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Drivers of contemporary landscape vegetation heterogeneity in the Canadian boreal forest: Integrating disturbances (natural and human) with climate and physical environment [1]

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Abstract: This study aims to demonstrate that contemporary landscape vegetation heterogeneity is controlled by a combination of natural disturbances with other sets of explanatory variables. Integration of these drivers should be considered the key to explaining vegetation changes along ecological gradients characterizing the boreal forest. Forest inventory plots and maps produced from about 1970 to 2000 were used to characterize a large area (175 000 km^2) according to 3 vegetation themes constituting distinct aspects of forest community composition (tree species, forest types, and potential vegetation–successional stages) and 4 sets of explanatory variables (climate, natural disturbances, physical environment, and human disturbances). Canonical ordinations were performed to define ecological gradients as well as the overlap between vegetation themes and sets of explanatory variables along each gradient. For each vegetation theme, we quantified the relative proportion of vegetation variation explained by unique as well as combined sets of explanatory variables. The landscape vegetation heterogeneity described by species and potential vegetation–successional stage was mostly explained by natural disturbances and climate in association with other sets of explanatory variables. The influence of physical environment was higher for landscape vegetation heterogeneity related to forest types than for the other themes, but this theme also was dominated by natural disturbances and climate. Compared to natural sets of explanatory variables, human disturbances played a secondary but significant role in the 3 vegetation themes. This research contributes to a better understanding of the relationship between vegetation and the factors underlying its development in the boreal forest and represents an important step toward ecosystem-based management.
Keywords: ecological gradients, integration of sets of factors, landscape heterogeneity, variation partitioning.

Résumé : Cette étude vise à démontrer que l'hétérogénéité des paysages contemporains est régie par les perturbations naturelles en combinaison avec d'autres familles de variables explicatives. L'intégration de ces facteurs (*drivers*) devrait être considérée comme l'élément clé permettant d'expliquer les changements de végétation survenant le long des gradients écologiques qui caractérisent la forêt boréale. Des placettes d'inventaire forestier et des cartes forestières produites de 1970 à 2000 ont été utilisées pour caractériser un vaste territoire (175 000 km^2) selon 3 thèmes associés à la végétation (espèces forestières, types forestiers, végétations potentielles-stades évolutifs) et 4 familles de variables explicatives (climat, perturbations naturelles, milieu physique et perturbations humaines). Des ordinations canoniques ont été effectuées pour définir les gradients écologiques et, le long de chacun d'eux, caractériser le chevauchement entre les thèmes de végétation et les familles de variables explicatives. Pour chaque thème, la proportion relative de la variation de la végétation expliquée par les familles seules (aucun chevauchement) ou en combinaison avec les autres a été quantifiée. L'hétérogénéité de la végétation décrite par les espèces ainsi que par les végétations potentielles-stades évolutifs s'explique principalement par les perturbations naturelles et le climat en association avec d'autres familles de variables explicatives. L'hétérogénéité de la végétation décrite par les types forestiers est aussi dominée par les perturbations naturelles et le climat, mais le milieu physique est plus important que dans les 2 autres thèmes. Par rapport aux familles de variables explicatives naturelles, les perturbations humaines jouent un rôle secondaire, mais significatif dans les 3 thèmes de végétation. L'ensemble de ces informations sur les relations entre la végétation et les facteurs à la base de son développement contribue à une meilleure connaissance du territoire d'étude et constitue un pas de plus vers son aménagement écosystémique.
Mots-clés : gradients écologiques, hétérogénéité du paysage, intégration de familles de variables explicatives, partitionnement de la variation.

Nomenclature: Scoggan, 1978.

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Introduction

Ecosystems are spatially heterogeneous because of the diversity created by vegetation and environmental characteristics (White, 1979; Milne, 1991; Wagner & Fortin, 2005). This heterogeneity characterizes the landscape, defined as an area fragmented into a mosaic of interconnected patches, each showing particular characteristics in terms of vegetation, abiotic variables (*e.g.*, physical environment), biotic factors (*e.g.*, species competition), and processes (natural and anthropogenic) (Daubenmire, 1968; Urban, O'Neill & Shugart, 1987; Perera & Euler, 2000). In this study, we defined landscape heterogeneity (diversity) on the basis of ecological gradients and evaluated the relative contribution of factors controlling this diversity, which are important concerns in landscape ecology (Turner, 1989; Wu & Loucks, 1995; White *et al.*, 1999).

As a first step toward defining the landscape heterogeneity of the study area, we used 3 vegetation themes (response variables) representing 3 distinct aspects of forest composition. The first theme describes tree species and their abundance. At this level, the distribution of vegetation is the result of migration, dispersal processes, interspecies competition, species autecology, and environmental factors (climate, physical environment, disturbances) along the ecological gradients of latitude, longitude, and altitude (Gleason, 1939; Whittaker, 1967; Ohmann & Spies, 1998; Hubbell, 2001). The second theme consists of forest types, namely, groups of tree species with similar ecological affinities. Each forest type has its own set of ecological preferences (ecological niches), having established at locations with appropriate living conditions (Hutchinson, 1957; Damman, 1964; Whittaker, 1967; Gauvin & Bouchard, 1983; Legendre, Borcard & Peres-Neto, 2005). The third theme is made up of potential vegetation assemblages, defined as specific assemblages of tree species that are linked by the dynamics of their successional stages (Dansereau, 1957; Rey, 1960; Daubenmire, 1968; Powell, 2000; Saucier *et al.*, 2009; Cyr, Gauthier & Bergeron, 2012). For example, in Quebec's boreal forest, *Betula papyrifera*, *Populus tremuloides*, *Abies balsamea*, and *Picea glauca* constitute an assemblage observed on sites with specific combinations of physical features, microclimate, and disturbances. The early-successional stage is dominated by light-demanding species (*e.g.*, *Betula papyrifera*); with increasing time since the last fire, these species are progressively replaced by the shade-tolerant species that compose the late-successional stage (*e.g.*, *Abies balsamea*) (Bergeron, 2000; Couillard, Payette & Grondin, 2012).

