RESEARCH ARTICLE

A new approach to ecological land classification for the Canadian boreal forest that integrates disturbances

Pierre Grondin · Sylvie Gauthier · Daniel Borcard · Yves Bergeron · Jean Noël

Abstract Traditional approaches to ecological land classification (ELC) can be enhanced by integrating, a priori, data describing disturbances (natural and human), in addition to the usual vegetation, climate, and physical environment data. To develop this new ELC model, we studied an area of about 175,000 km^2 in the *Abies balsamea–Betula papyrifera* and *Picea mariana*-feathermoss bioclimatic domains of the boreal forest of Québec, in eastern Canada. Forest inventory plots and maps produced by the Ministère des Ressources naturelles du Québec from 1970 to 2000 were used to characterize 606 ecological districts (average area 200 km^2) according to three vegetation themes (tree species, forest types, and potential vegetation-successional stages) and four sets of explanatory variables (climate, physical environment, natural and human disturbances). Redundancy, cluster (K-means) and variation partitioning analyses were used to delineate, describe, and compare homogeneous vegetation landscapes. The resulting ELC is hierarchical with three levels of observation. Among the 14 homogeneous landscapes composing the most detailed level, some are dominated by relatively young forests originating from fires dating back to the period centered on 1921. In others, forest stands are older (fires from the period centered on 1851), some are under the influence of insect outbreaks and fires (southern part), while the rest are strongly affected by human activities and *Populus tremuloides* expansion. For all the study area and for parts of it, partitioning reveals that natural disturbance is the dominant data set explaining spatial variation in vegetation. However, the combination of natural disturbances, climate, physical environment and human disturbances always explains a high proportion of variation. Our approach, called "ecological land classification of homogeneous vegetation landscapes", is more comprehensive than previous ELCs in that it combines the concepts and goals of both landscape ecology and ecosystem-based management.

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Introduction

In natural and human-dominated environments, the
interplay between biotic and abiotic forces creates
spatial heterogeneity. This heterogeneity generally
takes the form of a mosaic composed of patches, each
defined by specific relationships between vegetation
and environmental conditions (Jenny 1958; Whittaker
1967; White 1979; Urban et al. 1987; Legendre and
Fortin 1989; Wu and Loucks 1995; Grossman et al.
1999; Wagner and Fortin 2005). The patches, as
represented on a forest map delimiting numerous
stands, can be analyzed to define the ecological forces
(e.g., latitudinal gradient) structuring the heterogene-
ity of an area (beta diversity) (Hills 1960; Damman
1979; Zonneveld 1989; Gerardin and Ducruc 1990).
Patches can be positioned on an ordination diagram
along ecological gradients (continuum concept) and
then grouped to form homogeneous vegetation land-
scapes (community concept) (Whittaker 1967; Ahti
et al. 1968; Rowe and Sheard 1981; Zonneveld 1989;
Borcard and Legendre 1994; McGarrigal and Cush-
man 2005). A homogeneous landscape is a portion of
land with specific vegetation, physical environment,
climate, and disturbance characteristics (both natural
and human) (Rowe 1962; Daubenmire 1968; Dufrêne
and Legendre 1991). From the macro to the micro
scale, a hierarchy of increasingly homogeneous land-
scapes can be defined (Bailey 1987; Urban et al. 1987;
Allen and Hoekstra 1992; Klijn and de Haes 1994;
White and Jentsch 2001). At the macro scale, climate
is the main driver explaining vegetation distribution
(Damman 1979; Bailey 1983; Pojar et al. 1987; Allen
and Hoekstra 1992; Payette 1992; Bailey 2009).
Bioclimatic zones are at this level (Halliday 1937;
Hare 1950; Saucier et al. 2009). At the meso scale,
climate, physical features, and disturbances are con-
sidered. Finally, at the micro scale, the scale of a field
observer, microclimate, physical environment, and
disturbances are important variables (Bailey 1987;
Lertzman and Fall 1998).

Understanding the causes of spatial heterogeneity
and how they vary with scale is a central theme in
landscape ecology (Turner 1989; Turner et al. 1993;
White et al. 1999). Statistical methods have been
developed to test hypotheses about beta diversity
(Borcard et al. 1992; Legendre et al. 2005; Peres-Neto
et al. 2006; Tuomisto and Ruokolainen 2006). Ecolog-
ical land classification (ELC), a field related to
landscape and numerical ecology, aims to divide large
territories into relatively homogeneous landscapes at
different levels of observation, and to characterize the
contribution of various sets of explanatory variables to
vegetation variation. Knowledge of these patterns and
processes, and the ecological gradients creating them, is
important for ecosystem-based management and biodi-
versity conservation (Bailey 1983; Gauthier et al. 2001;
Legendre et al. 2005; Bailey 2009). Historically, ELC
has adopted two main approaches. The first approach is
based on vegetation–climate relationships and the
second on relationships between vegetation, climate,
and the physical environment (Bailey et al. 1985).

The first approach was mainly used from the
beginning of the twentieth century to the 1970s. The
aim was to identify vegetation changes on mesic soils
along ecological gradients (latitudinal, longitudinal,
altitudinal) and to associate these changes to macro-
climatic variations (temperature and precipitation).
Changes in regional (or zonal) vegetation and climate
along gradients justified the delineation of bioclimatic
units on a subcontinental scale (Halliday 1937; Hustich
1949; Hare 1950; Dansereau 1957; Rey 1960; Küchler
1964; Grandtner 1966; Ahti et al. 1968; Rowe 1972).

The second approach evolved with the influence of
geomorphology and a desire to understand ecosystem
relationships at a finer scale to help guide resource
management decision making. Using ground plots,
aerial photographs and satellite images, the physical
environment (edaphic-topographic criteria) and its
relationship with vegetation and climate were analyzed
to delineate biogeoclimatic units. These studies gener-
ally covered smaller areas (meso scale) than the
vegetation-climate approach (macro scale). From this
perspective, within homogeneous ecological units,
similar site conditions are expected to support the same
type of plant community, including the assemblage of
tree species. Together, *Betula papyrifera*, *Populus
tremuloides*, *Abies balsamea*, and *Picea glauca* consti-
tute an example of an assemblage existing on sites
with specific combinations of physical features,

microclimate, and disturbances. The early-successional stage is dominated by the light-demanding species (e.g., *B. papyrifera*) of this assemblage, which are progressively replaced in late-successional stages by shade-tolerant species (e.g., *A. balsamea*), as time since the last disturbance increases. Landscapes with high fire frequencies (e.g., <150 years) are characterized by a large proportion of area occupied by early-successional species (Bergeron et al. 2001; Gauthier et al. 2001; Couillard et al. 2012). This description of forest dynamics corresponds to the notions of potential vegetation (Küchler 1964; Powell 2000; Saucier et al. 2009), habitat type (Daubenmire 1968), site type (Hills 1960; Pojar et al. 1987), and *série de végétation* (vegetation series) (Rey 1960; Grandtner 1966).

Landscapes can be viewed as a continuum of potential vegetation assemblages along a site gradient (toposequence). Climate–site–vegetation relationships, climatic and edaphic climaxes, site potential and toposequence are key words within this second approach. (Hills 1960; Rowe 1962; Whittaker 1967; Jurdant et al. 1977; Bailey 1983, 2009). The concept of permanence comes into play in this approach, which doesn't explicitly deal with disturbances.

