Comparison of two plant functional approaches to evaluate natural restoration along an old-field – deciduous forest chronosequence

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Abstract

Question: Are direct and indirect trait-based approaches similar in their usefulness to synthesize species responses to successional stages?

Location: Northern hardwood forests, Québec, Canada (45°01′–45°08′N; 73°58′–74°21′W).

Methods: Two different trait-based approaches were used to relate plant functional traits to succession on an old-field – deciduous forest chronosequence: (i) a frequently used approach based on co-occurrence of traits (emergent groups), and (ii) a new version of a direct functional approach at the trait level (the fourth-corner method). Additionally, we selected two different cut-off levels for the herb subset of the emergent group classification in order to test its robustness and ecological relevance.

Results: Clear patterns of trait associations with stand developmental stages emerged from both the emergent group and the direct approach at the trait level. However, the emergent group classification was found to hide some trait-level differences such as a shift in seed size, light requirement and plant form along the chronosequence. Contrasting results were obtained for the seven or nine group classification of the herbaceous subset, illustrating how critical is the number of groups for emergent group classification.

Conclusion: The simultaneous use of two different trait-based approaches provided a robust and comprehensive characterization of vegetation responses in the old-field – deciduous forest chronosequence. It also underlines the different goals as well as the limitations and benefits of these two approaches. Both approaches indicated that abandoned pastures of the northern hardwood biome have good potential for natural recovery. Conversion of these lands to other functions may lead to irremediable loss of biodiversity.

Introduction

Over the past decade, trait-based approaches have become increasingly popular in community ecology. They can provide valuable insights into mechanisms of community development, because the potential of a species to establish or persist under any given set of environmental conditions is largely determined by its biological traits (Lavorel et al. 2007). The underlying assumption is that the most important processes in an ecosystem are the product of those operating at the level of the populations that compose it, while these processes are the consequence of the species traits (Peet 1992). The biological traits of species are used as an alternative to taxonomic classification, thereby offering the possibility for large-scale comparisons that could reveal patterns of organization that are otherwise difficult to detect using a traditional taxonomic approach.

Trait-based or functional type approaches have been used as a framework for understanding complex ecosystem responses to human disturbance. At first essentially limited to open grasslands (e.g. Lavorel et al. 1998; Barbaro et al. 2000), they have rapidly gained utility in characterizing human impacts on forests (e.g. Graae & Sunde 2000;

Verheyen et al. 2003; Aubin et al. 2007) and on heavily human-transformed ecosystems such as hedgerows (Deckers et al. 2004; Roy & De Blois 2006) and plantations (Herault et al. 2005; Aubin et al. 2008).

Numerous trait-based approaches exist. They can be differentiated in terms of their level of straightforwardness, i.e. whether the analysis is performed at an individual trait level or for groups, based on the co-occurrence of traits (Lavorel et al. 1997). A major difference between these approaches lies in how they account for the relationship between plant traits and environmental variables (Lavorel et al. 1997). Most studies using a trait-based approach search for a community response to an environmental gradient, but few have directly related traits to the environment. The most frequently encountered trait-based approach is based on groups of species sharing similar traits (emergent groups *sensu* Lavorel et al. 1997) that are not directly related to an environmental gradient. Trait-based approaches are said to be "direct" when plant traits are related directly to environmental variables by simultaneously analysing three matrices (abundance or presence – absence of species, their traits and the environmental variables), or "indirect", when the species and traits matrices are linked in a first step and related in a second step to the environmental gradient (Dray & Legendre 2008).

Trait-based approaches were used in the present study to obtain a synthetic view of the diversified plant community that developed during old-field succession. Since abandoned farmlands are considered a transitional stage, the vegetation composition varies greatly both in terms of species traits and in time and space, from herb-dominated communities to communities dominated by shrubs and pioneer trees (Benjamin et al. 2005). The pressure to convert these lands into other uses begets the question of their ecological value and their potential to develop into a functional forest ecosystem.

Two different trait-based approaches were compared in this study. First, emergent group analysis (EG) identified groups of species that share similar traits (Lavorel et al. 1997). This has been widely used to study ecosystem responses to human-induced changes (e.g. Verheyen et al. 2003). Second, a direct functional approach was attempted at the trait level, using a new version of the fourth-corner method (Legendre et al. 1997). When first developed, this latter method was based on presence-absence species data. A new version (Dray & Legendre 2008) allows the use of species abundance data. The new computer program allows testing for the significance of the relationship between all species traits and all environmental variables in a single step. Our primary goal was to compare the performance of the two approaches for linking plant functional traits to ecological succession. Although these two trait-based approaches differ in how they account for the relationship between plant traits and environmental variables (Lavorel et al. 1997), they have never been used on the same data set. We evaluated their limits and benefits, as well as comparing the type and precision of the information they produce. This type of comparison is very important for improving our insights into the robustness and utility of various trait-based approaches. Using the characterization of trait responses via these two approaches, we evaluated the potential for natural restoration of abandoned agricultural land, asking the question: to what extent does the understorey flora recover on former pastures?

Methods

Study area

The study was conducted in the Upper St. Lawrence Regional County Municipality (45°01'-45°08'N; 73°58'-74°21'W) of southern Quebec, Canada. The area is within the deciduous forest of the Great Lakes-St. Lawrence River forest region (Rowe 1972). The regional mean annual temperature is 5°C, precipitation ranges from 900 to 1000 mm, and the mean annual growing season typically lasts between 190 and 200 days (Robitaille & Saucier 1998).