As a second step toward defining the landscape heterogeneity of the study area, we used 4 sets of explanatory variables (factors): climate, natural disturbances, physical environment, and human disturbances. It is well known that, at a continental scale (biomes), patterns of vegetation are associated with large-scale climatic variations (Hare, 1950; Whittaker, 1960; Damman, 1979; Bailey, 1987; Ohmann & Spies, 1998). The climate–fire connection is a key process affecting contemporary and Holocene boreal vegetation diversity, dynamics, and resilience (Heinselman, 1973; Payette, 1992). Major differences in vegetation can be observed between maritime areas and the continent's interior, due to specific climate–fire relationships (fire-cycle and species responses) (Ohmann & Spies, 1998; Parisien & Sirois, 2003; Cyr, Gauthier & Bergeron, 2007; Bouchard, Pothier & Gauthier, 2008). The effects of natural disturbances, mostly fires, are influenced by the physical environment. Landscape configuration, including topography and abundance of wetlands and water bodies, is a major determinant of fire behaviour and landscape heterogeneity (Whittaker, 1960; Rowe & Scotter, 1973; Zackrisson, 1977; Peet, 1978; Romme & Knight, 1981). The relationship between climate and physical environment (elevation, altitude) becomes a dominant factor in regions where stand-replacing disturbances are relatively rare (long fire cycle), as in the mountainous wet maritime landscapes of northwestern North America (Whittaker, 1960; Reiners & Lang, 1979; Swanson *et al.*, 1988; Turner & Romme, 1994; Lertzman & Fall, 1998; Ohmann & Spies, 1998). Landscape vegetation heterogeneity is also influenced by human disturbances. The combined action of naturally occurring fires, human-caused fires, and logging has a major impact, increasing the proportion of early-successional species and the loss of old-growth forests (Grimm, 1984; White & Mladenoff, 1994; Foster, Motzkin & Slater, 1998; Cushman & Wallin, 2002; Grondin & Cimon, 2003; Ohmann, Gregory & Spies, 2007; Boucher *et al.*, 2009). Our study area has been subjected to human activities, particularly forest harvesting and fires in the southern part, for almost 150 y.

A holistic approach to explaining landscape heterogeneity, based on the integration of several sets of variables (climate, physical environment, natural disturbances, and human disturbances), has evolved since the early 20th century (Daubenmire, 1936; Jenny, 1958; White, 1979; Turner, 1989). Daubenmire (1936) demonstrated in the relatively natural Big Woods area (Minnesota, USA) that the spatial transition from prairie to woodland to forest ecosystems was related to the combination of climate, natural disturbances, and physical environment. In the same area, Grimm (1983; 1984) showed that landscapes had been strongly modified over a period of decades by human activities, which are now considered to be the main factor controlling landscape dynamics.

However, these approaches, although holistic in their conception, did not take into account all of these themes and factors at the same time. Here, we quantify the relative contribution of 4 sets of explanatory variables, including recent anthropogenic influences, to the landscape heterogeneity of a vast territory described according to 3 vegetation themes. Although Quebec has a rich history of ecological land classification (Jurdant *et al.*, 1977; Grondin, Noël & Hotte, 2007; Saucier *et al.*, 2009), quantitative estimates of the natural and human drivers that modulated its landscape heterogeneity are still in the embryonic stage. This study aims first to demonstrate that the proportion of vegetation heterogeneity explained by various sets of explanatory variables (factors) differs according to the 3 vegetation themes. More specifically, we expect the strongest links to be 1) between the tree species theme and climate, 2) between the forest types theme and physical environment, and 3) between the potential vegetation–successional stages theme and natural disturbances. Second, we will show that despite the specificity of themes, landscape vegetation heterogeneity is mainly related to the integration of natural disturbances with other sets of explanatory variables. Finally, we will establish that human disturbances are a secondary, yet important, cause of landscape heterogeneity, despite their relatively recent appearance in the study area (about 150 y).

Methods

STUDY AREA

The 175 000-km^2 study area forms part of Quebec's boreal forest, more precisely the *Abies balsamea–Betula papyrifera* domain in the south and the *Picea mariana*–feathermoss domain in the north (Saucier *et al.*, 2009; Figure 1, study area centre at 49°15'N, 75°35'W). This area is appropriate for the objectives of our study because of its very diverse natural and human forest landscapes and large size (Robitaille & Saucier, 1998; Grondin, Noël & Hotte, 2007; Saucier *et al.*, 2009). The forest vegetation consists mainly of 6 tree species: *Picea mariana*, *Abies balsamea*, *Picea glauca*, *Pinus banksiana*, *Betula papyrifera*, and *Populus tremuloides*.