Although they had received some attention since the beginning of the twentieth century (Clements 1910), natural disturbances have been studied more intensively since 1970 (Heinselman 1973; Payette 1992; Turner et al. 1993; Bergeron et al. 2001). Emphasis has been placed on characterizing the spatial and temporal variability of disturbance regimes (e.g., fire frequency). These studies have demonstrated that forest landscapes are more complex and diversified than originally estimated. Dynamic equilibrium, landscape heterogeneity, and hierarchical patch dynamics are the main concepts structuring these analyses (White 1979; McCune and Allen 1985; Wu and Loucks 1995; Cleland et al. 1997; White et al. 1999; Powell 2000). ELCs were adapted to acknowledge this new approach, which assumes that vegetation is controlled mainly by climate and natural disturbances (Omi et al. 1979; Cissel et al. 1999). From this perspective emerged a landscape classification based on natural disturbance characteristics (fire) in connection with more or less stable vegetation (equilibrium). This approach was mostly applied to larger vegetation landscapes, but could also be considered at a finer scale to the dynamics of a site (Turner et al. 1993; Lertzman and Fall 1998; White et al. 1999).

More recently, human-caused disturbances have been identified as an important driver of landscape dynamics. Anthropogenic activities have altered landscape age class distribution by provoking the loss of old forests (Boucher et al. 2009; Cyr et al. 2009), and have homogenized forest composition by substantially increasing the frequency of early-successional stands on various sites along the toposequence. The relationship between vegetation and the physical environment then becomes much more diffuse than in natural environments (Carleton and MacLellan 1994; Östlund et al. 1997; Lorimer 2001; Schulte et al. 2007; Laquerre et al. 2009). However, ELCs have not yet incorporated human disturbances and are therefore missing an important driver of landscape change.

The first goal of this research is to classify the heterogeneity of the study area within a hierarchy of relatively homogeneous landscapes, on the basis of vegetation and four sets of explanatory variables (climate, physical environment, natural and human disturbances). The second goal is to quantify the proportion of vegetation variation explained by each set and their combinations for some levels of observation in the hierarchical classification.

Methods

Study area

The study region (175,000 km^2) belongs to the circumboreal zone, and forms an important part of two bioclimatic domains: the *A. balsamea–B. papyifera* in the south, and further north, the *Picea mariana*-feathermoss domain (Rowe 1972; Saucier et al. 2009) (Fig. 1). Six of the boreal zone's most common tree species are well represented. Three are shade-tolerant species: *Picea mariana* (Mill.) BSP., *A. balsamea* (L.) Mill., and *Picea glauca* (Moench) Voss. Three are light-demanding species: *Pinus banksiana* Lamb., *B. papyrifera* Marsh., and *P. tremuloides* Michx. The proportions of these species change along ecological gradients describing the climate, physical environment, and natural and human disturbances. These gradients are used to define and describe homogeneous landscapes. Human disturbances are included in the explanatory variables because some portions of the study area have been affected by anthropogenic activities for almost 100 years.
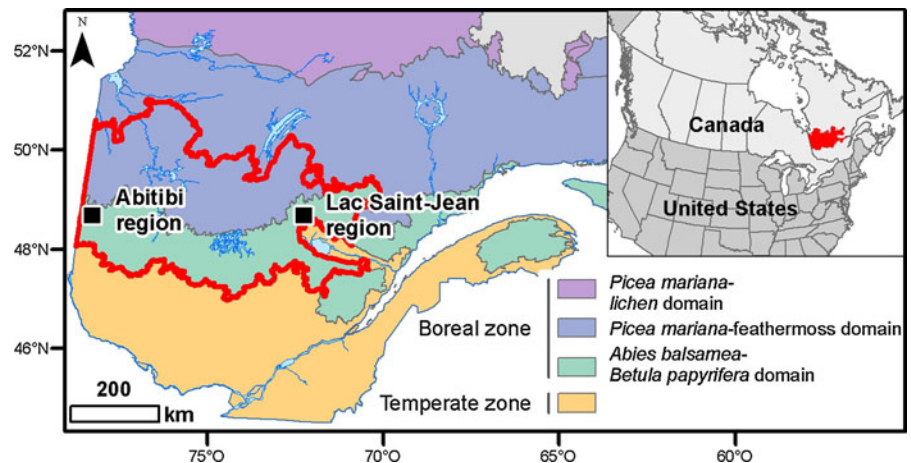
Sources of information

This study draws on two main contemporary sources
of information: forest inventory plots and geospatial
databases derived from forest maps. These databases
have been developed from Spatial Information on
Forest composition based on Tessera (SIFORT).
Forest maps from 1970 to 1980 make up the
SIFORT-1 database, and forest maps from 1980 to
1990, the SIFORT-2 database. These information
sources have been used to characterize 606 ecological
districts. The average area of the districts is 200 km^2.
Each ecological district corresponds to a uniform area
described by a specific pattern of surficial deposits,
topography, and regional vegetation (Robitaille and
Saucier 1998), and was characterized by vegetation
(Y-matrix) and explanatory variables (X-matrix).

The Y-matrix was constructed using three comple-
mentary vegetation themes, each corresponding to a
different aspect or organization level of the vegetation:
tree species (e.g., the abundance of *Pinus banksiana* as
a species in an ecological district), forest types (e.g.,
the abundance of forest stands dominated by *Pinus
banksiana*), and the combination of potential vegeta-
tion types and successional stages (e.g., Re2-S2: *Picea
mariana* potential vegetation-Re2 in the early stage of
succession-S2) (Appendix 1 in Supplementary Mate-
rial). The description of tree species and potential
vegetation-successional stages is based on forest
inventory plots (1970–2000). The SIFORT-2 database
was used to describe the forest types.

The X-matrix contains the description of the 606
ecological districts in relation to four sets of explan-
atory variables (Appendix 2 in Supplementary

Material). Climatic variables were estimated using
data recorded at meteorological stations and extrapo-
lated to each ecological district by the BioSIM
simulator (Régnière 1996). The physical environment
was characterized according to the Ministère des
Ressources naturelles (MRN) database describing each
ecological district, including the relative proportion of
area for each surficial deposit type and physiographic
variable (Robitaille and Saucier 1998). Natural distur-
bances were described in terms of the recent history of
fires, insect outbreaks, and windthrows over the last
100–150 years. Forest maps (SIFORT-2) were used to
evaluate the areas affected by light and severe
epidemics, windthrows, and fires. Forest inventory
plots (n = 53,635) were used to characterize fire
history relative to periods of origin (e.g.,
1901–1930). In this article, each of these periods is
named according to a year close to its central year (e.g.,
the 1901–1930 period is referred to as the period
centered on 1921). The number of years of infestation
by spruce budworm and the frequency of natural fires
per 100 km^2 from 1938 to 1998 were derived from
MRN archives. Human disturbances were described by
the relative proportions of agriculture, fallow land,
logging, and human-induced fires (from 1938 to 1998).
These variables were obtained from forest maps
(SIFORT-1 and 2).

Data analysis (Fig. 2)