European settlement in the 19th century brought intense forest exploitation to the region, first for wood and potash production, and subsequently for agriculture (Simard & Bouchard 1996; Domon & Bouchard 2007). As in many other agricultural regions of eastern North America, the traditional rural landscape changed during the 20th century towards intensified agriculture, resulting in the progressive abandonment of many agricultural fields (Bouchard & Domon 1997; Domon & Bouchard 2007). With time, vegetation that developed on these abandoned lands created a patchwork of various field and forest types (Meilleur et al. 1994; Pan et al. 1999).

Current and historical land uses are closely associated with geomorphological characteristics. Superficial deposits originated from the post-glacial

Champlain Sea; they comprise two major types: (i) moraine-type deposits in islets and ridges with stony soils, principally covered by forests and abandoned old-fields; and (ii) nutrient-rich marine clays, principally in low lying areas that are covered by agricultural fields (Domon & Bouchard 2007). Mature mesic forests are generally dominated by *Acer saccharum* in association with *Carya cordiformis*, *Ostrya virginiana*, *Tilia americana* and *Fagus grandifolia* (Bouchard & Brisson 1996). Young forests that developed after abandonment are dominated by *Betula populifolia*, *Populus tremuloides*, *Fraxinus* spp., *Acer rubrum* and *Ulmus americana* (Brisson et al. 1988; Meilleur et al. 1994).

Study plots

Protracted agricultural abandonment resulted in stands at different successional stages that co-occur throughout the study area, ranging from active pasture to secondary forest, which provide a chronosequence that allows the study of natural revegetation. Five successional stages of the tree stratum were chosen, based on the following structural and biological criteria: (PA) active pasture stands where cattle are still present; (LS) stands dominated by low shrubs (< 1.5 m), where pasture activity has been abandoned (10-25 years old); (TS) stands dominated by tall shrubs, where a relatively closed shrub and tree sapling canopy < 8-m high has developed (23-39 years old); (YT) young tree-dominated stands with a fully developed canopy $\geq$ 10-m high (28-60 years old); (MA) mature second growth forest with a canopy > 25-m high, composed of species characteristic of mature mesic forests (> 100 years old).

Six stands, representing each of the five stand stages, were selected for a total of 30 stands. Shrub stands were chosen based on the work of Benjamin et al. (2005), while selection of mature forests was based on the work of Carignan (2005). Young tree stands were identified based on the work of Delage et al. (2005). Six active pastures were chosen in the vicinity of these stands. All stands contained old barbed wire, indicating past agricultural use. We did not detect any evidence of ploughing as no stone piles were found; rocks and pit-mounds were visible in the ground. We thus considered that these stands had never been ploughed with modern heavy machinery. Year of land abandonment and recent land-use history was later validated through aerial photograph interpretation (1964-1966, 1975-1983) and by meeting private landowners (see Table 1, where the main characteristics of the study stands are described).

We set up a 25-m radius plot at the approximate centre of each stand. All plots were located at least 25 m away from roads, and between 25 and 300 m from adjacent mature forest. All stands were on flat ground at similar elevations and on morainal deposits. They all had stony soil and good drainage (Benjamin et al. 2005).

Field sampling

We determined floristic composition using linear vegetation surveys. In each plot, 13 circular points (15-cm radius) were systematically sampled along four 25-m transects for a total of 52 points per plot. Herbaceous and woody species within a sampling point were assigned an occurrence value of 1, with a possible total score of 52 when a species was present at all points. Species present in the plot but not in any of the sampling points were assigned an occurrence value of 0.5. The frequency of occurrence (%) for a species was determined as the

Table 1. Characteristics of the study plots. A different letter indicates a significant difference at $P < 0.05$ (one-way ANOVA followed by Tukey tests). und.:understorey; [‡]% PPFD: percentage of above-canopy photosynthetic photon flux density.

Stand	Class	Understorey stratum		Understorey environmental conditions					
Code	age (years)	Mean und. height (cm)	Richness	% PPFD[‡] at 200 cm/soil level	Substrate type (%)				
					Grass	Leaves	Mineral soil	Rock	DWD
Active pasture									
PA	0	36	34[d]	100.0[a]/100.0[a]	70[a]	0[c]	26[b]	4	0[d]
Low shrub-dominated stand									
LS	10-25	117	64[b]	93.2[b]/31.7[b]	71[a]	8[c]	16[c]	2	3[c]
Tall shrub-dominated stand									
TS	23-39	356	73[a]	29.2[c]/4.7[c]	35[b]	14[c]	37[a]	4	10[b]
Young tree-dominated stand									
YT	28-60	368	68[b]	5.6[d]/2.2[cd]	2[c]	47[b]	21[bc]	5	25[a]
Mature forest									
MA	~100	314	45[c]	2.1[e]/1.2[d]	0[c]	83[a]	5[d]	3	9[b]

proportion of points in the plot where the species was present. All woody species with a DBH < 5 cm and a height < 5 m were included. The plots were sampled three times from May to September 2003 to obtain data for all species present during the growing season. For logistical reasons, species within the families Poaceae and Cyperaceae, and in the genus *Crataegus* were not identified to species.

