vital functions in relation to prevailing environmental factors (Smith, Shugart & Woodward, 1997).

We evaluated assemblages of understory species in sugar maple (*Acer saccharum*) stands, a dominant forest type of the northern hardwood biome. These forests have a high level of diversity that is reflected in the broad range of life history strategies and physiological, morphological, and phenological traits that characterize the shrubs and herbs of these forests (Bierzchudek, 1982; Collins, Dunne & Pickett, 1985). From a conservation perspective, sugar maple forests have been and will very likely continue to be subjected to numerous human pressures. They contain many understory species threatened with local or regional extinction (*e.g.*, *Panax quinquefolius* and *Allium tricoccum*; Nantel, Gagnon & Nault, 1996) and, due to their proximity to major urban or agricultural areas, are increasingly faced with potentially invasive exotic species (*e.g.*, *Alliaria petiolata*; Luken, 2003).

Sugar maple forests are highly heterogeneous in their land use history. Regional variation in land use is frequently related to biophysical characteristics (Pan *et al.*, 1999). For example, in flat, productive regions, forests are typically residual fragments of second-growth forests embedded in an

agricultural or peri-urban matrix. In remote or hilly regions, sugar maple forests can occur in extensive tracts where the principal disturbance is forest harvesting. While stands with little history of human disturbance are found in these tracts, such stands are extremely rare in the agricultural matrix (Brisson & Villeneuve, 2003). This regional variation complicates the design of a sampling strategy that encompasses forests subjected to all of the possible types of human disturbance as well as unmanaged forests.

Because they are based on universal vegetation traits rather than on site-specific vegetation composition, PFT are independent of biogeographic barriers and offer the possibility of inter-regional comparisons (Tsuyuzaki & del Moral, 1995; Cramer, 1997; Leemans, 1997; Graae & Sunde, 2000; Verheyen *et al.*, 2003). This approach may reveal patterns of organization that are difficult to detect using an approach based solely on differences of floristic composition, as such differences can arise from regional variation in climate or geology. In other words, a PFT approach makes it possible to compare ecosystems that differ in composition but possess similar underlying ecological processes and functions.

Our objective was to evaluate the ecological integrity of sugar maple forests by comparing the understory of forests with a varying history of human disturbance and unmanaged old growth forests that represent natural states. As human disturbances are likely to affect species differently according to their particular biological traits (McIntyre, Lavorel & Tremont, 1995; Roberts & Gilliam, 2003), it may be possible to associate certain sets of traits with particular human disturbances (Table I) or, conversely, with natural unmanaged forests. The extent to which a given assemblage possesses the former trait set can reflect its history of human disturbance. Moreover, the abundance in a given stand of species possessing these "human-disturbance" traits indicates the degree to which the stand has been altered from its unmanaged state and may provide a surrogate measure of its ecological integrity.

In our study, PFT were combined with measures of vertical stratification of the understory vegetation to provide a more complete portrait of vegetation assemblages than that garnered by using functional types alone. Structure is the result of vegetation development and can greatly influence several ecological processes by, for example, modifying aspects of the abiotic environment such as light and moisture availability (Spies, 1998). Moreover, structural changes can provide the first indication of a modification in ecosystem functioning (Spies, 1998).

## Methods

We examined 30 maple-dominated stands of the Great Lakes–St. Lawrence forest region (Rowe, 1972) in southern Québec, Canada. These stands were located in 2 contiguous regions that differ in physiography and land use history: the Upper St. Lawrence and the Outaouais. In both regions, mean annual temperature ranges between 2.5 and 5 °C and precipitation between 900 and 1000 mm. The growing season typically lasts 190–200 d in the Upper St. Lawrence and 170–190 d in the Outaouais (Robitaille & Saucier, 1998).

The Upper St. Lawrence region is located in southernmost Québec (45° 01' – 45° 08' N, 73° 58' – 74° 21' W).

TABLE I. Literature review of biological traits associated positively (+) or negatively (–) with human disturbance types sampled in the present study.

Disturbance type	Biological traits
Forested matrix	+ Short geophytes <sup>12</sup> + Insect-pollinated species <sup>14</sup> + Gravity- or animal-dispersed perennial species <sup>12</sup>
Old growth forest	+ Perennial, native species <sup>3</sup> + Geophytes and hemicryptophytes <sup>13</sup> + Ant- or gravity-dispersed species with large seed size <sup>7, 18</sup> + Low seed production and with limited dispersal <sup>13</sup> + Species with large storage organ <sup>22, 23</sup> + Shade-tolerant species <sup>13, 22, 24</sup> + Saprophyte species <sup>11</sup>
Recent single-tree selection harvest*	+ Annuals <sup>10, 21</sup> + Shade intolerant and mid-shade tolerant species <sup>5</sup> + Species with seed bank <sup>8</sup> + Species dispersed by wind or animal ingestion <sup>10, 18</sup> + Species with strong vegetative propagation <sup>8</sup> + Summer or fall flowering species <sup>21</sup> – Shallow rooted herbs <sup>19</sup> – Slow-growing species <sup>19</sup> – Species with long juvenile period <sup>19</sup> – Saprophyte species <sup>11</sup> – Low seed production and limited dispersal <sup>19</sup>
Old single-tree selection harvest*	+ Tall herbs <sup>19</sup> + Woody species <sup>1, 10</sup> + Species dispersed by animal ingestion <sup>10</sup> + Species reproducing by vegetative propagation <sup>10</sup>
Agricultural matrix	+ Exotic species <sup>4</sup> – Wind-, animal-, and bird-dispersed species <sup>16, 20</sup> – Species dispersed by gravity, explosive discharge, or ants <sup>12, 20</sup> – <b>Insect-pollinated species</b> <sup>15</sup> – <b>Low stature species</b> <sup>15</sup> – <b>Species with heavy and short-lived seeds</b> <sup>15</sup>
Undisturbed forest	+ Chamaephytes and – therophytes <sup>9</sup> + Species with large seed size <sup>9</sup> dispersed by gravity or ants <sup>2, 9</sup> + Shade-tolerant species <sup>5</sup> + Species with early and short flowering time <sup>9</sup>
Maple syrup production stands	– <b>Tree seedlings and saplings</b> <sup>25</sup>
Second-growth forest of old pasture origin	+ Short life-span species <sup>6</sup> + Wind-pollinated species <sup>6</sup> + Species with long-distance seed dispersal <sup>2, 6, 17</sup> <b>by humans or animal adhesion</b> <sup>9</sup> + Species with seed bank <sup>2</sup> + Woody species <sup>2</sup> + Late-flowering species <sup>9</sup> – Species with limited seed dispersal <sup>2, 3, 17</sup>