Unconstrained analysis

An unconstrained analysis involving vegetation alone
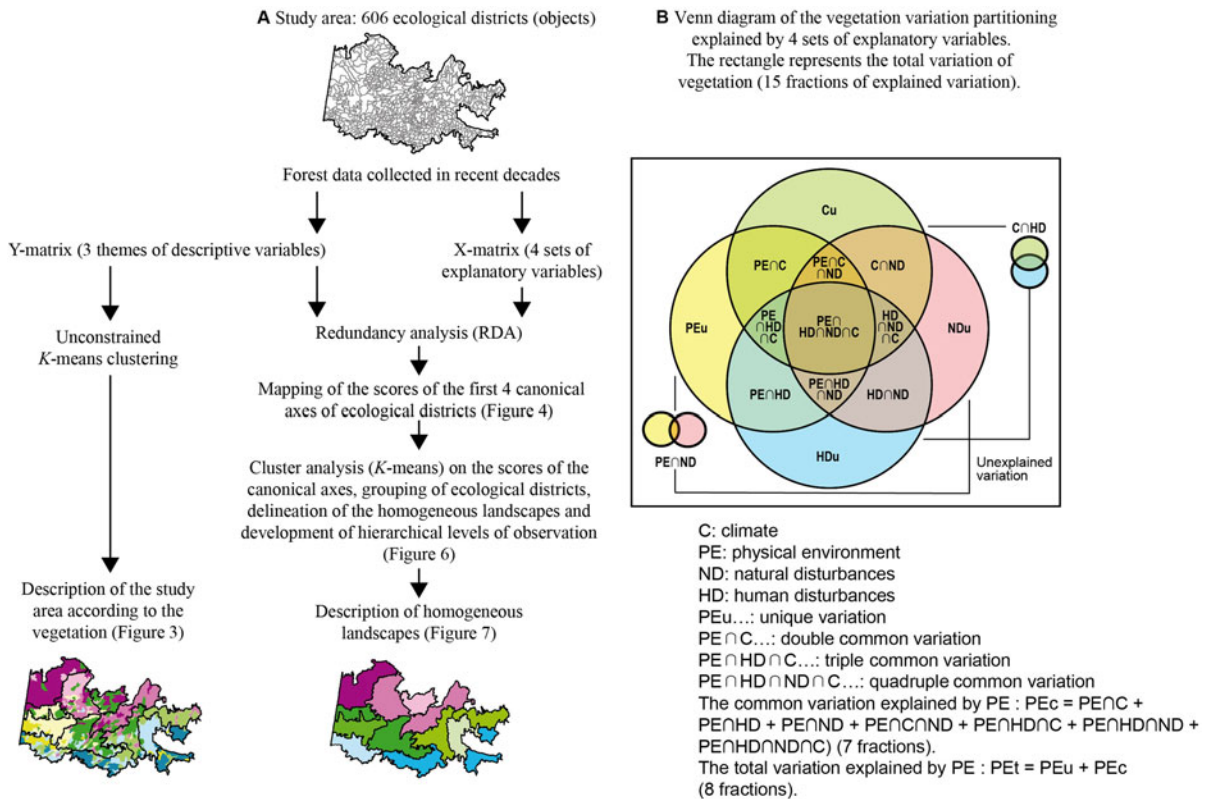was run to illustrate ELCs produced by pioneers in this

Fig. 2 Method used **a** to define the ecological land classification of homogeneous vegetation landscapes (ELCH) and **b** to quantify the proportion of vegetation variation explained by each set of explanatory variables and by their combinations

field (Halliday 1937; Dansereau 1957; Küchler 1964; Rowe 1972). This analysis was performed using the R statistical language (R Development Core Team 2010, version 2.11.1). A *K*-means clustering of the 606 districts was computed for the three vegetation themes (Legendre and Legendre 2012). Prior to clustering, the variables were subjected to a Hellinger transformation to give less weight to abundant tree species and preserve an ecologically meaningful distance among sites (Legendre and Gallagher 2001).

Constrained analysis, delineation of homogeneous landscapes, and variation partitioning of the vegetation

The ecological land classification of homogeneous vegetation landscapes (ELCH) was developed using a redundancy analysis (RDA) involving a Y-matrix formed by all vegetation themes (tree species, forest types, potential vegetation-successional stages) and constrained by an X-matrix composed of four sets of

explanatory variables (climate, natural disturbances, physical environment, and human disturbances). All canonical axes resulting from the RDA were submitted to *K*-means clustering in order to form groups of ecological districts. *K*-means clustering allows the formation of two or more groups of ecological districts. While *K*-means results can be completely hierarchical (smaller groups nested in larger ones), the method does not guarantee this outcome (Legendre and Legendre 2012). This gradual stratification was used to develop a hierarchy of homogeneous landscapes formed of three levels of observation. The landscapes were positioned on an ordination diagram according to the centroid of each landscape, as calculated using the canonical scores of each ecological district. Ordination axis 1 was positioned vertically and axis 2 horizontally, because this configuration represents north–south and east–west gradients in their usual orientation in the study area. The homogeneous landscapes were also characterized using histograms showing the relative proportions of

period of origin and disturbance type (fires or insect outbreaks) noted in each forest inventory plot. Variation partitioning of the vegetation was used to quantify the contribution of each set of explanatory variables to vegetation changes along the levels of observation considered in this study (Borcard et al. 1992; Legendre et al. 2005; Peres-Neto et al. 2006; Tuomisto and Ruokolainen 2006). Variation partitioning was performed following the steps proposed by Borcard et al. (2011).

Results

An overview of the vegetation of the study area is used as an introduction to the ELCH. Other descriptions in line with approaches presented in the introduction are described in Appendix 3 in Supplementary Material.

The vegetation of the study area

Nine classes of vegetation, combining dominant tree species, forest types, and potential vegetation-successional stages, describe the vegetation of the area. The following description is restricted to tree species because this theme provides a good overview of the vegetation heterogeneity (Fig. 3). Eastern units V-1, V-2, and V-3 are characterized by an abundance of *A. balsamea*, *B. papyrifera*, and *Picea mariana*. Towards the north (V-2, V-3), *Picea mariana* becomes more abundant than *A. balsamea* and *B. papyrifera*. In the central-eastern unit (V-3), early-successional species (*P. tremuloides* and *Pinus banksiana*) are abundant. In

the north-east, V-4 is dominated by *Picea mariana* and *A. balsamea*, the latter mainly confined to hills. *Pinus banksiana* is scattered and concentrated on sandy deposits. In the central unit (V-5), *Picea mariana* and *Pinus banksiana* are abundant. A composition similar to V-3 is found in the southern and central-western units (V-6 and V-7), but *A. balsamea* is less abundant than in the east (V-1, V-2, V-3). In the north-west, V-8 shows similarities to V-4 in terms of abundance of *Picea mariana*. Finally, the most northwestern unit V-9 consists mainly of non-forested peatlands and *Picea mariana* on organic deposits.

Ecological land classification of homogeneous vegetation landscapes (ELCH)

RDA and mapping of the scores of the first four canonical axes

The ELCH is based on a RDA, and mainly on scores of the first 4 canonical axes. These canonical axes are closely related to ecological gradients describing the heterogeneity of the study area (Fig. 2). These first 4 canonical axes of the RDA explain 37 % of the vegetation's variability. The first canonical axis (Fig. 4a) reflects the changes in vegetation and explanatory variables occurring from south to north in the study area. For example, changes along the latitudinal gradient are primarily related to the decrease in the annual number of growing degree-days and forest stands affected by the last spruce budworm outbreak (Sbom) (Fig. 5a). The second canonical axis (Fig. 4b) is described by three
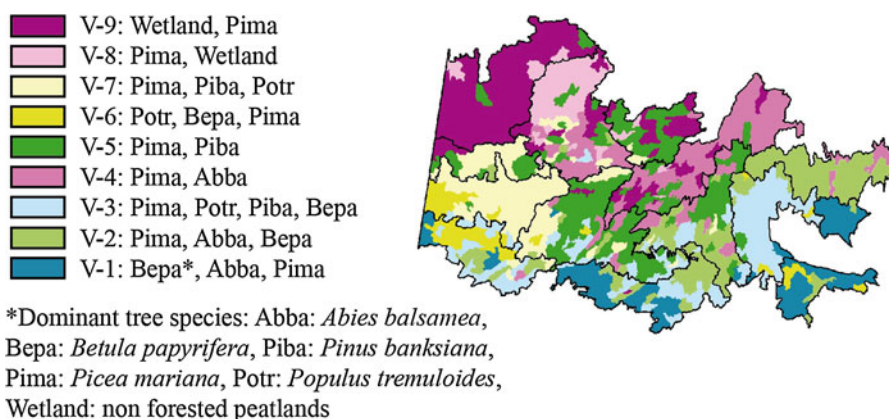
Fig. 3 Description of the study area according to vegetation (V). The homogeneous landscapes defined in Fig. 7a are outlined in *black*