To characterize the understorey environment, we quantified light availability and soil cover substrate for the 52 sampling points in each plot. The percentage of above-canopy photosynthetic photon flux density (% PPFD) was measured both at ground level and 2 m aboveground (but the understorey is > 3 m in some stages see Table 1), using a line quantum sensor (LI-COR, Lincoln, NE, USA). Light measurements were taken under a completely overcast sky following the methods of Messier & Puttonen (1995), and Gendron et al. (1998). We used the following categories of soil cover substrate types: grasses, herbs, deciduous shrub or tree leaf litter, conifer needles, mineral soil, rock and downed woody debris. The frequency of occurrence (%) of each substrate type was determined as the proportion of points in a plot where that substrate type was present.

Species ecological traits

Information on the species ecological traits was obtained from the TOPIQ data base (Traits Of Plants In Quebec, see Aubin et al. 2007). Eleven categorical traits and two quantitative traits were used (Table 2).

Data analyses

Two different trait-based approaches were used in the study: a two-step approach, referred to as emergent group analysis; and a direct functional approach, referred to as fourth-corner analysis.

Indirect functional approach – Emergent group analysis

The first step was to delineate emergent groups (EG) from the biological trait matrix using classification methods. EG were identified separately for the woody and herbaceous species following the hierarchical approach suggested by McIntyre et al. (1999), which was used by Deckers et al. (2004). Classes of traits not present in any of the woody species (indicated with an asterisk in Table 2) were omitted from their classification. Raunkiaer's phanerophyte forms and foliage structure were omitted for the herbaceous species classification. Gower's

Table 2. Plant biological traits compiled from the literature. *Omitted in analysis of the woody species subset of EG groups. †For the seed dispersal vector, a species can have more than one class;

Trait	Code	Description
Raunkiaer life form	RA	mg: mega- or meso-phanerophyte (≥ 8 m in height); mc: micro- or nano-phanerophyte (25 cm-8 m); ch: chamaephyte (herb or shrub, bud between 1 mm and 25 cm aboveground)*; 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	REP	1: seeds only; 2: vegetative propagation possible but mostly by seeds; 3: mostly by vegetative propagation
Foliage persistence	PFO	0: no; 1: yes
Foliage structure	SFO	For phanerophytes: m: one stem; mu: multi-stemmed; vi: vine 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-autumn *
Colour of chasmogous flower	CFL	w: white; g: unattractive (green or brown); b: bright (red, yellow or blue); na: not applicable
Seed dispersal vector†	DI	w: wind (anemochorous); ez: mammal (zoochorous); mammal, carried externally (epizoochorous)*; an: insect, mostly ant (myrmecochorous)*; bi: bird ingestion (avichorous); hd: human dispersal: (anthropochorous)*; ex: ballast or explosive discharge (ballistichorous)*
Seed size	SE	quantitative variable: 0.05-40 mm
Height	HT	quantitative variable: 10-3500 cm
Light requirement	LI	s: shade tolerant; m: mid-tolerant; i: intolerant
Status in Quebec	ST	0: native; 1: exotic

similarity coefficient (Gower 1971; we used the form of the coefficient that excludes double zeros from the comparison) was calculated for the woody and herbaceous subsets. This coefficient can handle both missing values and mixed data types (Legendre & Legendre 1998, Chapter 7). Ward's hierarchical classification method was used to cluster species,

based on these similarity matrices. The cut-off limit for defining clusters was determined subjectively after visual screening of the dendrogram using our botanical knowledge. To assess the impact of the number of groups on the results, two cut-off levels were chosen for the herbaceous species subset.

The second step required assessing EG differences among stand stages. We examined the relative occurrence of EG in different successional stages using a matrix of the species group occurrences, which was calculated as the product of the transposed species data matrix (253 species×30 plots, with percentage occurrence data of each species) by the binary matrix of emergent groups (253 species×13 or 15 EG, depending on the cut-off level). This new matrix (30 plots×13 or 15 EG) was then standardized by dividing the occurrences of each group by the total occurrence for all groups in each plot. Differences in the relative occurrences of the species groups among stand stages were analysed using one-way ANOVA, followed by Tukey tests when significant effects of stand stages were detected. A correction for multiple tests was done; only the relationships that remained significant after Holm's (1979) correction were considered ($P \leq 0.05$).

Direct functional approach at the trait level – Fourth-corner analysis

We used a new version of the fourth-corner analysis and program (Legendre et al. 1997) to assess how individual species traits were related to stand stages. In this new version (Dray & Legendre 2008), quantitative data can be used in the species data matrix, instead of presence-absence as intended in the original paper and program (Legendre et al. 1997). Fourth-corner analysis directly relates an **R** matrix of environmental variables to a **Q** matrix of species traits, by way of an **L** matrix of species occurrences measured in the field; the matrices **R**, **Q** and **L** (Dray & Legendre 2008) were originally designated **B**, **C** and **A** by Legendre et al. (1997). The analysis allows statistical tests of the significance of the links between all combinations of species traits and environmental variables to be carried out. The results of this analysis constituted the fourth-corner, in which the global statistic is denoted $\mathbf{S_{RLQ}}$ by Dray & Legendre (2008). A statistic is computed for each pair of environmental variables and species traits. Its definition depends on the mathematical type of both traits: (1) a squared correlation coefficient (r^2), if both traits are quantitative; (2) a Pearson χ^2 statistic divided by the sum of the abundances in Table L, if both traits are qualitative (based on a contingency table, each entry corresponding to the states of the two traits); and (3) a correlation ratio (η^2) if one variable is

qualitative and the other is quantitative, defined as the among-group sum-of-squares (groups denoted by the states of the qualitative variable) divided by the total sum-of-squares. A global statistic can also be calculated that links the complete matrix **R** and **Q**; this statistic is the sum of all r^2, Pearson χ^2 and η^2 values in the fourth-corner matrix (denoted $\mathbf{S_{RLQ}}$). The significance of all fourth-corner statistics can be tested using the permutation models presented in Dray & Legendre (2008).