1. Angers *et al.*, 2005; 2. Bellemare, Motzkin & Foster, 2002; 3. Bossuyt, Hermy & Deckers, 1999; 4. Charbonneau & Fahrig, 2004; 5. Collins, Dunne & Pickett, 1985; 6. Diaz *et al.*, 1999; 7. Froberg & Eriksson, 1997; 8. Gilliam & Roberts, 2003; 9. Graae & Sunde, 2000; 10. Halpern, 1989; 11. Haussler *et al.*, 2002; 12. Herault & Honnay, 2005; 13. Hermy *et al.*, 1999; 14. Jolls, 2003; 15. Kolb & Diekmann, 2005; 16. Mabry, Ackerly & Gerhardt, 2000; 17. Matlack, 1994; 18. McLachlan & Bazely, 2001; 19. Meier, Bratton & Duffy, 1995; 20. Moffat & McLachlan, 2004; 21. Moore & Vankat, 1986; 22. Olivero & Hix, 1998; 23. Rogers, 1982; 24. Scheller & Mladenoff, 2002; 25. Whitney & Upmeyer, 2004.

\*Studies reviewed for harvesting are clearcuts. We assumed selection cutting would have a similar but reduced impact on forest flora.

Agriculture dominates the region on the vast expanses of clay deposits originating from the post-glacial Champlain Sea. Isolated forest fragments cover 28% of the region, principally on moraine ridges and other land unsuitable for agriculture (Bouchard & Brisson, 1996; Robitaille & Saucier, 1998). Upper St. Lawrence vegetation dynamics and land use history have been the subject of numerous studies (Simard & Bouchard, 1996; Bouchard & Domon, 1997; Pan *et al.*, 1999; De Blois, Domon & Bouchard, 2001). Before the 19<sup>th</sup> century, the region was sparsely populated by a few groups of native people (Simard & Bouchard, 1996). European settlement after 1820 brought intense forest exploitation, first for wood and potash production and subsequently for agriculture. Some forests remained on private lands unsuitable for agriculture and were used for firewood or maple syrup production (Brisson & Bouchard, 2003). As agricultural activities changed in the 20<sup>th</sup> century, many fields were abandoned and allowed to reforest (Bouchard *et al.*, 1989). This history altered tree composition in the region: a climax of human origin, sugar maple–hickory forests, has replaced the pre-colonial climax of sugar maple–beech–hemlock forest (Bouchard & Domon, 1997; Doyon, Gagnon & Bouchard, 1998).

The Outaouais region extends west of the Upper St. Lawrence (45° 43' – 46° 06' N, 75° 00' – 75° 51' W). This sparsely inhabited area contains extensive forests on glacial tills with rocky outcrops (Robitaille & Saucier, 1998). Ninety-five percent of the region is forests (Robitaille & Saucier, 1998), with 75% of these in public ownership (MRNFP, 2003). The dominant disturbance in the region is industrial forestry. Until the latter half of the 20<sup>th</sup> century, harvesting consisted principally of targeted extraction of large-diameter pine, oak, and spruce along waterways. During the 1960s and 1970s, most of the area experienced selective, “diameter-limit” harvests. Currently, single-tree selection dominates the silvicultural regime, a system that removes approximately 30% of the basal area across all size classes every 20–30 y (Bédard & Majcen, 2003). A few unmanaged forests with very little history of direct human influence remain.

#### DESCRIPTION OF STUDY PLOTS

Twelve stands were chosen in the Upper St. Lawrence region: 4 stands exploited for maple syrup production, 4 second-growth stands originating from abandoned pastures, and 4 stands without recent human disturbance. From previous studies conducted in the region, we can assess that almost all these stands were entirely or partially cut in the 19<sup>th</sup> century and/or first part of the 20<sup>th</sup> century (Brisson, Bergeron & Bouchard, 1988). Vegetation dynamics after pasture and agriculture have been studied extensively in the region (De Blois & Bouchard, 1995; Benjamin, Domon & Bouchard, 2005). These studies were used to identify stands originating from the abandonment of pasture or agriculture. Old field stands had at least one visible sign of past agricultural use (*e.g.*, fence or large tree with a broad, open-grown crown). Syrup production stands were easily identified by presence of sap-collecting tubes. Undisturbed stands had no visible signs of pasturing, tree harvesting, or other human activities, either in the field or on aerial photographs. We assumed these stands were never cleared for pasture or agri-



culture and had had no important human disturbances during the second part of the 20<sup>th</sup> century at least.

We selected 18 stands in the Outaouais region: 6 old-growth stands, 6 stands harvested by single-tree selection 12 y ago (1990–1991), and 6 stands recently harvested (2000–2001) by single-tree selection. Old-growth stands were documented by the Exceptional Forest Ecosystems Working Group (Brisson & Villeneuve, 2003). Table II presents the principal characteristics of these study stands.

Stands were selected to reduce as much as possible any differences in edaphic conditions, aspect, and drainage. In addition to the studies mentioned above, information concerning the land use history of our study stands was compiled from the following sources: field observations, aerial photo-interpretation (1964–1966, 1975–1983), and meetings with officials from the provincial forest ministry in the Outaouais region and with private land owners in the Upper St. Lawrence region.

#### FIELD SAMPLING

Sugar maple dominated all of the study sites, representing > 25% of basal area and total tree stem density. American beech (*Fagus grandifolia*), American basswood (*Tilia americana*), and ironwood (*Ostrya virginiana*) were the most frequent companion tree species. None of the stands showed signs of recent fire, windthrow, or other natural disturbances. In each stand, a 25-m-radius plot was centred on plots previously surveyed by Carignan (2005) or Angers *et al.* (2005). To avoid edge effects, all plots were located at least 200 m away from any openings.

We determined floristic composition using linear vegetation surveys. In each plot, 52 circular points (15-cm radius) were systematically sampled along four 25-m transects. Species detected within a sampling point received an occurrence value of 1, for a possible score of 52 when a species was present in all points. Species present in the plot but not in any of the sampling points received an occurrence value of 0.5. The occurrence frequency (%) of a given species was the proportion of points in a plot where the species occurred. To describe vertical structure, we sampled the vegetation as described above every 50 cm in height, from the soil surface to the top of the understory (see Aubin, Beaudet and Messier [2000] for further details). We sampled the plots 3 times from May to September 2003 to obtain data for all species present during the growing

season. Grasses, sedges and hawthorns (*Crataegus* spp.) were not identified to species.