The average annual temperature varies from 1.5 °C in the south to –1.5 °C in the north. During the growing season (May to September), precipitation (rainfall) ranges from about 300 mm in the Abitibi region (west) to 350 mm in the Lac-Saint-Jean region (east), following a longitudinal gradient. Abitibi is characterized by organic and glaciolacustrine deposits and a relatively flat topography, while till, glaciofluvial deposits, and a relatively hilly topography are found in the Lac-Saint-Jean region (Robitaille & Saucier, 1998; Grondin, Noël & Hotte, 2007). Fires and spruce budworm outbreaks have been the main natural disturbances throughout the study area. Fires occurred over huge areas in the 1820s–1870s and 1920s (Bergeron *et al.*, 2001; Lesieur, Gauthier & Bergeron, 2002; Grondin, Noël & Hotte, 2007). Three spruce budworm outbreaks, peaking around 1910, 1950, and 1975–1980, affected the age structure and composition of vegetation in the 20th century (Morin, 1994; Bergeron *et al.*, 2001).

From 1870 to 1950, forest harvesting and land clearing were carried out in both the Abitibi and Lac-Saint-Jean regions, particularly along a railway line built between 1905 and 1910 that runs across the southern part of the territory. The line's early coal-powered steam locomotives contributed to human-caused forest fires in subsequent decades (Hardy & Seguin, 1984; Grondin & Cimon, 2003; Laquerre, Leduc & Harvey, 2009). During the second half of the 20th century, mechanized logging spread throughout the southern part of the study area (*Abies balsamea–Betula papyrifera* domain) and, gradually, towards the northern part (*Picea mariana*–feathermoss domain).

DATA SOURCES AND MATRICES

This study is based on forest maps and forest inventory plots produced between the 1970s and 2000 by the Ministère des Ressources naturelles du Québec (MRN) (Letarte *et al.*, 1995). These data were used to develop matrices describing 606 landscape units referred to as ecological districts (Figure 2a1). Each of the ecological districts (mean area of 200 km^2) is relatively homogeneous

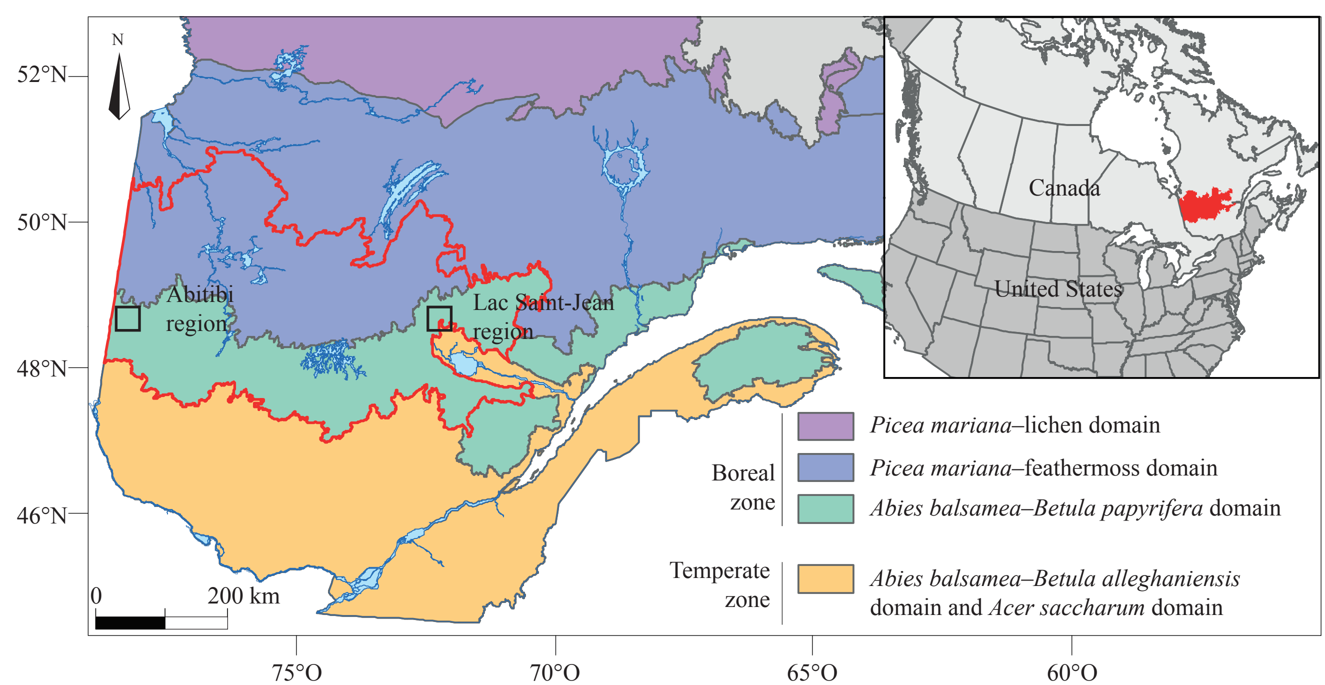

FIGURE 1. Location of the study area (outlined in red) according to the Ecological Land Classification Hierarchy of the Ministère des Ressources naturelles du Québec (Saucier *et al.*, 2009).