V-9: Wetland, Pima
V-8: Pima, Wetland
V-7: Pima, Piba, Potr
V-6: Potr, Bepa, Pima
V-5: Pima, Piba
V-4: Pima, Abba
V-3: Pima, Potr, Piba, Bepa
V-2: Pima, Abba, Bepa
V-1: Bepa*, Abba, Pima

*Dominant tree species: Abba: *Abies balsamea*, Bepa: *Betula papyrifera*, Piba: *Pinus banksiana*, Pima: *Picea mariana*, Potr: *Populus tremuloides*, Wetland: non forested peatlands

4A First canonical axis (20%)

- - - - - - - - - - → Fig. 6A

4B Second canonical axis (8%)

- - - - - - - - - - → Fig. 6B

4C Third canonical axis (5%)   **4D** Fourth canonical axis (4%)

→ Fig. 6C

Fig. 4 Maps of the scores of the first 4 canonical axes of the ecological districts of the RDA (Fig. 2). The *darker the gray*, the higher the positive scores. The variation explained by each canonical axis is indicated in *brackets*. The homogeneous landscapes defined in Fig. 7a are outlined in *black*

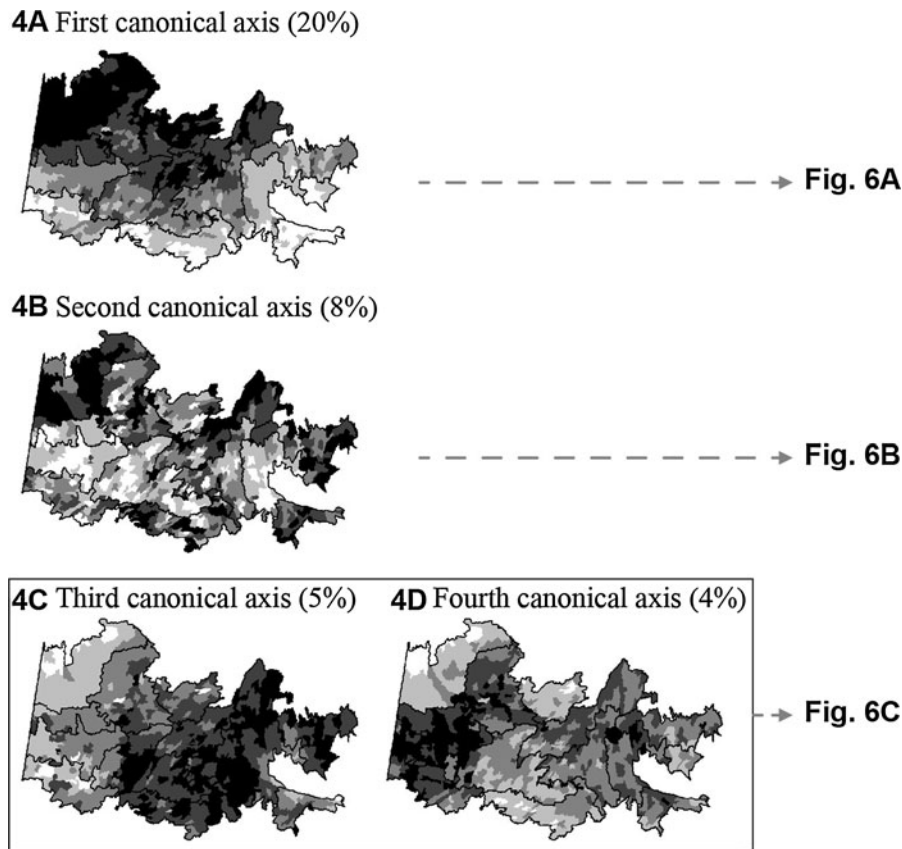longitudinal bands mostly reflecting natural disturbances (Fig. 5b). The central band is dominated by relatively young stands (1921f). It differs, on one hand, from the southern portion, which is well populated with *A. balsamea* (AbbaS) whose dynamics are related to Sbom and, on the other hand, from the northern part, where old stands (PimaF, Pima-AbbaF) from fires of the period centered on 1851 (before 1870) are well represented. In the central band, the abundance of sandy deposits favors the presence of young forests often dominated by *Pinus banksiana*.

The third canonical axis (Fig. 4c) characterizes changes that occur from south-east to north-west. This latitudinal-oblique gradient is strongly linked to changes in the physical environment (Ele variable, Fig. 5c), particularly the transition from a hilly (south-east) to relatively flat topography (north-west). These changes are accompanied by an increase in wetlands (D_7). The

fourth canonical axis (Fig. 4d) primarily defines the impact of human activities (Fig. 5d). From approximately 1880 to 1940, land clearing for agricultural settlement had a widespread impact on both the southeastern and southwestern sectors. Beginning in 1905, coal-fired steam locomotives were used in the southern part of the territory to link the agroforestry regions of Abitibi and Lac Saint-Jean (Fig. 1). These activities contributed to numerous human-induced fires (Hf1, Fig. 5, Hardy and Seguin 1984) and promoted changes in both age structure and forest composition. These changes consist mostly in the expansion of *P. tremuloides* (PotrF) and the presence of many stands originating from the period centered on 1951 (after 1930). During the second half of the twentieth century, mechanized logging spread throughout the *A. balsamea–B. papyrifera* domain, and gradually towards the north into the *Picea mariana*–feathermoss domain.
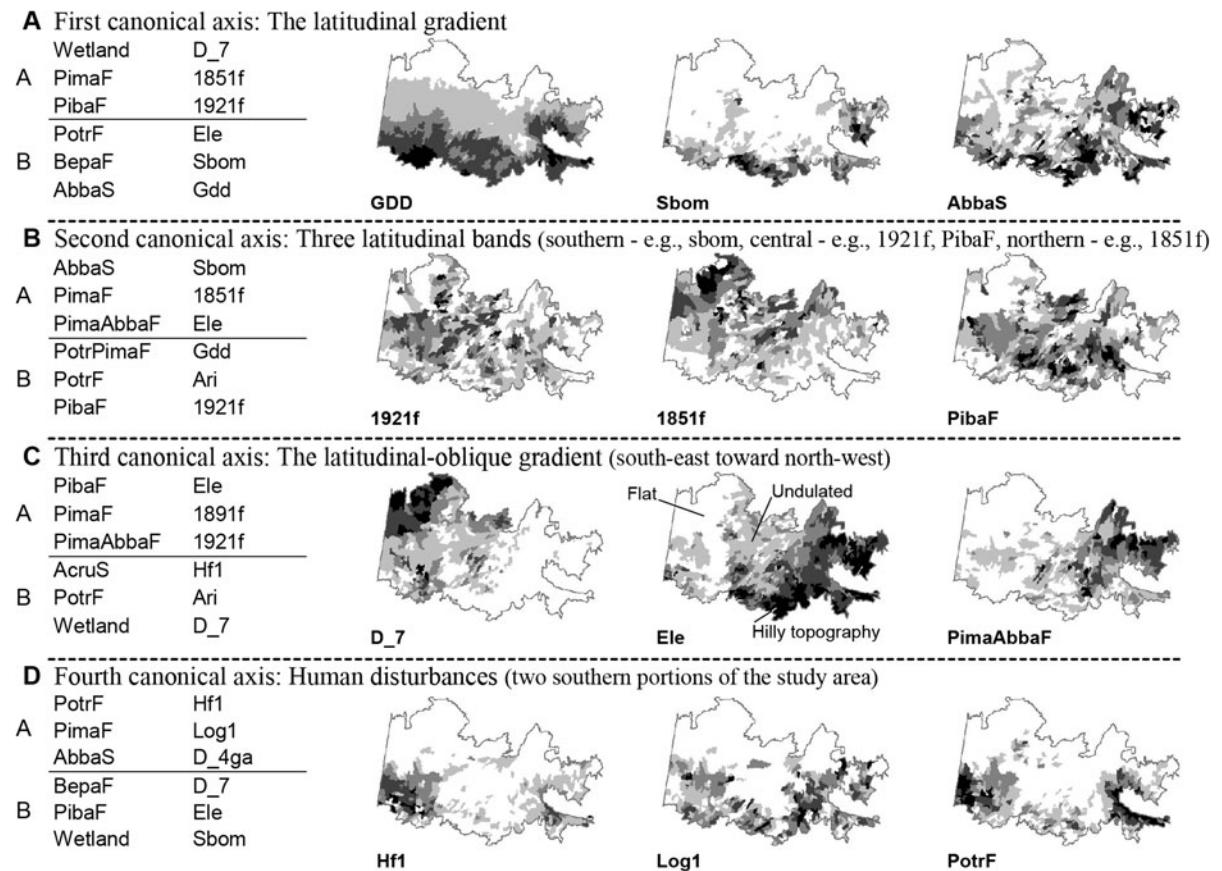
A First canonical axis: The latitudinal gradient