The following forest cover data were collected for each plot: tree composition, basal area ( $\text{m}^2\text{-ha}^{-1}$ ), and stem density ( $n\text{-ha}^{-1}$ ) measured for all stems with diameter at breast height (DBH) > 5 cm. The percentage of above-canopy photosynthetic photon flux density (% PPFD) was measured at each of the 52 sampling points, both at the ground level and at 2 m above the ground, using a line-quantum sensor (LI-COR, Lincoln, Nebraska, USA). All light measurements were taken under completely overcast sky conditions following the methods of Messier and Puttonen (1995) and Gendron, Messier, and Comeau (1998).

#### DATABASE OF BIOLOGICAL TRAITS (TOPIQ)

The elaboration of plant functional types (PFT) required the characterization of a set of carefully chosen biological traits for each of the species inventoried. Although several databases of biological traits exist (Kleyer, 1999; Gachet, Vêla & Taton, 2005), none was available for the Québec flora. We thus created a Québec-specific database, Traits Of Plants In Québec (TOPIQ). The database structure was based on the model of Grime, Hodgson, and Hunt (1988), using traits associated with regeneration and establishment. Due to the large number of species, we considered only traits for which information was available from published sources or herbarium specimens. Traits were chosen from a comprehensive literature review, with validation, *i.e.*, several sources were needed to include a given trait for a given species; contradictions among sources were settled by experts. A complete list of sources is available in the data repository of Écoscience. Thirteen categorical traits were used in the present study, resulting in a total of 51 classes after expansion into binary form for analysis (Table III).

#### DATA ANALYSIS

##### PLANT FUNCTIONAL TYPES: EMERGENT GROUPS

PFT used in this study are emergent groups, *i.e.*, species are grouped according to their biological traits (Lavorel *et al.*, 1997). To develop the emergent groups and test for their responses to human disturbance, we conducted a 3-step analysis. First, a Correspondence Analysis (CA) was done on the data matrix of plant biological traits (214 species  $\times$  51 classes) to create an overall portrait of life history strate-

TABLE II. Characteristics of sampled stands. No significant differences were detected in the diversity indices between the 2 regions and among disturbance types ( $P > 0.05$ , one-way ANOVA).

			Basal area	Tree stem density	% PPFD <sup>i</sup>	Diversity indices <sup>ii</sup>		
Code	Disturbance type	<i>n</i> plots	(m <sup>2</sup> ·ha <sup>-1</sup> )	( <i>n</i> ·ha <sup>-1</sup> )	at 200 cm / soil level	S	H'	J
UPPER ST. LAWRENCE REGION – AGRICULTURAL MATRIX								
UND	No recent disturbance	4	38	752	1.9 / 1.3	21.5	3.350	0.758
ACE	Maple syrup production	4	34	581	3.7 / 2.2	18.3	2.992	0.716
PAS	Origin from pasture abandonment	4	36	672	2.3 / 1.4	21.0	3.344	0.770
OUTAOUAIS REGION – FORESTED MATRIX								
OGF	None (old growth)	6	28	447	3.9 / 2.5	12.5	2.687	0.762
OSH	Single-tree selection (1990-1991)	6	20	369	2.4 / 1.5	16.0	2.898	0.744
RSH	Single-tree selection (2000–2001)	6	20	403	17.1 / 5.3	19.0	3.089	0.750

<sup>i</sup> % PPFD: percentage of above-canopy photosynthetic photon flux density.

<sup>ii</sup> Diversity indices: S: species richness; H': Shannon's diversity index; J: evenness.

TABLE III. Biological traits of understory plants in sugar maple forests as compiled from the literature. In parentheses: number of missing values.

Trait	Code	Description
Raunkier life form	RA	mg: mega or meso-phanerophyte ( $\geq 8$ m in height); mc: micro or nano-phanerophyte (25 cm to 8 m); ch: chamaephyte (herb or shrub, bud between 1 mm and 25 cm above ground); h: hemicryptophyte (herb with bud at the ground surface); g: geophyte (herb with underground bud); t: therophyte (annual)
Life cycle	PER	1: annual; 2: biennial; 3: perennial
Principal means of reproduction (39)	REP	se: seeds only; ms: vegetative propagation possible but mostly by seeds; ve: mostly by vegetative propagation
Foliage persistence	PFO	0: no; 1: yes
Foliage structure	SFO	For phanerophytes: ms: spread out stem; me: erect stem; mu: multi-stemmed For other life forms: No stem: r: rosette or semi-rosette; g: graminoid; e: erect leaves; With stem: el: erect leafy stem; de: decumbent stem; um: umbel-shaped stem; vi: vine; Non-leafy stem: nl: saprophyte
Physical defences (e.g., thorns)	DEF	0: no; 1: yes
Flowering phenology	FPH	sp: spring; su: summer; sf: summer–fall
Pollination vector (35)*	POL	a: abiotic; b: biotic; n: no pollination or vector; na: non applicable (e.g., pteridophytes)
Seed dispersal vector*	DI	w: wind (anemochorous); ez: animal ingestion (endozoochorous); an: insect, mostly ant (myrmecochorous); bi: bird ingestion (avichorous); hd: human dispersal: (anthropochorous); ex: ballasts or explosive discharge (ballistichorous)
Seed size	SE	1: < 0.1 mm; 2: 0.1 to 1.99 mm; 3: 2 to 2.99 mm; 4: 3 to 4.99 mm; 5: 5 to 40 mm
Seed dormancy (67) *	DO	nd: non dormant; sc: physical dormancy; dp: physiological or morphophysiological dormancy
Light requirement (9)	LI	s: shade tolerant; m: mid tolerant; i: intolerant
Status in Québec	ST	0: native; 1: exotic

\*For these traits, a species may have more than one class.

gies and trait associations for flora in sugar maple forests (results not shown). Second, to delineate emergent groups, a Ward-type ascending hierarchical classification was done on the axis scores of this CA (Euclidean distance, weighted by 1). The cut-off was determined by visual inspection of the dendrogram in accordance with our botanical knowledge. Third, we examined the relative occurrence of these groups in the human-disturbance types. To do this, a matrix of species groups' occurrence was calculated as the product of the species data matrix (214 species  $\times$  30 plots, with percent occurrence data of each species) and the binary matrix of emergent groups (214 species  $\times$  13 emergent groups). This new matrix was standardized by dividing the occurrence of each group by the total occurrence for all groups in each plot. Differences in the relative occurrence of species groups among disturbance types were analyzed using a one-way ANOVA followed by a multiple comparison Bonferroni test in cases where significant effects of disturbance type were detected. The Bonferroni test is based on Student's *t* statistic and corrects the significance level for multiple analyses.