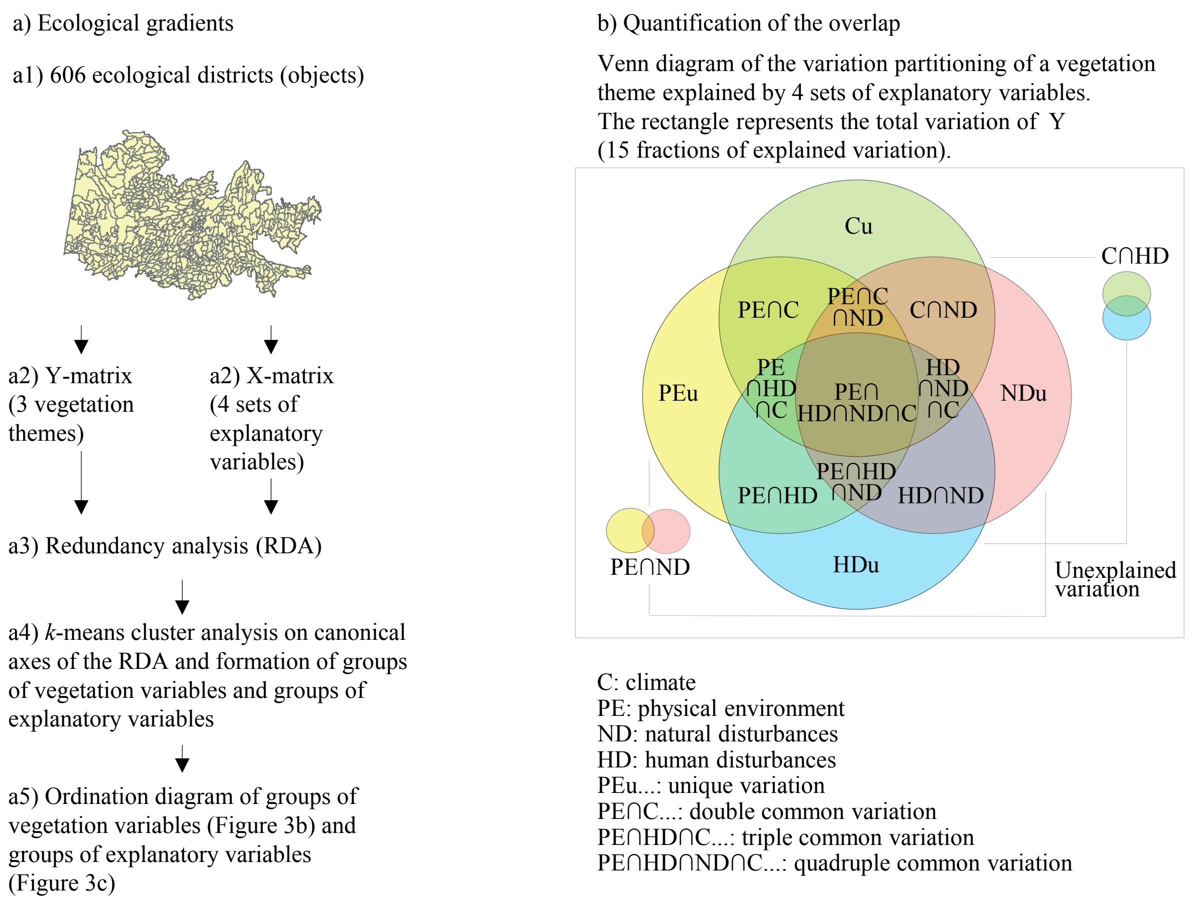

FIGURE 2. Method used a) to define the ecological gradients and b) to quantify the overlap for each of the 3 vegetation themes (tree species, forest types, potential vegetation–successional stages) relative to 4 sets of explanatory variables (climate [C], natural disturbances [ND], physical environment [PE], and human disturbances [HD]).

in terms of surficial deposits, topography, geology, and regional vegetation (Robitaille & Saucier, 1998). Each was described with regard to 2 matrices: vegetation (Y-matrix of response variables) and factors (X-matrix of explanatory variables) (Figure 2a2). The rows of the 2 matrices represent the ecological districts, and the columns, the response or explanatory variables.

The Y-matrix contains 3 vegetation themes: tree species composition (botanical aspect, $m = 10$), forest types (site aspect, $m = 14$), and potential vegetation–successional stages (forest dynamics aspect, $m = 12$), for a total of 36 variables (Appendix I). The first theme describes the relative proportion of 10 tree species in each ecological district based on forest inventory plots ($n = 53\,635$). The second theme describes the relative proportion of 14 forest types in each ecological district based on forest maps. The third theme describes the vegetation with respect to the potential vegetation types ($n = 3$) and successional stages ($n = 4$) associated with each forest inventory plot. Three types of potential vegetation were considered: *Abies balsamea–Betula papyrifera* (Ms2), *Abies balsamea–Picea mariana* (Rs2), and *Picea mariana* (Re2).

The X-matrix contains 4 sets of explanatory variables: climate ($m = 8$), natural disturbances ($m = 12$), physical environment ($m = 16$), and human disturbances ($m = 8$), for a total of 44 variables (Appendix II). The climate (C) of each of the 606 ecological districts was characterized using the BioSIM simulator designed by the Canadian Forest Service (Régnière, 1996). The climatic variables were estimated for the centre of each ecological district using data from 37 meteorological stations located in the study area. Natural disturbances (ND) were described relative to the history of fires and spruce budworm outbreaks over the last 150 y. Forest maps were used to describe the relative proportion of each ecological district affected by light or severe insect outbreaks and natural fires. Forest inventory plots provided information concerning the time since the last fire and type of disturbance (spruce budworm outbreaks). Post-fire forest types (1851f, 1891f, 1921f) formed distinct categories from post-spruce budworm outbreak forest types (1851o, 1891o, 1921o). Physical environment (PE) was described using an MRN database containing the relative proportion of surficial deposits and physiographic variables (*e.g.*, mean altitude) for each ecological district (Robitaille & Saucier, 1998). Human disturbances (HD) were analyzed based on forest maps, forest inventory plots, and archival data on human disturbances (MRN). The history of contemporary human activities was presented in Grondin *et al.* (2014).