	Wetland	D_7
A	PimaF	1851f
	PibaF	1921f
	PotrF	Ele
B	BepaF	Sbom
	AbbaS	Gdd

GDD Sbom AbbaS

B Second canonical axis: Three latitudinal bands (southern - e.g., sbom, central - e.g., 1921f, PibaF, northern - e.g., 1851f)

	AbbaS	Sbom
A	PimaF	1851f
	PimaAbbaF	Ele
	PotrPimaF	Gdd
B	PotrF	Ari
	PibaF	1921f

1921f 1851f PibaF

C Third canonical axis: The latitudinal-oblique gradient (south-east toward north-west)

	PibaF	Ele
A	PimaF	1891f
	PimaAbbaF	1921f
	AcruS	Hf1
B	PotrF	Ari
	Wetland	D_7

D_7 Ele PimaAbbaF

Flat Undulated Hilly topography

D Fourth canonical axis: Human disturbances (two southern portions of the study area)

	PotrF	Hf1
A	PimaF	Log1
	AbbaS	D_4ga
	BepaF	D_7
B	PibaF	Ele
	Wetland	Sbom

Hf1 Log1 PotrF

Fig. 5 Vegetation and explanatory variables related to the first 4 canonical axes of the redundancy analysis (RDA, Fig. 2). *A* Variables with the highest positive scores on the canonical axis. *B* Va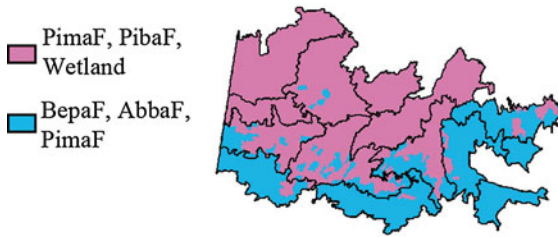riables with the highest negative scores on the canonical axis. Codes and description of variables are presented in Table 2. On the maps, *the darker the gray*, the greater the proportion of the variable

K-means cluster analysis and grouping of ecological districts

A *K*-means clustering applied to the scores of the canonical axes relative to the ecological districts (Fig. 2) allows the formation of three groupings of ecological districts (Fig. 6). In the first grouping (Fig. 6a), ecological districts strongly associated with the *A. balsamea–B. papyrifera* domain are distinguished from those belonging to the *Picea mariana*-feathermoss domain. In the second grouping (Fig. 6b), the *Picea mariana*-feathermoss domain is split to highlight the wide central band described by the RDA (previous section). In the third grouping (Fig. 6c), the northern part of this last domain (pink) is characterized according to the proportion of wetlands and related attributes (group 5 vs. group 6). The central band (green, Fig. 6b) is divided into an eastern (group 3, Fig. 6c) and a western subsection (group 4). *A. balsamea* is more abundant and relief is well defined (hilly) in the eastern subsection (Fig. 5). The southern portion (blue) is described relative to the effects of Sboms (group 1) and human disturbances (group 2).
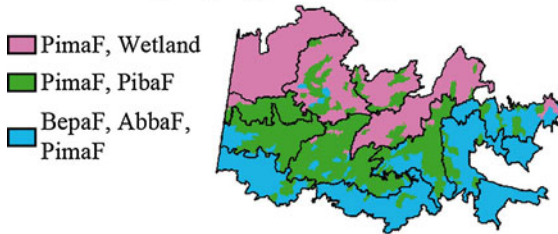
Ecological land classification of homogeneous vegetation landscapes (ELCH)

The development of the ELCH is based on ecological gradients described in the two previous sections. The sequence of analyses highlights four results of particular importance in the delineation and description of the ELCH: the third grouping of ecological districts (Fig. 6c), the delineation of the homogeneous landscapes (Fig. 7a), the ordination diagram showing the position of homogeneous landscapes along ecological gradients (Fig. 7c), and the period-disturbance

6A First grouping of ecological districts

- ■ (pink) PimaF, PibaF, Wetland
- ■ (blue) BepaF, AbbaF, PimaF

- -

6B Second grouping of ecological districts

- □ (pink) PimaF, Wetland
- ■ (green) PimaF, PibaF
- ■ (blue) BepaF, AbbaF, PimaF

- -

6C Third grouping of ecological districts

- ■ 6. Wetland, PimaF
- ■ 5. PimaF
- ■ 4. PimaF, PibaF
- ■ 3. PimaF, AbbaF
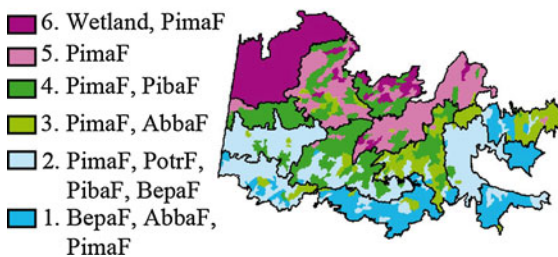- □ 2. PimaF, PotrF, PibaF, BepaF
- ■ 1. BepaF, AbbaF, PimaF

Fig. 6 Gradual segmentation of the study area based on a *K*-means clustering (Fig. 2). Codes and description of forest types are presented in Table 2. The homogeneous landscapes defined in Fig. 7a are outlined in *black*

histograms (Fig. 7c). The ELCH is hierarchical with three levels of observation (Fig. 7). The first level (n = 2, Fig. 7b, c) is the most general and highlights the major territory subdivisions corresponding to bioclimatic domains. The second level (n = 4) distinguishes homogeneous landscapes characterizing the southern and the northern portions of the two bioclimatic domains. The third level is composed of nine elements of landscape classification and 14 geographically distinct homogeneous landscapes. Some of the 14 landscapes are dominated by young forests originating from fires dating back to the period centered on 1921 (222, 221, 24, 131). In others, located in the northern part, forest landscapes are older (period centered on 1851: 132, 231, 232, 25). In the southern part, landscapes are under the influence of insect outbreaks and fires (121, 123). In the two

southern extremities, landscapes are strongly affected by human activities (21-pe, 14-pe, 11-pe, 122-pe) and *P. tremuloides* expansion (Fig. 7; Table 1, Appendices 4 to 7 in Supplementary Material). Homogeneous landscape 122-pe was not classified as a managed landscape by the numerical analysis (Figs. 7a, 6c, dark blue-color). Considering the importance of the human activities, we decided to classify this landscape with those affected by human activities (Table 1; Fig. 5d).