#### PLANT FUNCTIONAL TYPES: INDIVIDUAL TRAITS

As emergent groups may be too general to reveal differences among species at the trait level, individual biological traits were also related to human-disturbance types. A matrix of the prevalence of each trait in each plot was created by multiplying the plant species data matrix by the traits data matrix. This new matrix was standardized by dividing the occurrence of each class by the total occurrence for all classes in each plot. This biological spectra matrix (30 plots  $\times$  51 classes) comprises the relative abundance of species of a plot with a particular trait. A Principal Component Analysis (PCA) was done on this matrix to compare the distribution of classes among the different disturbance types.

#### VERTICAL UNDERSTORY STRATIFICATION

We used the matrix of occurrence of species groups as determined for individual strata to examine the vertical occupancy of different groups. The impact of human disturbance on the development of understory vertical strata was also tested. Total species occurrence by vertical strata of 50 cm was analyzed using a one-way ANOVA and a multiple comparison Bonferroni test.

In addition to these analyses, the following indices were calculated for each plot: species richness, Shannon's diversity index (Whittaker, 1972), and species evenness (Magurran, 1988). The functional diversity, or the richness of each emergent group, was also calculated. A one-way ANOVA followed by a multiple comparison Bonferroni test was done to check for index differences among the disturbance types.

Where necessary, we performed a natural log transformation on the dependent variables to ensure normality and homoscedasticity. A significance level of 0.05 was used. The XLStat program (Addinsoft, 2006) was used for all analyses.

## Results

A total of 142 species were recorded in the Upper St. Lawrence, while 163 species were recorded in the

Outaouais, with 91 species in common. No significant differences were detected in the diversity indices between the 2 regions and among disturbance types (Table II).

#### EMERGENT GROUP IDENTIFICATION

Cluster analysis allowed 13 emergent groups to be delineated (Table IV). The following traits characterized the groups: (1) annuals (therophytes); (2) exotic, wind-dispersed (anemochorous) hemicryptophytes, with a high proportion of biennials and rosette-form species; (3) exotic hemicryptophytes dispersed mainly by animal ingestion (endozoochorous) that were perennial species with a decumbent or vine form; (4) native, wind-dispersed hemicryptophytes, with a high proportion of late-flowering species; (5) native hemicryptophytes dispersed by animal ingestion or bird (avichorous) with a decumbent form; (6) spring geophytes, which are mainly dispersed by ants (myrmecochorous) or animal ingestion; and (7) shade-tolerant herbs that are mostly wind-dispersed and contain particular sub-groups such as the *Orchidaceae*. Pteridophytes, which have distinct biological traits, were separated by the analysis into (8) ferns and (9) the genus *Lycopodium*. (10) The next group comprised the genus *Viola*. Finally, the phanerophytes were separated into 3 groups: (11) trees dispersed by wind; (12)

trees or vines dispersed by birds; and (13) shrubs dispersed by birds.

#### RESPONSES OF EMERGENT GROUPS TO HUMAN DISTURBANCES

The disturbance types differed in the relative occurrence of emergent species groups (Table V). Old growth forests had the lowest proportion of exotic, wind-dispersed hemicryptophytes and trees or vines dispersed by birds. Undisturbed forests were not significantly different from old growth stands. Undisturbed stands possessed the highest proportion of spring geophytes. Maple syrup production forests possessed a higher proportion of trees or vines dispersed by birds than old growth stands but were not significantly different from undisturbed stands. They had the lowest occurrence of shrubs. Old pasture stands had a significantly higher proportion of trees or vines dispersed by birds than old growth stands and a significantly higher proportion of shrubs than undisturbed stands. Stands partially harvested 12 y ago were not significantly different than from old growth stands. They possessed the lowest proportion of spring geophytes. Recently partially harvested stands had a significantly higher proportion of exotic, wind-dispersed hemicryptophytes and of native decumbent hemicryptophytes dispersed by animals or birds than old growth stands.

TABLE IV. Characteristic biological traits of the identified emergent groups computed from a cluster analysis done on the axis scores of a Correspondence Analysis on the biological traits data matrix.

Group	Characteristic trait														Characteristic species	<i>n</i>
	RA	PER	PFO	SFO	DEF	FPH	POL	DI	SE	DO	LI	ST	REP			
Annuals	t	1	0	el, r	0	su	b	-	2, 4	dp	i	0	se	<i>Bidens frondosa</i> <i>Erigeron canadensis</i>	13	
Exotic wind-dispersed hemicryptophytes	h	2, 3	0	r	-	su	b, n	w	-	dp	i	1	-	<i>Cirsium arvense</i> <i>Hieracium pratense</i>	18	
Exotic hemicryptophytes dispersed by animal ingestion	h	3	0	de, vi	0	su	b	ez	3	sc, dp	i, m	1	-	<i>Trifolium pratense</i> <i>Vicia cracca</i>	5	
Native wind-dispersed hemicryptophytes	h	3	0	el, <i>r</i>	0	su, <i>sf</i>	b	w	2, 3	dp	-	0	ve	<i>Anaphalis margaritae</i> <i>Solidago canadensis</i>	28	
Animal- or bird-dispersed decumbent hemicryptophytes	h	3	0	de	<i>l</i>	sp, su	b	ez, bi	3	dp	-	0	ve	<i>Rubus idaeus</i> <i>Galium triflorum</i>	17	
Spring geophytes	g	3	0	<i>um</i>	0	sp	b	ez, an	4	dp	s, <i>i</i>	0	ve, ms	<i>Medeola virginiana</i> <i>Uvularia grandiflora</i>	26	
Shade herbs	g, h	3	0	el, <i>nl</i> , r	0	<i>sp</i>	-	<i>w</i>	-	-	s, <i>m</i>	0	ve	<i>Epiphaeus virginiana</i> <i>Oxalis montana</i>	22	
Ferns	g, h	3	<i>l</i>	e	0	-	na	w, ex	1	na	s	0	ve	<i>Adiantum pedatum</i> <i>Dryopteris spinulosa</i>	20	
<i>Lycopodium</i>	ch	3	1	de	0	-	na	w	1	na	s	0	ve	<i>Lycopodium lucidulum</i> <i>Lycopodium obscurum</i>	3	
<i>Viola</i>	h	3	0	r, <i>e</i>	0	sp	b	an, ex	3, 2	sc, dp	s, <i>m</i>	0	ve	<i>Viola blanda</i> <i>Viola canadensis</i>	6	
Wind-dispersed trees	mg	3	<i>l</i>	ms	0	sp	a	w, ez	5	dp	-	0	ms	<i>Acer saccharum</i> <i>Fraxinus americana</i>	25	
Bird-dispersed trees or vines	mg	3	0	vi, ms	0	su	b	bi	5	dp	m, s	0	ms, ve	<i>Vitis riparia</i> <i>Prunus serotina</i>	5	
Shrubs	mc	3	0	mu	<i>l</i>	sp	b	bi	4, 5	dp	m, s	0	ve	<i>Cornus sericea</i> <i>Prunus virginiana</i>	26	

See Table III for code definitions. Codes in italic indicate that this class is present but in lower proportion.