Data analysis

Multivariate analyses such as redundancy analysis are invaluable tools for studying landscape heterogeneity (Legendre & Legendre, 2012). The 2 matrices (Y, response variables, and X, explanatory variables) were analyzed in order to describe and associate ecological gradients characterizing the vegetation and explanatory variables (Figure 2; Appendix I, II; Whittaker, 1960; 1967; Peet, 1978.). Comparison of the ordination of response variables and the ordination of explanatory variables allowed us to understand the overlap between the 2 sources of information (Appendix III). Variation partitioning then provided the statistical means to quantify the relative contribution of different sets of explanatory variables to vegetation heterogeneity (Borcard, Legendre & Drapeau, 1992; Ohmann & Spies, 1998; Legendre, Borcard & Peres-Neto, 2005; Dray *et al.*, 2012).

To model ecological gradients, a redundancy analysis (RDA) was performed on the Y and X matrices (Figure 2a2) (Borcard, Gillet & Legendre, 2011; Dray *et al.*, 2012; Legendre & Legendre, 2012) using the vegan package (Oksanen *et al.*, 2010) of the R statistical language (R Development Core Team, 2010). The objective of an RDA is to extract the variation of a set of response variables (Y matrix) explained by a set of explanatory variables (X matrix). In an RDA, we perform a regression analysis (first step) of all explanatory variables on each response variable and then produce a matrix of fitted values, which is then subjected to a principal component analysis (PCA; second step). The RDA results in an ordination diagram that summarizes, by canonical axes, the spatial patterns and heterogeneity of the Y matrix that is explained by the X matrix.

Given the large number of response (36) and explanatory (44) variables, it was useful to group them in order to provide a summary of the information. RDA and *k*-means clustering were conducted using vegan (Figure 2a3). *K*-means clustering was carried out on all canonical axes of the RDA in order to group the variables belonging to the vegetation themes (9 groups were retained) as well as the variables composing the sets of explanatory variables (11 groups were retained) (Figure 2a4). Each group was named and described using the most representative variable for the group. The groups of response variables and the groups of explanatory variables are presented on distinct ordinations (Figure 2a5).

Variation partitioning uses a series of linear regressions or RDA (Borcard, Legendre & Drapeau, 1992; Legendre, Borcard & Peres-Neto, 2005; Legendre & Legendre, 2012; Peres-Neto *et al.*, 2006). To complete a Venn diagram depicting 4 sets of explanatory variables (Figure 2b), 16 partial RDAs are required, each one resulting in an adjusted R^2 of the variation explained by a unique set or by a combination of 2, 3, or 4 sets of explanatory variables. Variation partitioning was computed using the varpart function of the vegan package, following the steps proposed by Borcard, Gillet, and Legendre (2011) (Appendix IV).

Results

The results consist first of a description of the ecological gradients used to characterize the study area in terms of vegetation (first ordination) and explanatory variables (second ordination). This description allows us to understand the organization (landscape heterogeneity) of the study area and the overlap between the response and explanatory variables. Once the area has been described, variation partitioning (second section) is used in order to achieve the 3 aims of the study. Thus, the ecological gradients are a prerequisite to understanding the variation partitioning.

Ecological gradients

Groups of response variables and explanatory variables were considered in terms of geographical distribution (maps), position on the ordination diagrams, and gradual changes along ecological gradients. For clarity, the groups are illustrated on 2 separate ordination diagrams. Axes 1 (vertical) and 2 (horizontal) reflect the geographic organization of the territory. Each of the 9 groups of vegetation variables is composed of variables belonging to the 3 vegetation themes (Figures 3a, 3b, Table I, Appendix I). Each of the 11 groups of explanatory variables is made up of variables belonging to the 4 sets of explanatory variables (Figures 3c, 3d, Table I, Appendix II).

The first 3 canonical axes of the RDA explain 33% of vegetation heterogeneity. On both ordination diagrams (Figures 3b, 3c), axis 1 describes the changes along the latitudinal gradients, *i.e.*, the gradual transition from the *Abies balsamea–Betula papyrifera* bioclimatic domain (south) to the *Picea mariana*–feathermoss domain (north). The vegetation characterizing the southern part of the latitudinal gradient is dominated by the *Betula papyrifera* forest type (GBepaF) and *Abies balsamea* species (GAbbaS) (Figures 3a, 3b). In the more northern landscapes, these groups gradually give way to the *Picea mariana* forest type (GPimaF) and wetlands groups (GWetlands). The southern landscapes include some temperate zone tree species, grouped under GAcruS, including *Acer rubrum*, *Betula alleghaniensis*, and *Thuja occidentalis*. The study area is also characterized by a southeast to northwest latitudinal-oblique gradient, which shows a gradual transition from the *Picea mariana–Abies balsamea* forest type (GPimaAbbaF, southeast) to non-forested wetlands (GWetland, northwest). Along the latitudinal gradient, the explanatory variables (Figures 3c, 3d) first show a decrease in the annual number of growing degree-days (GGdd) both in areas affected by light spruce budworm outbreaks (GSbom) and in those characterized by significant logging (GLog1). Second, they show an increase in fires during the 1851 period (G1851f). The latitudinal-oblique gradient describes the gradual transition from southeastern hilly landscapes (high GEle values) to flatter northwestern landscapes dominated by organic soils (GD_7).