The transition from 9 to 14 landscapes of level III is mainly justified by disjunctions in geographic distribution (Fig. 7a, b). For example, landscape 12 is divided into three landscapes 121, 122, and 123-pe (pe: *Populus* expansion), each occupying a specific portion of the study area. Some landscapes are also distinguished in reference to the geographical units delineated on Fig. 6a and b. For example, landscapes 131 and 132 (Fig. 7a), which forms a large unit in Fig. 6c (pale green), is separated into two landscapes in Fig. 6a and b. Landscape 131 is placed high along axis 1 of the ordination diagram (Fig. 7c), revealing its affinities with the *Picea mariana*-feathermoss domain. Considering the hilly topography, the relative abundance of *A. balsamea* and its grouping with homogeneous landscape 132 in some analyses (Fig. 3), we classified homogeneous landscape 131 within the northern portion of the *A. balsamea–B. papyrifera* domain.

Proportion of variation explained by sets of variables along spatial levels of observation (variation partitioning of vegetation)

After presenting the ELCH, we are now interested in quantifying the relative importance of the four sets of explanatory variables in explaining the vegetation heterogeneity. To achieve this goal, we used the partitioning of vegetation throughout the study area as well as in three portions of it (Fig. 8). The analyses reveal that the explained vegetation variation is always greater than the unexplained portion. This suggests that the heterogeneity of the study area, its beta diversity, is structured along ecological gradients. This structure indicates that portions of the territory are different from others, allowing the delineation of homogeneous landscapes.

The total proportion of variation attributed to natural disturbances is relatively high, regardless of geographical entity (Fig. 8, NDt). The unique fractions of variation (e.g., NDu) explained by each set of
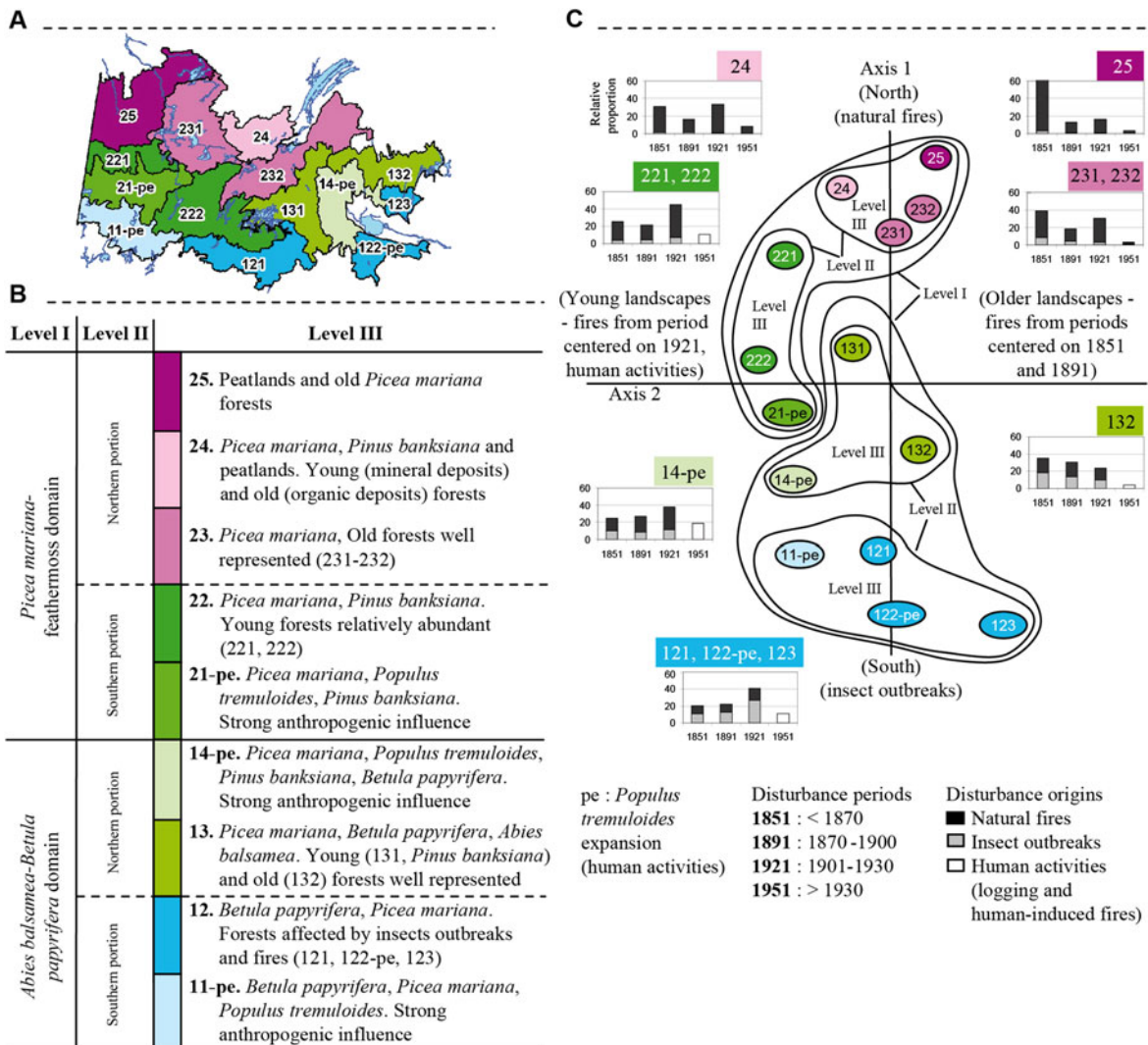
Fig. 7 Ecological land classification of homogeneous vegetation landscapes (ELCH). **a** Map of homogeneous vegetation landscapes. **b** Description of homogeneous landscapes at three levels of observation. **c** Homogeneous landscapes positioned on an ordination diagram (ecological gradients) and described on disturbance histograms. The ordination diagram is related to the RDA (redundancy analysis) of two matrices: Y-vegetation and X-explanatory variables (Fig. 2)

explanatory variables are generally small, except for natural disturbances. This indicates that some changes in natural disturbances are relatively independent of changes in other sets, especially physical environment. The three large latitudinal bands presented previously (southern, central, northern) and characterizing the natural disturbances are the main examples (Figs. 4b, 6b).

The common fractions of variation explained by the sets of explanatory variables are generally high, especially for natural disturbances. The common variation of natural disturbances is mainly attributed to triple and quadruple combinations. This result confirms that changes in vegetation are closely related to changes in natural disturbances, in combination with other sets. The variation explained by climate (unique and double combinations) is higher for the entire area than the two bioclimatic domains. The impact of human disturbances is generally low, except in the western portion (mainly the Abitibi region), where a high proportion of variation is explained by this set of variables, in combination with the three

Table 1 Synthetic description of homogeneous landscapes

		Natural homogeneous landscapes										Homogeneous landscapes affected by human activities			
		121	123	131	132	221	222	231	232	24	25	11-pe	122-pe	14-pe	21-pe
	Area (%)	7	2	8	6	4	11	11	10	5	12	6	3	7	7
Vegetation	BepaF	43	43	13	20	4	13	4	7	3	0	20	32	16	9
	AbbaF	4	9	4	11	0	1	0	2	0	0	1	3	3	1
	PimaAbbaF	3	9	7	12	1	2	1	5	1	0	1	4	5	2
	PotrF	7	9	5	4	16	7	6	1	2	1	23	31	23	21
	PibaF	10	3	22	8	19	26	8	11	24	4	6	3	20	16
	PimaF	25	21	38	38	41	33	59	57	40	33	25	18	25	34
Climate	Gdd	1295	1276	1210	1195	1201	1274	1165	1149	1139	1111	1345	1340	1281	1258
	Preci	342	359	328	346	312	334	312	330	316	287	303	345	316	312
Physical environment	Ele	77	90	56	73	23	39	25	38	26	11	27	70	64	24
	D_4ga	0	0	0	0	58	4	40	0	3	7	34	0	0	44
	D_7	1	1	4	2	16	12	13	9	23	59	17	2	1	18
Natural disturbances	Sbom	26	34	3	12	2	4	3	1	0	0	11	14	3	3
	1921f	15	7	24	14	45	33	31	23	32	16	19	14	29	37
	1891f	11	6	23	17	14	23	13	16	15	12	12	7	15	15
	1851f	11	10	16	17	28	18	29	32	30	60	10	5	13	19
Human disturbances	Log1	16	22	14	10	8	7	1	1	1	0	10	13	15	13
	Hf1	2	5	2	3	3	4	1	1	2	0	32	18	7	15
	Ag1-Fa1	0	0	0	0	0	0	0	0	0	0	5	3	0	6
	1951	11	9	10	4	5	13	0	0	0	0	16	7	28	14

Codes and description of variables are presented in Table 2

others (quadruple combination). This indicates that changes in vegetation are closely integrated or dependent on changes in all of the sets, from southern to northern Abitibi (Fig. 3, Appendix 7 in Supplementary Material).