TABLE V. Mean relative occurrence (O%) of emergent groups and functional diversity (r: richness of each emergent group) among disturbance types. UND: undisturbed; ACE: maple syrup production; PAS: old pasture; OGF: old growth; OSH: old harvested; RSH: recent harvested stands. For each emergent group (row) a different letter indicates a significant difference at  $P < 0.05$  (one-way ANOVA followed by a multiple comparison Bonferroni test). See Table IV for a detailed description of the groups.

Groups	P		UND		ACE		PAS		OGF		OSH		RSH	
	O%	r	O%	r	O%	r	O%	r	O%	r	O%	r	O%	r
Annuals	-	*	0.1	0.3 <sup>ab</sup>	1.3	1.3 <sup>ab</sup>	0.2	0.50 <sup>ab</sup>	0.1	0.2 <sup>a</sup>	0.3	0.7 <sup>ab</sup>	0.8	2.8 <sup>b</sup>
Exotic wind-dispersed hemicryptophytes	*	**	0.6 <sup>ab</sup>	1.5 <sup>ab</sup>	0.7 <sup>ab</sup>	1.5 <sup>ab</sup>	0.6 <sup>ab</sup>	1.8 <sup>ab</sup>	0.1 <sup>a</sup>	0.2 <sup>a</sup>	0.1 <sup>a</sup>	0.3 <sup>a</sup>	1.3 <sup>b</sup>	3.7 <sup>b</sup>
Exotic animal-dispersed hemicryptophytes	-	-	0	0	0.1	0.3	0	0	0	0	0.1	0.2	0.3	0.5
Native wind-dispersed hemicryptophytes	* <sup>i</sup>	* <sup>i</sup>	5.6	4.3	6.0	6.3	4.2	3.8	1.2	2.7	1.7	4.0	2.1	5.7
Animal- or bird-dispersed decumbent hemicryptophytes	***	**	3.1 <sup>a</sup>	3.3 <sup>a</sup>	3.4 <sup>a</sup>	6.3 <sup>ab</sup>	0.9 <sup>a</sup>	2.8 <sup>a</sup>	1.8 <sup>a</sup>	2.8 <sup>a</sup>	4.2 <sup>a</sup>	5.3 <sup>ab</sup>	12.4 <sup>b</sup>	7.7 <sup>b</sup>
Spring geophytes	*	*	34.4 <sup>b</sup>	11.8 <sup>b</sup>	24.6 <sup>ab</sup>	11.5 <sup>ab</sup>	19.3 <sup>ab</sup>	9.3 <sup>ab</sup>	29.1 <sup>ab</sup>	7.5 <sup>ab</sup>	15.2 <sup>a</sup>	8.3 <sup>ab</sup>	18.8 <sup>ab</sup>	7.3 <sup>a</sup>
Shade herbs	-	-	5.1	5.0	2.3	4.3	3.4	3.5	2.4	5.0	4.0	5.8	5.3	5.5
Ferns	-	-	6.1	5.0	3.8	5.5	0.6	1.8	4.2	4.8	4.4	5.7	3.9	5.0
<i>Lycopodium</i>	-	*	0.1	0.3 <sup>ab</sup>	0	0 <sup>a</sup>	0	0 <sup>a</sup>	3.0	0.5 <sup>ab</sup>	0.8	1.3 <sup>b</sup>	0.4	1.0 <sup>ab</sup>
<i>Viola</i>	-	-	0.7	1.0	0.8	1.3	0.5	0.5	0.6	0.8	1.0	0.7	1.6	1.2
Wind-dispersed trees	-	***	38.6	7.3 <sup>ab</sup>	48.9	8.0 <sup>ab</sup>	55.7	8.5 <sup>ab</sup>	51.6	5.3 <sup>a</sup>	62.6	9.3 <sup>b</sup>	46.5	10.5 <sup>b</sup>
Bird-dispersed trees or vines	***	***	2.4 <sup>abc</sup>	2.8 <sup>bc</sup>	5.2 <sup>c</sup>	3.0 <sup>bc</sup>	3.9 <sup>bc</sup>	3.8 <sup>c</sup>	0.4 <sup>a</sup>	0.8 <sup>a</sup>	0.9 <sup>a</sup>	1.2 <sup>ab</sup>	1.2 <sup>ab</sup>	1.5 <sup>ab</sup>
Shrubs	*	-	3.3 <sup>a</sup>	6.3	2.8 <sup>a</sup>	4.5	10.8 <sup>b</sup>	7.3	5.6 <sup>ab</sup>	5.0	4.9 <sup>ab</sup>	5.8	5.4 <sup>ab</sup>	6.8

\*  $P \leq 0.05$ ; \*\*  $P \leq 0.01$ ; \*\*\*  $P \leq 0.001$ ; -  $P > 0.05$ .

<sup>i</sup> But Bonferroni test  $P > 0.05$ .

Functional diversity (richness in each emergent group) differed among disturbance types (Table V). Old growth stands possessed the lowest diversity of annuals, of exotic, wind-dispersed hemicryptophytes, of animal- or bird-dispersed decumbent hemicryptophytes, and of trees. Undisturbed stands had a higher diversity in bird-dispersed trees or vines than old growth forests. Undisturbed stands had the highest spring geophytes diversity. Maple syrup production and old pasture stands had a higher diversity of trees or vines dispersed by birds than old growth stands but were not significantly different than undisturbed stands. These stands had no *Lycopodium* species. Old growth, undisturbed, and old pasture stands had no exotic hemicryptophytes dispersed by animal ingestion. The older partially harvested stands possessed a significantly higher diversity of trees dispersed by wind than old growth and the highest diversity of *Lycopodium*. Recently partially harvested stands were the most distinct from the old growth because of their significantly higher diversity of annuals, of exotic, wind-dispersed hemicryptophytes, of native, decumbent hemicryptophytes dispersed by animals or birds, and of trees dispersed by wind. They possessed the lowest diversity in spring geophytes.