In our study, the environmental matrix (**R**) contained the five successional stand stages coded 0 or 1. The species trait matrix contained the variables described in Table 2. The pairwise statistics reported in the Supporting Information, Table S2, comparing successional stages to species traits, are Pearson correlation coefficients for quantitative traits.

Five models of permutation (i.e. ways of permuting **L** at random), following five different ecological hypotheses, are presented in Dray & Legendre (2008). Here, we used their model 1, where the cell values were permuted within the columns of **L**. This model tests the null hypothesis, that the species are randomly distributed with respect to characteristics of the sites. The alternative hypothesis states that individuals of a species are distributed according to their environmental preferences. This corresponds to our data, as there are strong environmental gradients along succession (e.g. light) that regulate the species assemblages.

The probabilities resulting from the tests of significance of all statistics in the fourth-corner matrix were adjusted for multiple testing using Holm's procedure (1979). Before analysis, a Hellinger transformation (for details, see Legendre & Gallagher 2001) was applied to the species occurrence data table to adjust for the effect of decreasing occurrences along successional stages.

The analyses were carried out using the R 3.0 package (Casgrain & Legendre 2005) and the XLStat program (Addinsoft 2006). The 'fourthcorner2' R function of the 'fourthcorner' package, available from http://www.biomserv.univ-lyon1.fr/~dray/software.php, was used for fourth-corner analyses.

Results

Species richness

Of the 253 species recorded in the studied old-fields, 190 were herbaceous and 63 were woody. Species richness was highest in mid-successional stages, the tall shrub-dominated stands possessing

the highest richness (73, Table 1). Thirty-three forest herb species that were described as typical of maple forests by Dansereau (1943) were found in our mature stands (see Supporting Information Appendix, Table S1). Of these 33 forest herbs, ten species were unique to mature forests. *Circea lutetiana, Sanguinaria canadensis, Smilacina racemosa* and *Trillium grandiflorum* were found in all stand stages, except active pastures. *Erythronium americanum* was found in all stand stages, including one active pasture (Supporting Information, Table S1).

Emergent group identification

Cluster analysis revealed four groups for the woody species and seven for the herbaceous species, both at a cut-off level $S = 0.82$. Woody species groups (Table 3a) were characterized by the following traits: (group W1; $n = 11$) tall phanerophytes, reproducing by large seeds that are mainly dispersed by mammals (zoochorous); (W2; $n = 22$) wind-dispersed (anemochorous) phanerophytes; (W3; $n = 22$) short, mid- or shade-tolerant multi-stemmed phanerophytes, producing seeds that are mainly dispersed by birds (avichorous), a fairly large proportion of these species possess physical defences (e.g. thorns); (W4; $n = 8$) summer flowering bird-dispersed phanerophytes, mainly vines.

For herbaceous species (Table 3b), the following traits characterized the groups: (group H1; $n = 41$) exotic shade-intolerant summer flowering species, with erect leafy stems or a rosette form, dispersed by wind or mammals (this group contains all the biennials; (H2; $n = 16$) annuals that possess traits similar to H1, but composed of both native and exotic species; (H3; $n = 27$) other summer flowering native perennials, with erect leaf stems or a decumbent form that are dispersed mainly by mammals, with many species possessing physical defences; (H4; $n = 28$) tall summer or late flowering native perennials dispersed by wind; (H5; $n = 16$) ferns and allies that have distinct biological traits, along with other shade-tolerant species with very small seeds; (H6; $n = 29$) shade-tolerant, spring flowering native perennials dispersed by mammals; and (H7; $n = 33$) short, spring flowering native perennials mainly dispersed by gravity (barochorous) or ants (myrmecochorous).

To test the robustness of this classification, we selected a second cut-off level for the herbs at a similarity level of 0.72. This limit resulted in nine groups (Table 3b). After a visual screening of the dendrogram based on our botanical knowledge, this classification was considered to provide another ecologically interesting choice. The group of exotic species (H1) was thus split into: (H1a; $n = 21$) short exotics mainly dispersed by mammals, and (H1b; $n = 20$) tall exotics dispersed by wind. Spring flowering, short perennials (H7) were split into: (H7a; $n = 18$) wind- or gravity-dispersed species, comprising light-demanding hemicryptophytes, many of which are exotics or have persistent foliage; and (H7b; $n = 15$) ant-dispersed species, comprising native, short shade-tolerant or spring ephemeral geophytes with a variety of shapes.

Table 3a. Classification by species group of woody species having similar biological traits computed from a cluster analysis using the biological traits data matrix ($n = 63$). Cut-off limit at $S = 0.82$. See Table 2 for code definitions. Codes in parentheses indicate that this class is present but at lower proportion. Sp: characteristic species.