Discussion

The ELCH supplements ELCs based solely on vegetation

The ELCH is strongly influenced by the pioneers and others authors interested by landscape ecology (e.g., Rowe 1972). The similarity between the vegetation map of the study area (Fig. 3) and that of the homogeneous landscapes (Fig. 7) reveals that vegetation alone is a faithful indicator, a phytometer, of explanatory variables at the meso scale (Halliday 1937; Hills 1960; Damman 1964; Barnes et al. 1982). However, the ELCH better describes landscapes patterns than ELCs based on vegetation and climate (e.g., Halliday 1937) or using vegetation, climate, and the physical environment (e.g., Hills 1960) (Fig. 9).

The ELCH considers natural disturbances and other sets of natural explanatory variables

The usefulness of the ELCH lies in its a priori inclusion of natural disturbances and other natural sets of explanatory variables (climate, physical environment). We have shown that natural disturbances are the predominant set explaining vegetation variation (the sum of unique and common variations). The unique variation explained by natural disturbances is considered to be part of the total variation independent of the other sets of explanatory variables. This unique variation might also be defined as the expression of the dominance of natural disturbances over the other sets. This concurs with authors who consider natural disturbances as overlaying other environmental gradients (Heinselman 1973; White 1987; Payette 1992). In addition, this study has shown that natural disturbances vary regionally (White 1987; Mansuy et al. 2010). Some homogeneous landscapes are dominated by young forests, others are older, some are under the influence of insect outbreaks and fires, while the rest are strongly affected by human activities. These landscape types (younger vs. older), based on natural disturbances criteria, are described by specific age class distributions and are in line with those proposed

Table 2 Codes and description of variables used to describe the homogeneous landscapes

	Code	Description
Vegetation	AbbaF	Relative area covered by *Abies balsamea* forest type
	AbbaS	Relative basal area for *Abies balsamea* species
	AcruS	Relative basal area for *Acer rubrum* species
	BepaF	Relative area covered by *Betula papyrifera* forest type
	PibaF	Relative area covered by *Pinus banksiana* forest type
	PimaF	Relative area covered by *Picea mariana* forest type
	PimaAbbaF	Relative area covered by *Picea mariana* and *Abies balsamea* forest type
	PotrF	Relative area covered by *Populus tremuloides* forest type
	PotrPimaF	Relative area covered by *Populus tremuloides* and *Picea mariana* forest type
	Wetland	Relative area covered by non-forested wetlands
Climate	Gdd	Annual number of growing degree-days
	Preci	Rainfall during the growing season (mm)
	Ari	Aridity index
Physical environment	Ele	Absolute difference of topographic elevation (m)
	D_4ga	Relative area covered by glaciolacustrine fine-textured (clay) surficial deposits
	D_7	Relative area covered by organic deposits
Natural disturbances	Sbom	Relative area covered by light spruce budworm outbreak (last outbreak 1975–1985)
	1921f	Relative proportion of forest inventory plots originating from fires between 1901 and 1930
	1891f	Relative proportion of forest inventory plots originating from fires between 1870 and 1900
	1851f	Relative proportion of forest inventory plots originating from fires before 1870
Human disturbances	Log1	Area covered by logging during the 1970s
	Hf1	Frequency of human-induced fires per 100 km^2 from 1938 to 1998
	Ag1	Relative area covered by agriculture during the 1970s
	Fa1	Relative area covered by fallow farmland during the 1970s
	1951	Relative proportion of forest inventory plots originating from logging since 1930

by Turner et al. (1993) and discussed by Lertzman and Fall (1998) and White et al. (1999). Using the vocabulary of these authors, some landscapes of the study area are more stable than others, or are closer to their equilibrium stage.

Although natural disturbances are the main factor, the variation in vegetation explained by this set in combination with others is larger than the unique variation. Consequently, the control of the vegetation by environmental variables is mainly related to the integration of several sets. This paradigm of multiple factors controlling landscape heterogeneity follows numerous authors (Jenny 1958; White 1979, 1987), including those interested by vegetation variation partitioning (Borcard et al. 1992 and following). The integration of multiple factors is maintained for the entire territory and parts of it, all considered at the meso scale (Damman 1979; Bailey 1987; Lertzman and Fall 1998). At this scale, climate is never the

dominant set of variables (Ohmann and Spies 1998). We attribute this result to small changes in temperature and precipitation along the latitudinal gradient of the study area. Two bioclimatic domains are present but the same six main species are still present in the landscapes. Climate rather becomes the main driver of landscape heterogeneity in larger territories (macro scale), such as bioclimatic zones (Damman 1979; Bailey 1983; Allen and Hoekstra 1992; Payette 1992; Wu and Loucks 1995; Grondin et al. 2007).