#### RESPONSES TO HUMAN DISTURBANCES AT THE TRAIT LEVEL

Figure 1 presents the ordination of all the study plots ( $n = 30$ ) and species' biological traits that contributed the most to building the axes ( $n = 31$  of a total of 51) along the 2 PCA axes of the biological spectra matrix. The eigenvalues of the first 2 axes were 15.88 and 10.13, corresponding respectively to 29% and 19% of the total variance observed. The primary axis of variation distinguished between recently partially harvested stands on the left and old growth stands, a more or less homogeneous group, to the right. The secondary axis of variation separated the 2 study regions, with Outaouais plots mostly located near the top of axis F2. The primary variation (Axis 1, Figure 1) reflects principally a gradient of flowering phenology, life cycle, provenance, seed characteristics, and plant form classes. The secondary

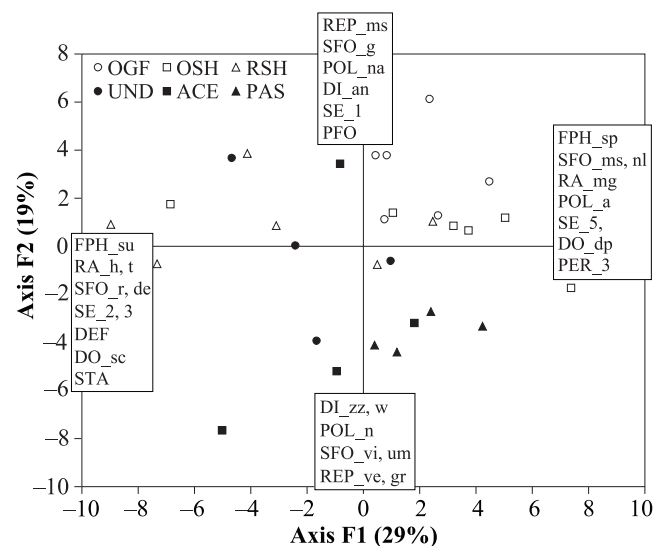


FIGURE 1. Principal Components Analysis (PCA) diagram (axes 1 and 2) of the biological spectra matrix (plots  $\times$  traits). Indicated are study plots (see Table II for code definitions) and biological traits contributing strongly to building the axes (see Table III for code definitions).

axis of variation (Axis 2, Figure 1) highlights differences in the principal means of reproduction, seed dispersal, pollination vector, plant form classes, and leaf persistence.

The PCA elucidated differences in how classes of traits are represented among the disturbance types. Old growth stands possessed a high proportion of spring flowering species (FPH\_sp), species capable of vegetative propagation but that reproduce mostly by seeds (REP\_ms), myrmecochorous species (DI\_an), species with graminoid form (SFO\_g), and saprophytes (SFO\_nl). Old field stands possessed a large proportion of wind-dispersed species (DI\_w) and of species reproducing either solely by seeds (REP\_gr) or by strong vegetative reproduction (REP\_ve), but no saprophyte species (SFO\_nl). Recently partially harvested



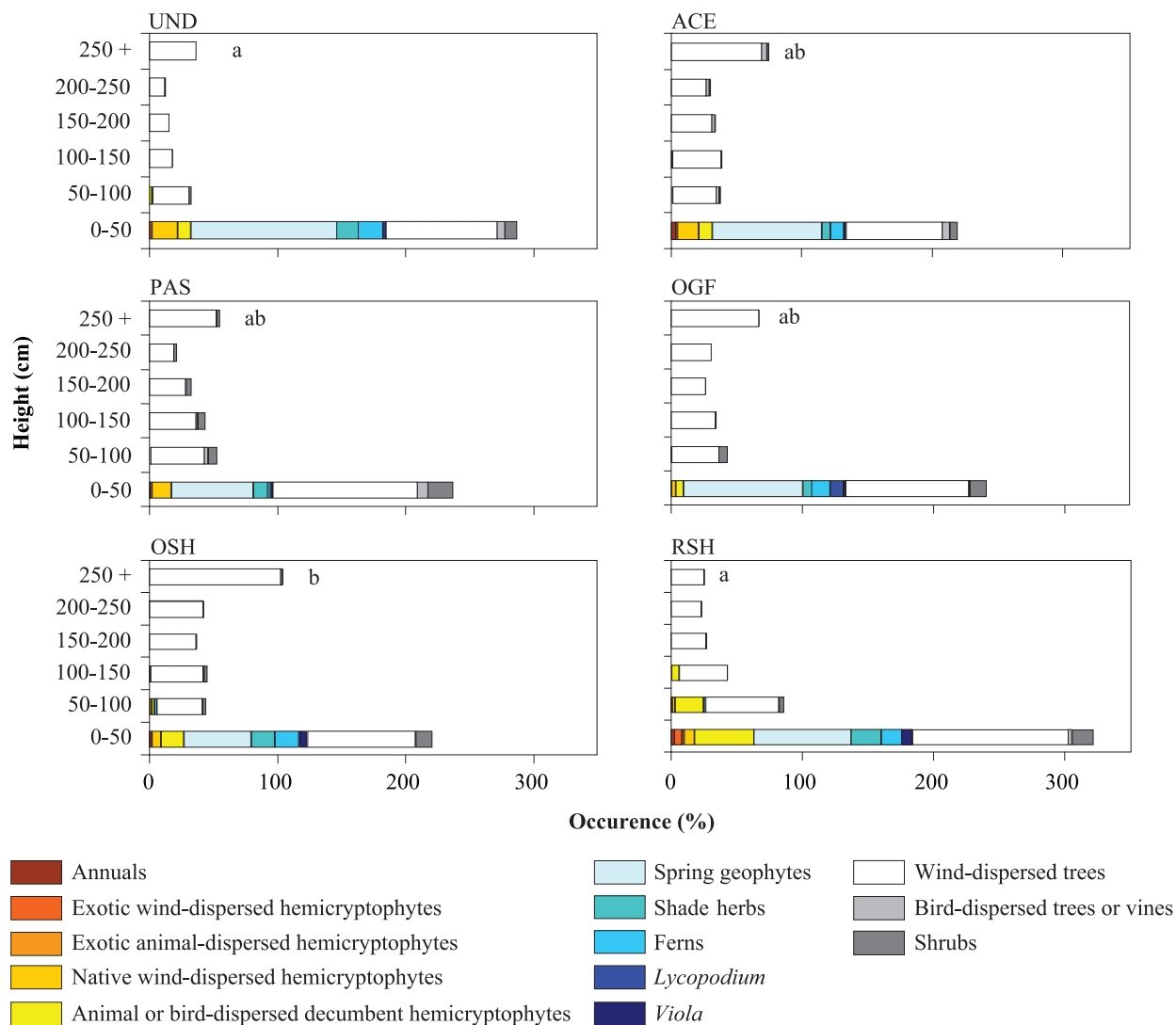


FIGURE 2. Vertical stratification of the vegetation by emergent groups for each type of human disturbance. UND: undisturbed; ACE: maple syrup production; PAS: old pasture; OGF: old growth; OSH: old harvested; RSH: recent harvested stands. For the stratum 250 cm and higher, a different letter indicates a significant difference among disturbance type at  $P < 0.05$  (multiple comparison Bonferroni test). No significant difference was found for the lower strata. See Table IV for a detailed description of the groups.