Axis 2 describes the changes along the longitudinal gradient. The vectors associated with this axis are short, indicating that they have less influence on the distribution of the vegetation than axis 1. For vegetation

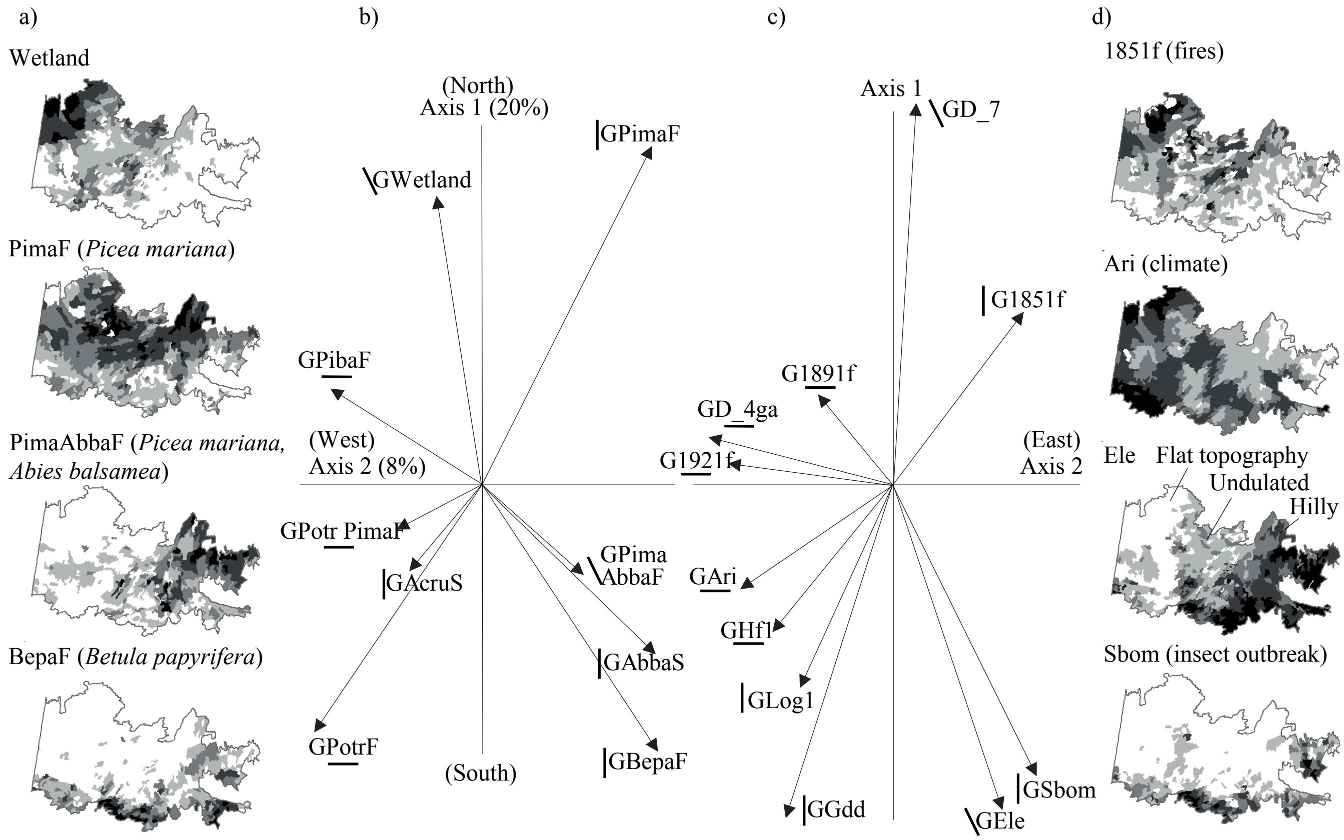

FIGURE 3. Distribution maps of variables for vegetation themes (a) and sets of explanatory variables (d), and ordination diagrams of vegetation theme variables (b) and sets of explanatory variables (c). On each map, the abundance of the variable is proportional to the darkness of the shade of grey. On the ordination diagrams, arrows indicate the direction of change, with their length reflecting their importance in structuring the landscape heterogeneity of the study area. Each group of variables is characterized by an ecological gradient (latitudinal |, latitudinal-oblique \, or longitudinal —) deduced from the distribution of the variables. The groups of variables are defined in Table I.

TABLE I. Codes used to describe groups (prefix G) of vegetation variables and groups of explanatory variables (climate [C], natural disturbances [ND], physical environment [PE], and human disturbances [HD]). Each group is composed of variables presented in Appendix I and II.