Traits	Tall mammal-dispersed phanerophyte W1	Wind-dispersed phanerophyte W2	Short bird-dispersed multi-stemmed phanerophyte W3	Summer flowering bird-dispersed phanerophyte W4
RA	mg	mg, (mc)	mc	mc, mg
REP	2	2 (3)	3, 2	3
PFO	(1)	0	0	0
FPH	sp	sp	sp	su
SFO	m	m, (mu)	mu	(vi)
CFL	–	–	–	w, g
DEF	0	0	(1)	0
DI	ez, (bi, w)	w	bi, (ez)	bi
LI	–	–	m, s	(m)
ST	0	0	0	0
HT	2336	1948	471	1025
SE	13.9	5.3	4.4	4.7
Sp	*Carya cordiformis*	*Acer saccharum*	*Cornus sericea*	*Celastrus scandens*
	Pinus strobus	*Ostrya virginiana*	*Corylus cornuta*	*Rhus typhina*
	Thuja occidentalis	*Ulmus americana*	*Dirca palustris*	*Vitis riparia*
n	11	22	22	8

Table 3b. Classification by species group of herb species having similar biological traits computed from a cluster analysis using the biological traits data matrix ($n = 190$). Cut-off limits at $S = 0.82$ and $S = 0.72$. See Table 2 for code definitions. Codes in parentheses indicate that this class is present but at lower proportions. Sp: characteristics species.

Traits	Exotic H1	At S = 0.72		Annual H2	Summer flowering perennial H3	Late-flowering wind-dispersed perennial H4	Ferns and allies H5	Spring flowering mammal-dispersed perennial H6	Spring flowering gravity- or ant-dispersed perennial H7	At S = 0.72	
		Short exotic dispersed by mammals H1a	Wind-dispersed tall exotic H1b							Wind- or gravity-dispersed hemicryptophyte H7a	Ant-dispersed geophyte H7b
RA	h	h	h	t	h	h	h, g	g, h	h, g	h	g (h)
PER	3 (2)	3	2, 3	1	3	3	3	3	3	3	3
REP	–	3 (2)	1 (3)	1	–	3	3	3	3	3	3
PFO	0	0	0	0	0	0	(1)	0	0	(1)	0
FPH	su	su	su	su	su	su, sf	su	sp	sp	sp	sp
SFO	(r, el)	r, el, de	r (el)	el, (r)	el, de	el, (r)	e	–	–	r (el, de)	–
CFL	b	b (w)	b	w, b	w, b	w, b	na	–	b, w	b (w)	b (w)
DEF	0	0	(1)	0	(1)	0	0	0	0	0	0
DI	w, ez	(ez)	w	–	(ez)	w	w, ex	ez (bi)	(an)	g (w)	an (ex)
LI	i	i	i	i	–	(i)	(s)	s	–	–	s (m)
ST	1	1	1	(1)	0	0	0	0	0	(1)	0
HT	110	71	152	156	122	156	67	102	46	5.5	35
SE	2.6	1.8	3.5	1.9	2.3	1.9	<0.1	3.2	2.2	1.8	2.6
Sp	Hypericum punctatum Nepeta cataria Rumex crispus		Cichorium intybus Hieracium caespitosum Lactuca serriola	Chenopodium album Erigeron strigosus Erysimum cheiranthoides	Rubus alleghaniensis Rubus idaeus Verbena urticifolia	Aster novae-angliae Solidago canadensis Solidago rugosa	Adiantum pedatum Demnstaedtia punctilobula Dryopteris marginalis	Arisaema triphyllum Medeola virginiana Smilacina racemosa		Aquilegia canadensis Stellaria graminea Veronica serpyllifolia	Asarum canadense Sanguinaria canadensis Trillium grandiflorum
n	41	21	20	16	27	28	16	29	33	18	15

Responses of emergent groups to stand stages

Except for the summer flowering perennials (H3) and the spring flowering short perennials (H7), all EG varied significantly in their proportions among stand stages (Table 4). Exotics (H1), annuals (H2) and spring flowering mammal-dispersed perennials (H6) had decreasing relative occurrence from active pasture to mature forest. Ferns (H5) and tall phanerophytes (W1, W2) increased in occurrence with stand stage. Late flowering wind-dispersed perennials (H4) had their highest relative occurrence in the two shrub stages, while short, bird-dispersed multi-stemmed phanerophytes (W3) and summer flowering, bird-dispersed phanerophytes (W4) had their highest occurrences in the tall shrub and young tree stages.

In the nine-group classification of the herbaceous subset (Table 3b), the two exotic subgroups, H1a and H1b, showed similar trends across the chronosequence, with decreasing relative occurrence from active pastures to mature forests (Table 4). In contrast, the two spring flowering subgroups, H7a and H7b, had a different response to stand stages. Relative occurrence of the wind- or gravity-dispersed subgroup H7a decreased significantly among stand stages, while the relative occurrence of the ant-dispersed subgroup H7b increased significantly (Table 4).

Table 4. Mean relative occurrences of emergent groups among stand stages. PA: active pasture; LS: low shrub; TS: tall shrub; YT: young tree; MA: mature forest. $*P \leq 0.05$; $**P \leq 0.01$; $***P \leq 0.001$; $-P > 0.05$. For each emergent group (row), a different letter indicates a significant difference at $P < 0.05$ (one-way ANOVA followed by Tukey tests). Detailed descriptions of the groups are given in Table 3.