stands had a large proportion of hemicryptophytes and therophytes (RA\_h, t), exotic species (STA), summer flowering species (FPH\_su), species with small seeds (SE\_2, 3), species with physical defences (DEF), and species with rosette form (SFO\_R). No saprophyte species (SFO\_nl) was found in old field stands. Maple syrup production stands had a large proportion of species reproducing by seed (REP\_se) and dispersed by wind (DI\_W). Stands partially harvested 12 y ago had a large proportion of spring flowering (FPH\_sp) perennials (PER\_3) and tree saplings (SFO\_ms). Little difference in the representation of traits was found for undisturbed stands.

#### VERTICAL STRATIFICATION AND HUMAN DISTURBANCE

In general, the recurring pattern of vertical stratification of the understory vegetation observed for all types of stands was the presence of a low stratum (0–50 cm) that was well-developed and diversified, strata between 50 and 200 cm

that had little vegetation, and a high stratum ( $\geq 250$  cm) that was moderately developed but not very diversified (Figure 2). The vertical stratification was quite similar among disturbance types. The only significant difference was that stands partially harvested 12 y ago possessed an understory high stratum more developed than recently harvested and undisturbed stands (ANOVA  $P = 0.006$ ).

## Discussion

#### BIOLOGICAL TRAITS AND ECOSYSTEM FUNCTIONING

Plant functional groups developed in this study were objectively constructed from a classification of the principal biological traits of the flora in sugar maple forests of Québec. These 13 groups possessed a set of common traits that can be associated with a similar life history strategy and particular roles in the ecosystem (Mooney, 1997). These groups represent different life history strategies as well as responses and adaptations to disturbance.

First, annuals and the 2 groups of exotic species were associated with open environments. These species were almost exclusively shade intolerant, of short longevity, capable of long-distance seed dispersal, and associated with recently harvested stands where ground-level light is plentiful (Table II). Second, native, wind-dispersed and animal- or bird-dispersed decumbent hemicryptophytes comprised species with various light requirements. While the wind-dispersed group was mainly composed of open field species and seems adapted to the agricultural landscape of the Upper St. Lawrence, the latter group was associated with recently harvested stands. Third, the spring geophytes, ferns and allies, and *Viola* groups were mostly shade-tolerant species and thus can be considered as shade forbs. Adaptations, such as foliage/stem form, phenology, or saprophytic nature, allow these plants to tolerate the deep summertime shade prevalent in the understory of sugar maple forests (Collins, Dunne & Pickett, 1985; Givnish, 1987; Neufeld & Young, 2003). Many of these species have low colonization capacity and are recognized as sensitive to human disturbances (Bierzchudek, 1982; Meier, Bratton & Duffy, 1995; Flinn & Vellend, 2005). Even the pteridophytes, which produce spores that can travel long distances, need specific microsites for establishment and therefore possess limited capacity for colonization (Flinn, 2005). It was surprising that 3 of the 5 shade forbs did not vary in occurrence according to human-disturbance type. The lack of significant difference for the fern group despite their reduced presence in old pasture stands relative to undisturbed or old growth stands may be explained by the large variability among stands. For the shade forbs and *Viola* groups, phylogeny may explain the unresponsiveness to disturbance type. These groups are composed of species with convergent traits due to phylogeny but which differ in life history. This relatively frequently occurring problem with emergent group classification (Lavorel *et al.*, 1997) highlights the need to combine emergent group classification with trait level analyses.

Finally, the 3 phanerophyte groups, which contain shrubs, tree seedlings, and saplings, occupy the upper strata of the understory. They serve as a "sapling bank" (Wilson, 1993) for the tree stratum and contribute strongly to understory structure (Harcombe & Marks, 1977). The phanerophyte groups possess regeneration and dispersal strategies that differ from all the above groups (Gilliam & Roberts, 2003), being almost all native species adapted for long-distance seed dispersal. The phanerophytes responded positively to human disturbance, corroborating the findings of Royo and Carson (2006), who documented that increases in canopy disturbance generally favour the development of a dense phanerophyte stratum.

#### HUMAN EFFECTS ON UNDERSTORY ASSEMBLAGES

We used an approach combining PFT and vertical stratification of the understory vegetation to evaluate the effects of human disturbance on the ecological integrity of sugar maple stands. Ecological integrity of a forest was evaluated by the divergence of its understory assemblage from that observed in comparable unmanaged old growth forest, the most natural stands available in the region (Brisson & Villeneuve, 2003). Even though they are subjected to indirect influences such as air pollution and population increas-

es in deer and exotic earthworms, these forests show relatively little direct human influence. Unlike most of the old growth of eastern deciduous forest, which is located in human-dominated matrix (Foster, Orwig & McLachlan, 1996; McCarthy, 2003), old growth stands in Outaouais are embedded in a large forested matrix far from urban centres and are representative of the regional forest in terms of soil characteristics and topography. It therefore seems reasonable to assume these forests are the best extant reference we can find. To prevent a potential bias due to regional differences, we also evaluated undisturbed stands for the Upper St. Lawrence region.

Although understory vegetation assemblages were generally similar across all the disturbance types (Figure 2), some distinctions can be made. In old growth stands, the shade forbs were predominant. Moreover, despite the presence of gaps, a relatively open canopy, and a diversified structure in the tree stratum characteristic of old growth stands, the diversity and occurrence of open environment groups were low. Corroborating what is generally reported in the literature (Table I), our analyses at the trait level revealed that the following traits are associated with old growth stands (Figure 1): spring flowering native perennial species with ant-dispersed large seeds or saprophyte species with small seeds. Species that possess these traits, such as spring geophytes and some shade forbs, may therefore be potentially sensitive to human disturbance.