Groups of response variables	
GAcruS	Relative proportion of basal area for *Acer rubrum*
GBepaF	Relative proportion of area for *Betula papyrifera* forest type
GAbbaS	Relative proportion of basal area for *Abies balsamea*
GPimaAbbaF	Relative proportion of area for *Picea mariana* and *Abies balsamea* forest types
GPotrF	Relative proportion of area for *Populus tremuloides* forest type
GPotrPimaF	Relative proportion of area for *Populus tremuloides* and *Picea mariana* forest types
GPibaF	Relative proportion of area for *Pinus banksian*a forest type
GWetland	Relative proportion of area for non-forested wetlands
GPimaF	Relative proportion of area for *Picea mariana* forest type
Groups of explanatory variables	
GGdd	C - Annual number of growing degree-days
GSbom	ND - Relative proportion of area covered by light spruce budworm outbreaks
GLog1	HD - Relative proportion of area covered by logging during the 1970 period
GEle	PE - Relief amplitude: difference in elevation between upper and lower portions of the landscape (m)
GHf1	HD - Number of human-caused fires per 100 km^2 during the 1938–1998 period
GAri	C - Aridity index
G1921f	ND - Relative proportion of plots originating from fires between 1901 and 1930
GD_4ga	PE - Relative proportion of area covered by glaciolacustrine fine-textured (clay) surficial deposits
G1891f	ND - Relative proportion of plots originating from fires between 1870 and 1900
G1851f	ND - Relative proportion of plots originating from fires before 1870
GD_7	PE - Relative proportion of area covered by organic deposits

themes (Figure 3b), the western (left) portion of the diagram is mainly occupied by the *Populus tremuloides* (GPotrF), *Populus tremuloides–Picea mariana* (GPotrPimaF), and *Pinus banksiana* (GPibaF) forest types. The explanatory variables (Figure 3c) defining the longitudinal gradient are 1) relatively high atmospheric aridity (GAri) and a high frequency of human-induced fires (GHf1) in the southwest, 2) glaciolacustrine clay surficial deposits (GD_4ga) and fires during the 1921 period (G1921f) characterizing the western central area, and 3) fires during the 1891 period (G1891f) in the central part (slightly west) of the study area.

Comparing a position on the ordination of the groups of response variables (Figure 3b) with the same position on the ordination of the groups of explanatory variables (Figure 3c) allows us to confirm the overlap of these groups. For example, on the ordination of response variables, the *Abies balsamea* group (GAbbaS, Figure 3b) occupies the same position occupied by the spruce budworm outbreaks group on the ordination of explanatory variables (GSbom, Figure 3c). The 2 groups thus overlap in the same location: the southern and south-eastern parts of the study area (Appendix III).

VARIATION PARTITIONING

Variation partitioning shows that the total variation of the vegetation explained by the explanatory variables is relatively high and increases from the potential vegetation–successional stages theme (55%) to the tree species theme (58%) and again to the forest types theme (69%) (Table II, upper part). The total relative proportion of explained variation associated with natural disturbances (NDt) is high for the potential vegetation–successional stages (89%) and tree species (78%) themes. This variation (NDt) is lower for the forest types (67%), but still remains the most important set. The variation associated with unique fractions is generally low, except for natural disturbances (NDu) in the tree species theme (25%) and the potential vegetation–successional stage theme (37%) (Figure 4; Table II). These 2 fractions represent the highest of the 15 fractions composing the variation partitioning. The total variation explained by common fractions (*e.g.*, NDc) is always much higher than the total variation explained by unique fractions (*e.g.*, NDu). For the tree species and potential vegetation–successional stage themes, the common fractions of vegetation variation (double, triple, and quadruple combinations) decrease from natural disturbances (NDc) to climate (Cc), physical environment (PEc), and human disturbances (HDc). For the forest types theme, the common fractions related to NDc (55%), PEc (49%), and Cc (47%) are high and relatively similar (Figure 4; Table II). These results demonstrate the strong influence of natural disturbances on vegetation variation.

In the forest types theme, the variation described by natural disturbances (NDt, 67%) is high, but similar to that of the physical environment (PEt, 62%) (Table II). Values of R^2_{adj} for vegetation themes and each natural set of explanatory variables (PE, C, ND) are similar for the tree species and potential vegetation–successional stages themes; they are higher for the physical environment (43%) and climate (36%) under the forest type theme (Table III). These results demonstrate that the 3 vegetation themes are different in regard to their variation partitioning.

Among the double combinations of natural sets of explanatory variables (*i.e.*, those that do not involve human disturbances), the PE∩ND combination explains the largest fraction of vegetation variation, while the double combinations including climate (PE∩C, C∩ND) explain smaller fractions (Table II, lower section). The triple combination of natural sets (PE∩C∩ND) explains the largest fraction of variation. These results show the relatively high proportion of vegetation variation explained by the combinations of natural sets of explanatory variables.

TABLE II. Detailed view of the relative proportion of vegetation variation (%) explained by 4 sets of explanatory variables (climate [C], natural disturbances [ND], physical environment [PE], and human disturbances [HD]) in relation to 3 vegetation themes. Partial canonical analysis (Y- and X-matrices) is used to estimate the total explained and unexplained variation. The explained variation is divided into 15 fractions (Figure 2b). The unique fractions (*e.g.*, PEu) are associated with only 1 set of explanatory variables, while the common fractions (*e.g.*, PE∩C) are associated with more than 1 set. The common relative variation by a set is the sum of double, triple, and quadruple fractions containing this set (*e.g.*, PEc = [PE∩C] + [PE∩HD] + [PE∩ND] + [PE∩C∩ND] + [PE∩HD∩C] + [PE∩HD∩ND] + [PE∩HD∩ND∩C] – 7 fractions). The total relative variation by a set is the sum of unique and common fractions (*e.g.*, [PEt] = [PEu] + [PEc] – 8 fractions). See also Figure 4 for a synthetic presentation of the results.