The ELCH considers human disturbances

The ELCH is also novel by its a priori inclusion of human disturbances. We have demonstrated that human activities do not play a major role in explaining the vegetation variation when the entire territory is considered. However, in the southern two ends which
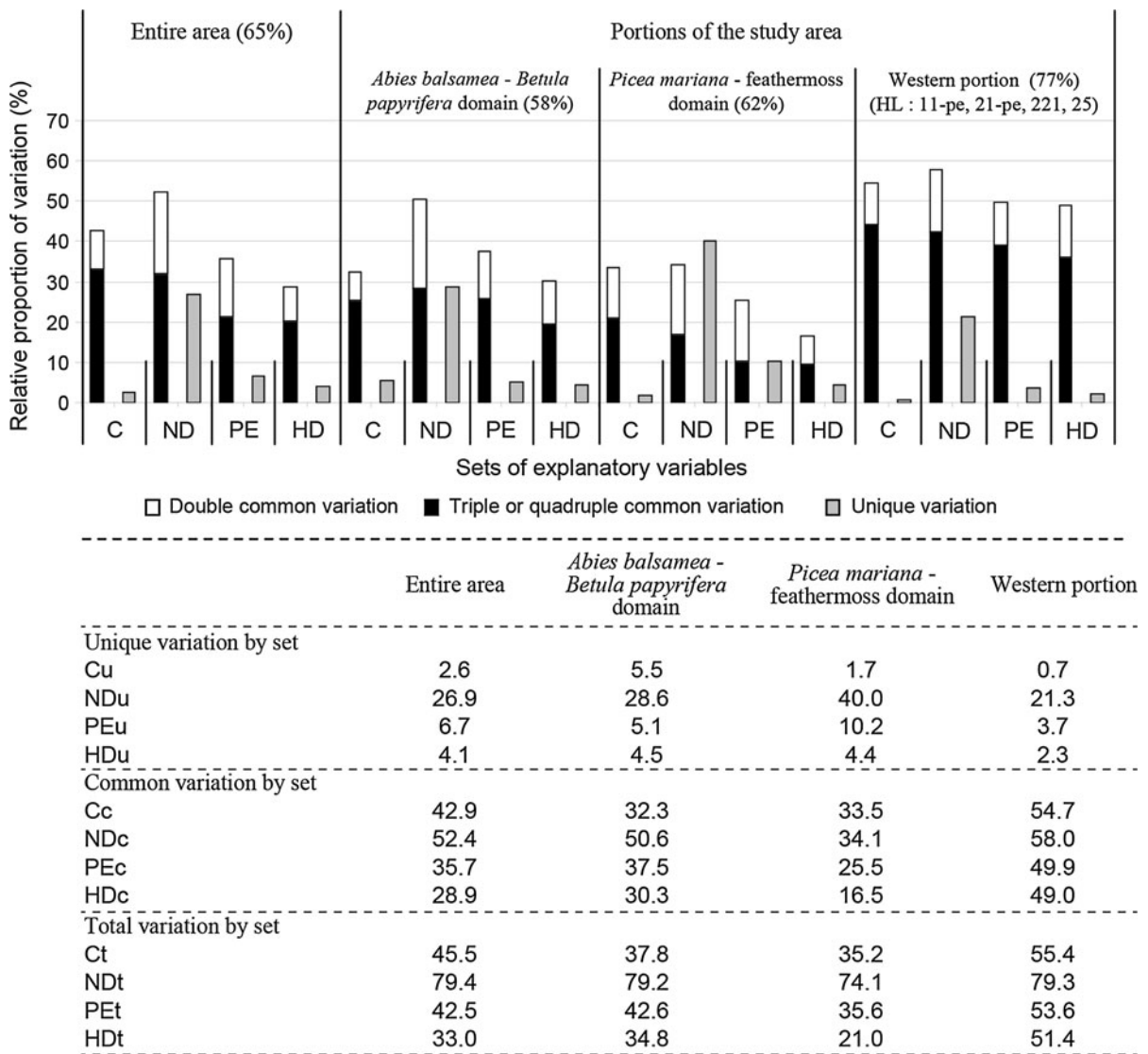
Fig. 8 Relative proportion of vegetation variation (%) explained by each of the four sets of explanatory variables (climate [C], natural disturbances [ND], physical environment [PE], and human disturbances [HD]) in relation to the entire area and three of its portions. The variation explained by the four sets in each portion is indicated in *brackets*. The double common variation by a set is the sum of the double fractions containing this set (e.g., double common fraction of the set C = PE∩C + C∩ND + C∩HD). The triple common variation by a set is the sum of the triple fractions containing this set (e.g., triple common fraction of the set C = PE∩C∩ND + PE∩HD∩C + HD∩ND∩C) (Fig. 2)

	Entire area	*Abies balsamea - Betula papyrifera* domain	*Picea mariana - feathermoss* domain	Western portion
Unique variation by set				
Cu	2.6	5.5	1.7	0.7
NDu	26.9	28.6	40.0	21.3
PEu	6.7	5.1	10.2	3.7
HDu	4.1	4.5	4.4	2.3
Common variation by set				
Cc	42.9	32.3	33.5	54.7
NDc	52.4	50.6	34.1	58.0
PEc	35.7	37.5	25.5	49.9
HDc	28.9	30.3	16.5	49.0
Total variation by set				
Ct	45.5	37.8	35.2	55.4
NDt	79.4	79.2	74.1	79.3
PEt	42.5	42.6	35.6	53.6
HDt	33.0	34.8	21.0	51.4

are closest to human settlement, four homogeneous landscapes show a strong anthropogenic influence. These four landscapes are well integrated into the sequence of canonical axes formed by the RDA (Fig. 2) and take their place after the sets of natural variables (Figs. 4d, 6c). These results concur with authors who consider human disturbances as an important factor in natural landscapes transformation,

and one of the major issues in the context of ecosystem-based management implementation (Urban et al. 1987; White and Mladenoff 1994; Schulte et al. 2007; Boucher et al. 2009). In Abitibi (western portion of the study area), where human activities have had the greatest impact, two homogeneous landscapes (21-pe and 221) are superimposed on a uniform area with respect to the physical

Fig. 9 Conceptual model comparing: 1- the traditional ELC (ecological land classification) approach based on climate (C) and physical environment (PE). Natural and human disturbances are considered a posteriori, 2- the proposed ELCH (ELC of homogeneous vegetation landscapes). In this last approach, all the sets of variables are considered a priori, with special emphasis on natural (ND) and human disturbances (HD)
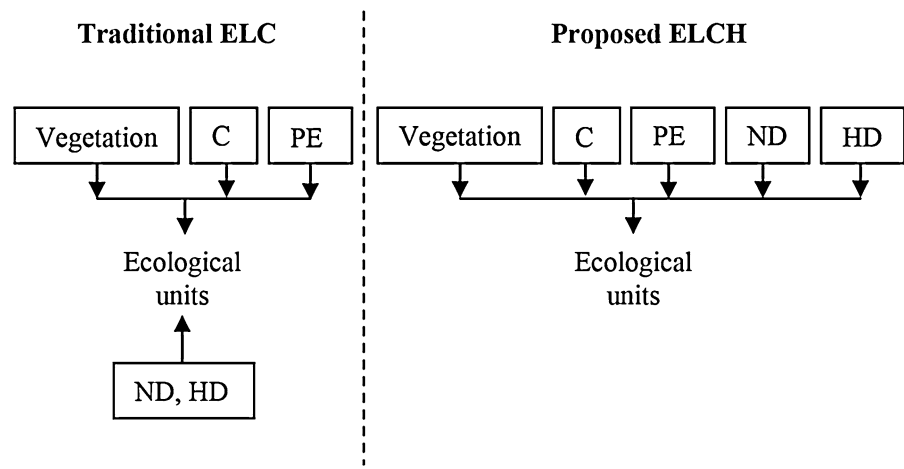
environment (mesic clay deposit), climate, and natural disturbances (abundance of fires centered on the period 1921). This indicates that anthropogenic disturbances can generate specific homogeneous landscapes. On mesic clay deposits, the expansion of *P. tremuloides* and *A. balsamea* could eventually continue northward, under the influence of logging, to the northern natural limit of *P. tremuloides.* The abundance of these two species and the consistent decrease of *Picea mariana* in mixed stands of the *Picea mariana*-feathermoss domain, favoured by intensive management practices and, possibly, climatic change, could contribute to the northward expansion of the *A. balsamea*–*B. papyrifera* domain into the northern boreal forest currently dominated by *Picea mariana* (Grondin and Cimon 2003; Laquerre et al. 2009; Arbour and Bergeron 2011).

Conclusion

This study builds on the research of authors who have described ecological gradients and used them to define an ELC. Our approach, the ELCH, is original in including, a priori, landscape disturbance patterns (natural and human) as sets of variables. A sequence of numerical analyses (RDA, *K*-means clustering, variation partitioning) has been used to describe the ecological gradients and define an ELC. We have shown that it is possible to elaborate on an ELC by integrating the main factors structuring landscape heterogeneity, even in areas with great variability of

natural disturbances and a strong local influence of human disturbances. Landscape spatial heterogeneity of the study area, considered at the meso scale, is mainly explained by natural disturbances in synchronicity and overlapping with changes in the physical environment, climate, and human activities. Our integrative and quantitative approach of ecological gradients enhance and perhaps slightly modifies our perception and understanding of factors causing landscape heterogeneity in the circumboreal forest zone. This study could not have been carried out without the large databases available at the MRN. More detailed data, especially with respect to natural disturbances (fire origin maps), could lead to slightly different and more accurate results. Other numerical analyses could also be tried (e.g., fuzzy clustering). This first ELCH should be considered as a point of reference to define and compare natural and managed landscapes, to initiate more detailed studies on forest dynamics (e.g., natural variability of homogeneous landscapes), and to estimate the effects of climate changes on vegetation.

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