Stands recently harvested by single-tree selection had an understory assemblage that differed most from that of old growth. Annuals, exotic species, and animal- or bird-dispersed decumbent hemicryptophytes had a higher occurrence and richness in these stands than in old growth. Certain shade forbs described as sensitive to harvesting by Moola and Vasseur (2004), such as the saprophyte species and *Oxalis montana*, were absent. The apparent lack of difference between stands partially harvested 12 y ago and old growth stands, in conjunction with our observation that shade forbs absent in recently harvested selection stands were present in the older harvested selection stands, suggests that the understory eventually recovers from such partial harvesting treatment.

Although the canopy was not entirely closed in the older partially harvested stands, a dense sapling layer of wind-dispersed tree species above 250 cm greatly reduced light transmission to the forest floor. Therefore, structural changes in the understory following logging may lead to the partial exclusion of species groups associated with open environments, as these groups were infrequent in the older partially harvested stands. Moreover, occurrence of spring geophytes in these older harvested stands was lower than in all other stand types. As suggested by Meier, Bratton, and Duffy (1995), spring geophytes may be affected by a strong post-logging response of tree seedlings and saplings. While several authors have documented a re-establishment or persistence of most species after logging, many have also observed a decline of certain forbs following clearcuts (Halpern, 1989; Elliott *et al.*, 1997; Ruben *et al.*, 1999; Roberts & Gilliam, 2003; Moola & Vasseur, 2004). Clearcutting apparently reduces populations of the rarer herb species (Meier, Bratton & Duffy, 1995; Jolls, 2003).

Single-tree selection, by harvesting only part of the canopy, possibly has a lower impact on the forest flora than clearcutting. For example, Reader and Bricker (1992) did not detect negative impacts on forest flora 2, 5, and 9 y after selective harvests in deciduous forests.

Corroborating previous studies (see Table I), we observed that former pastures tend to have fewer species groups with limited colonization capacity, such as the spring geophytes and the pteridophytes. Species in second-growth forests regenerating after agriculture abandonment are good colonizers, capable of maintaining a persistent seed bank in the soil, or able to survive in a non-forested environment (Graae & Sunde, 2000; Bellemare, Motzkin & Foster, 2002). But occasional long-distance seed dispersal is of noticeable importance for the colonization of species with a short-distance dispersal vector (Cain, Damman & Muir, 1998). The initial floristic composition in these forests, resulting from cattle grazing, which acted as a "selective agent" (*sensu* Hadar, Noy-Meir & Perevoltsky, 1999), was still apparent in the now mature maple forests. For example, the shrub group, which contains species avoided by cattle such as prickly ash (*Zanthoxylum americanum*), had its highest occurrence in these stands.

Activities associated with maple syrup production affect structural diversity, particularly by eliminating tree species other than sugar maple and by cutting saplings (Messier & Beaudet, 2000; Whitney & Upmeyer, 2004; Lenière & Houle, 2006). Surprisingly, the low observed structural diversity of the tree stratum was not reflected in the understory assemblage of sampled syrup production stands as we found a high occurrence of seedlings and saplings of trees or vines dispersed by birds. Few differences were found between this forest type and either old growth or undisturbed forests, perhaps due to the large variation observed in syrup production stands arising from inter-stand differences in management practices.

Undisturbed stands were quite similar to old growth stands. These stand types had the highest occurrence of spring geophytes. The undisturbed stands located in the Upper St. Lawrence region had more exotic species than old growth stands located in the Outaouais, presumably because of land-use history and the nature of the dominant regional matrix. Most, if not all, forests in the Upper St. Lawrence have had episodes of human disturbance (De Blois, Domon & Bouchard, 2001), and legacies of these influences remain in the presence of certain groups of species of open environments. Moreover, the Upper St. Lawrence forests are located within an agricultural matrix that affects species differently according to their biological traits (Table I). Conversely, the Outaouais remains generally forested, with a considerably less frequent, intense, and extensive history of human disturbance. The forested matrix has a buffering effect against the introduction of species of open environments and favours the reintroduction of existing forest species after disturbance (Ruben *et al.*, 1999; Charbonneau & Fahrig, 2004).

Undisturbed stands of the Upper St. Lawrence and old growth stands of the Outaouais showed little evidence of regional variations in PFT groups. The generally higher

occurrence and diversity of wind-dispersed hemicryptophytes and of trees and vines dispersed by birds in the Upper St. Lawrence is quite likely attributable to landscape context and land-use history. The higher occurrence of *Lycopodium* in the Outaouais region might be attributable to a regional difference in climate. However, it may also be related to nurse log availability as *Lycopodium lucidulum*, which is the most abundant *Lycopodium* species in our study, is known to need this specialized microhabitat for its establishment (Scheller & Mladenoff, 2002).

#### LONG-TERM CONSEQUENCES FOR PLANT COMMUNITIES

A principal finding of this study is the remarkable stability of understory vegetation in sugar maple forests. It appears that the majority of understory forest plants are well adapted to the range of human disturbances we studied. After 200 y of human disturbance, sugar maple forests still possess an understory community that appears to retain its ability to recover from human disturbance. However, our results suggest some issues of possible conservation concern in the long term. An increase in the frequency, extent, and severity of human disturbances may affect the understory assemblage of these forests by (i) increasing the occurrence of groups associated with open environments, including exotic species; (ii) decreasing the diversity and occurrence of spring geophytes; (iii) decreasing the occurrence of certain shade forbs, such as saprophytes; and (iv) modifying understory structure by increased development of phanerophytes, thereby modifying understory abiotic conditions and potentially negatively affecting recruitment of species in the lower strata. These modifications in the understory assemblage could alter the natural character of the understory of sugar maple forests over the long term.

#### Conclusion

The use of plant functional types provides a synthetic view of vegetation response to disturbance. By enabling comparisons of similar ecosystems in different regions, this approach offers a new methodological framework that can be applied to the study of human effects on vegetation processes as well as to many aspects of forest management. For instance, this approach provides an avenue for monitoring human effects on ecological integrity even where it is difficult to find unmanaged forest to serve as a reference state.

The northern hardwood forest of southern Québec is now seriously degraded from a market value perspective in terms of tree stem quality (Coulombe *et al.*, 2004). However, our study shows that the understory has so far kept its functionality. Possession of a functional understory is a determining factor in ensuring the long-term establishment and survival of the trees that will dominate the system in the future. Thus, all the studied forests seem to retain their potential for a natural recovery of the tree stratum in the long term.

From these results, it appears that disturbed forests remain valuable from the perspective of conserving biodiversity and ecological integrity. It is thus still possible to respond to the urgent need for more protected areas in



southern Québec by including a proportion of these disturbed forests in our conservation strategy.

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