EG	P	PA	LS	TS	YT	MA
H1	***	40.2a	32.7b	11.5c	4.8d	1.8d
H1a	***	30.7a	25.1b	8.8c	3.6d	1.1d
H1b	***	9.5a	7.6b	2.7c	1.2d	0.7d
H2	***	10.6a	2.6b	1.0c	0.3c	0.3c
H3	-	3.9	6.8	7.5	6.9	5.0
H4	***	6.9d	18.4b	20.2a	12.8c	3.5e
H5	**	0.0b	0.0b	0.1b	5.0a	0.5b
H6	***	22.3a	17.2b	14.4c	9.7d	6.1e
H7	-	14.6	8.6	11.8	7.2	14.7
H7a	***	14.3a	7.6b	7.0b	2.8c	2.0c
H7b	***	0.3c	1.0c	4.8b	4.4b	12.7a
W1	***	0.0c	0.9b	1.3b	4.1a	4.8a
W2	***	0.2d	1.3d	6.4c	20.8b	50.5a
W3	***	1.1d	9.4c	21.0a	22.3a	11.1b
W4	***	0.1d	2.0c	4.6b	6.0a	1.7c

Directly relating species ecological traits to stand stages

Based on the fourth-corner analysis, the relationship between stand stages and species ecological traits was significant for most traits (Table 5). Seed size and plant height significantly increased along the chronosequence. A clear shift along the chronosequence was also observed for light requirement,

Table 5. Synthesis of the results of the fourth-corner analysis, in which successional stages are related to species traits (see Supporting Information, Table S2 for details). For significant relationships at the 5% significance level after Holm correction, the sign indicates if the statistic is above (+) or below (−) the expected value (mean of the permutation results). Blank: non-significant relationship. PA = active pasture; LS = low shrub; TS = tall shrub; YT = young tree; MA = mature forest.

Traits	Code		PA	LS	TS	YT	MA
Raunkiaer life form	RA	mg	−	−	+	+	
		mc	−		+	+	−
		ch			+		−
		h	−	+	+		−
		g	−	−	−	+	+
		t	+				−
Life cycle	PER	1	+				−
		2		+		−	−
		3	−	+	+	+	−
Means of reproduction	REP	se		+			
		ms	−		+	+	−
		ve	−	+	+	+	−
Foliage persistence	PFO	1					
Foliage structure	SFO	ms	−	−	+	+	
		mu	−		+	+	
		r		+		−	−
		g					
		e	−			+	
		el	−	+	+		−
		de					−
		um	−	−	−		+
		vi	−		+	+	−
		nl			+		
Physical defences	DEF	1					
Flowering phenology	FPH	sp	−	−	+	+	
		su	−	+	+		−
		sf	−	+	+		−
Colour of flower	CFL	w	−		+	+	
		g	−		+	+	
		b	−	+	+		−
		na	−			+	
Seed dispersal vector	DI	ez					
		hd	+	+			−
		bi	−		+	+	−
		w					
		an	−				+
		ex					
Seed size	SE		−				+
Height	HT		−	−		+	+
Light requirement	LI	i		+	+	−	−
		m	−		+	+	−
		s	−	−		+	+
Status in Quebec	ST	1	+	+		−	−

life cycle and plant form. The statistically significant ecological profile of species in active pastures was: short exotic herbs, mainly annuals, with by small seeds dispersed by humans (anthropochorous). For the low-shrub stage, a positive correlation was found for short summer or late summer, bright flowering biennial or perennial hemicryptophytes that had a rosette or erect leafy stem shape, were exotic, and were light demanding and mainly anthropochorous. For the tall-shrub stage, a positive correlation was found with perennial mid-tolerant or light-demanding hemicryptophytes, phanerophytes or chamaephytes, with a tree, shrub, vine or erect leafy stem foliage structure. Species in the tall shrub stage were mainly dispersed by birds and could propagate vegetatively. Species in the young tree stage were native mid- or shade-tolerant spring flowering perennials, which were mainly phanerophytes or geophytes with a tree, shrub, vine or erect leaves foliage structure and mainly dispersed by birds. Saprophytes were only found in this last stand stage. Species traits that were associated with the mature forest stage were native, shade-tolerant geophytes with umbel-shaped foliage structure and seeds dispersed by ants.

Discussion

Traits associated with the different developmental stages

Clear patterns of trait associations with stand developmental stages emerged from both the emergent group (Table 4) and the direct approach at the trait level (Table 5). Both approaches found that short-lived rosette-shaped species with small seeds were associated with active pastures and low-shrub stages, which corroborates the results of other studies conducted in the Mediterranean biome (e.g. Lavorel et al. 1998). Many of these species were exotics. With the fourth-corner trait-level analysis, shifts in seed size, light requirement and plant form and height were clearly observed along the chronosequence, while these patterns were not obvious in the emergent group classification.

In our study, canopy closure led to a sharp decrease in light availability, a decrease in grasses, and an increase in bare soil and leaf litter substrate (Table 1), conditions that provided some advantage to forest herbs (Collins et al. 1985; Facelli & Pickett 1991). Accordingly, at the trait level we found an increasing proportion of mid-tolerant species in the tall shrub stand stage. This mixture of shrubs and tree saplings increased the structural complexity of the vegetation, thereby creating variability in environmental conditions and favouring floral diversity. In addition, many of these shrubs bore fruits that are attractive to birds (e.g. *Crataegus*), and therefore may aid in the introduction of forest bird-dispersed species, such as *Smilacina racemosa* and *Actea* spp. Hence, the direct approach found that the large seeds dispersed by birds were positively associated with this stand type, and similar to the woody species dispersed by birds for the emergent group approach.

Analysis at the trait level revealed that traits associated with our sampled second-growth mature maple forests (shade-tolerant geophytes dispersed by ants) were equivalent to those reported for natural unmanaged forests or ancient forests (Froborg & Eriksson 1997; Verheyen et al. 2003). For the emergent group approach, a group with a similar set of traits was clearly associated with mature forest for the nine-group classification, although this was not the case for the seven-group classification. Aubin et al. (2007) compared such second-growth forests on abandoned pasturelands with old-growth forests, and found that they possess a similar understorey assemblage, although this was slightly impoverished in spring geophytes and ferns.

Comparison of indirect and direct trait-based approaches

Our simultaneous use of two different trait-based approaches provided a robust and comprehensive characterization of vegetation responses in the old-field – deciduous forest chronosequence. It also highlights the different objectives of these two approaches. Below we discuss their usefulness, limitations and benefits.

Indirect functional approach – emergent group analysis

Emergent groups provided an easy method to construct an objective classification of the flora according to its biological traits. Each group was composed of species sharing a similar set of traits that could be associated with a similar life history strategy (Lavorel et al. 1997). The main utility of emergent group classification is to allow independence from taxonomy and to provide a synthetic portrait of the plant communities. This approach was particularly suited for identification of a functionally coherent group of indicator species. However, by themselves, the emergent groups

were purely descriptive and did not provide information on vegetation processes or ecosystem changes. A second step of analysis was necessary to relate these groups to an environmental gradient.

Although easy to implement, a relevant emergent group classification is not in itself an easy task to accomplish. Choice of a relevant list of traits has remained a major issue for functional classification (Kleyer 1999; Pillar 1999; Weiher et al. 1999). A consensus is emerging on a standardized worldwide shortlist of traits, which are closely related to vegetation responses to major environmental gradients (Cornelissen et al. 2003). In our study, a lack of knowledge regarding the biological traits of many forest herbs greatly reduced the significance of the identified pattern. Until now, a large majority of trait-based studies around the world have used "soft traits" (i.e. easily measured; e.g. dispersal mode and seed mass) as surrogates for "hard traits" (*sensu* Hodgson et al. 1999; e.g. dispersal distance). Analysis based on hard traits would be more closely related to ecosystem properties, but these traits are still inaccessible for most species (Cornelissen et al. 2003).

A major criticism of functional classifications related to the above question is the correlation among traits (Kleyer 1999; Lavorel et al. 1999). For the emergent group approach, correlation among traits may influence group determination. As Kleyer (1999) suggested, traits that are important for ecosystem functions may not have sufficient weight in cluster analysis. The more complex relationships between emergent groups and ecosystem processes (Kleyer 1999), or phylogeny (Chazdon et al. 2003), are further problems that have been encountered in developing emergent group classifications, and may further complicate their ecological interpretation.

Emergent groups may be too general and thus hide trait-level differences. In our study, fourth-corner analysis showed a shift in seed size, light requirement, plant form and height along the chronosequence, which was not easily revealed by emergent group classification. Additionally, the contrasting results obtained with a seven- or nine-group classification of the herbaceous subset illustrated how critical the number of groups is for emergent group classification (Table 3b). Choosing seven groups, rather than nine, would have hidden the response of a well-known and sensitive group – the spring flowering ant-dispersed geophytes (H7b); otherwise, this group would have been merged with the spring flowering, wind- or gravity-dispersed hemicryptophytes (H7a). Although possessing similar traits, these two closely related groups of short stature, spring flowering, short-dispersal perennials responded in vastly different ways to succession (Table 4). The latter group (H7a) contains both open-field exotics (e.g. *Veronica serpyllifolia*) and native forest herbs (e.g. *Coptis groenlandica*), but the ant-dispersed former group (H7b) is composed of herbs that Dansereau (1943) described as characteristic of maple forests, including *Asarum canadense* and species within the genus *Viola*. One could argue that the number of groups might only have a small impact on the results if we assume that closely related groups, in sharing similar traits, share a similar response to an environmental gradient. However, such an assumption must be regarded with caution, as it did not apply in our study.

Although arbitrary, visual screening of the cluster diagram has remained the most common method to delineate the final partitioning. Statistical methods such as the efficiency criteria of Legendre & Legendre (1998) exist but are rarely used. The final number of groups in emergent group classification must be based on sound botanical knowledge. While the number should be small enough to provide a synthesis of the information, ecologically relevant information may be lost if the classification is too coarse.

Direct functional approach at the trait level – fourth-corner analysis

The new direct functional approach directly related plant traits to environmental variables in a one-step analysis. By allowing simultaneous analysis of three matrices, direct functional analysis can offer new possibilities for plant community studies. To our knowledge, three such methods have been independently developed: RLQ analysis (Doledec et al. 1996), double CCA (Lavorel et al. 1998) and fourth-corner analysis (Legendre et al. 1997). Direct functional analysis is a recent development and not widely known among ecologists. The first two methods are quite complex to use and, in its original form (Legendre et al. 1997), the fourth-corner method could only deal with presence-absence data in the species data matrix. This problem has been solved in the new version of the method and program proposed by Dray & Legendre (2008). The fourth-corner method has the distinction of producing statistical tests for the significance of links between all combinations of species traits and environmental variables in a correlation-type analysis. The higher the statistical significance (smaller *P*-value), the stronger the link between species trait and environmental variable. An exhaustive and

precise analysis of the relationship between a species trait and an environmental variable can thus be obtained, helping ecologists to identify the relative importance of specific traits.

However, at this time, fourth-corner analysis does not provide the possibility of developing groups of species (which would be response groups *sensu* Lavorel et al. 1997). This analysis also has to consider the question of trait selection. In fourth-corner analysis, a correlation among traits may also lead to misinterpretation. For example, if two species traits are strongly correlated, and one is related to a specific environmental variable, these two traits will be assessed as strongly correlated to that environment variable in fourth-corner analysis. This has the effect of greatly inflating the value of the general statistic (sum of all $S_{RLQ}s$) and could lead to higher Type-I error in some permutation models (i.e. models where the link between L and Q is broken when L is permuted). This has not been thoroughly studied; therefore further work needs to be done to assess the outcome in such a situation. The solution to this problem is to carry out a correlation analysis of the species traits and eliminate redundant traits prior to the fourth-corner analysis.

The new fourth-corner analysis needs to be tested and utilized with a wider variety of situations and data to improve its usefulness and efficiency. It still has many unexplored applications for major questions in community ecology, and for studies at the landscape or biome scale. It provides a mechanistic understanding of how traits vary along relevant environmental gradients. It is also a simple and efficient starting point to establish general rules, and pinpoint key functional traits, based on their links to environmental characteristics. Such traits should have stronger predictive power when used in models. The fourth-corner analysis, for instance, could be use as a starting point for prioritizing factors (traits or environmental variables) prior to analyses in a different emerging quantitative trait-based framework (e.g. McGill et al. 2006; Shipley et al. 2006; Ackerly & Cornwell 2007).

With development of knowledge in both the field of biometry and in species autecology, we believe that trait-based approaches will have increased utility in answering key questions in community ecology, such as the fundamental niche (McGill et al. 2006), and at larger scales, such as vegetation responses to global change (Lavorel et al. 2007). Work is required to make these methods more accessible to ecologists, and further research is needed to develop an ideal clustering procedure.

To what extent do forest herbs recover in former pastures?

The shift in trait dominance observed along the successional stages indicated convergence of the developing understorey community toward that of a natural forest, suggesting a strong potential for natural recovery. However, forest herb species showed a variable capacity for recovery. Our results (and particularly those at the trait level) showed the effectiveness of animal or bird dispersal for early recovery. Indeed, forest herbs with seeds dispersed by mammal ingestion (e.g. *Smilacina racemosa*) or by adhesion to animal fur (e.g. *Circea lutetiana*) were found relatively frequently in the young stand stages. Surprisingly, some spring flowering herbs with short-distance dispersal, such as *Erythronium americanum*, *Trillium grandiflorum* and *Sanguinaria canadensis*, were found to possess good recovery ability (see Supporting Information, Table S1). These species, usually adapted for ant dispersal, could have been dispersed by other mechanisms, such as occasional long-distance events or animal ingestion (Cain et al. 1998; Vellend et al. 2003). Another explanation is that hedgerows and shrub thickets could have provided shelter for these long-lived perennials (Corbit et al. 1999). Secondary forests, such as these abandoned pastures, may take a long time to fully recover. In fact, this recovery is likely to be still ongoing in 100-year-old mature forest stands of old pasture origin. Some rare herbs with poor colonization ability or with specific environmental requirements may never reestablish. However, some high-conservation value species do colonize these stands, via relict populations, occasional events or animal dispersal. These forests are thus viable habitats for native forest flora, and possibly for other ecosystem components that are closely associated with the understorey vegetation (e.g. fungi, insects and herbivores).

Conclusions

Ecologists generally use emergent groups when referring to a trait-based approach. However, such studies are most often searching for vegetation responses to an environmental gradient. In this sense, the new functional approaches that directly relate plant traits to environmental variables are far more accurate. Nevertheless, the direct approaches may have to be complemented by a search for appropriate plant functional groups. The simplicity of the statistical procedure and the possibility of classify-

ing species into groups could explain the popularity of the emergent group approach. Although some imprecision has been noted, our results have shown the effectiveness of the emergent group approach to synthesize species diversity into diversity of functions (Lavorel et al. 1997). To ensure the robustness of trait-based analysis, we believe that a combination of the two approaches is best for exploring species responses to an environmental gradient.

In our study, the trait-based approaches clearly illustrated the potential for abandoned pastures in the northern hardwood biome to develop a functional understorey. With the importance of loss of forest habitat, which has occurred in the deciduous temperate biome, conservation strategies in this region need to include the potential for these lands to recover naturally.

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Supporting Information

The following supporting information is available for this article.

Table S1. Mean occurrences and frequencies of forest herbs among stand successional stages.

Table S2. Pairwise statistics of the fourth-corner analysis, in which successional stages are related to the species traits.

Supporting Information may be found in the online version of this article.

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