	Vegetation theme		
	Tree species	Forest types	Potential vegetation–successional stages
Total variation			
Explained	58.3	69.4	55.5
Unexplained	41.7	30.6	44.5
Relative proportion of explained variation (15 fractions)			
Unique variation			
Cu	2.7	4	2.3
NDu	25.5	11.6	36.7
PEu	7.1	13.2	2.7
HDu	3.9	2.7	3.2
Common variation			
PE∩ND	9.6	11.4	8.7
PE∩C	3	6.4	0.5
C∩ND	5.6	6.3	7
PE∩C∩ND	14.8	15.8	12.3
PE∩HD	2	3.1	0.4
C∩HD	1.5	1.7	1.1
HD∩ND	5.4	4.4	5
HD∩ND∩C	10.1	7	9.7
PE∩HD∩C	1.7	2.2	0.6
PE∩HD∩ND	0.4	0.8	1.1
PE∩HD∩ND∩C	6.6	9.3	8.6
Explained variation	100	100	100
Sums of relative proportion of explained variation			
Total unique relative variation	39.3	31.5	45
Total common relative variation	60.7	68.5	55
Total relative variation by set			
Ct	44.4	51	41
NDt	77.9	66.7	89.1
PEt	45.3	62.3	34.9
HDt	31.6	31.2	29.8
Common relative variation by set			
Cc	41.8	47	38.7
NDc	52.4	55.1	52.4
PEc	38.1	49	32.2
HDc	27.7	28.5	26.6
Double and triple variation			
PE∩ND	24.5	27.3	21
Double and triple variation			
HD∩ND	15.5	11.5	14.7

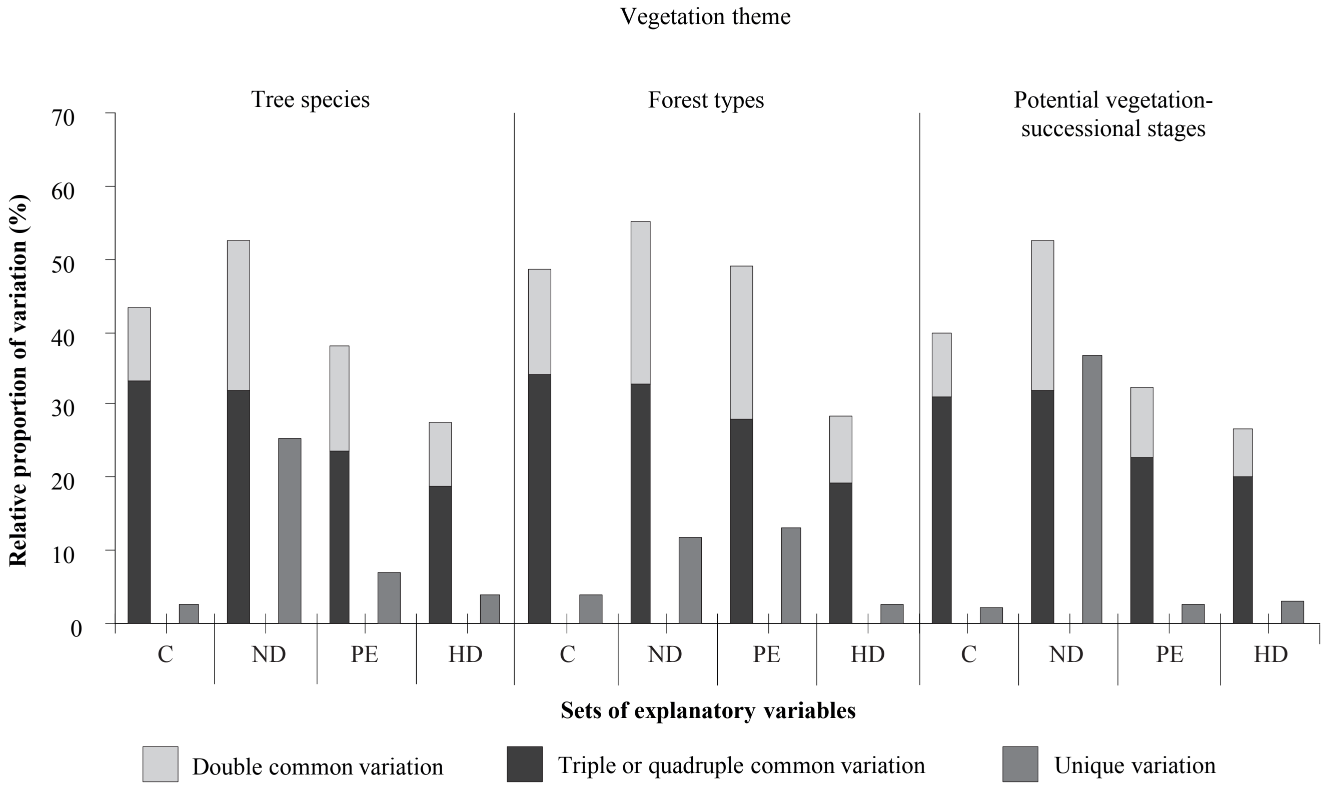

FIGURE 4. Synthetic view of the relative proportion of variation (%) explained by each of the 4 sets of explanatory variables (climate [C], natural disturbances [ND], physical environment [PE], and human disturbances [HD]) in relation to 3 vegetation themes. The variation is defined by the common and unique fractions illustrated in Figure 2b and described in Table II.

Human disturbances explain smaller fractions of total and common relative variation (approximately 30% for HDt and 25% for HDc) than natural sets of explanatory variables; they also show low values of R^2_{adj} for all vegetation themes (Table III). Some combinations including HD and ND are significant and reflect the overlap of these 2 sets. The triple combination of HD∩ND∩C is larger than any double (PE∩HD, C∩HD, and HD∩ND) or triple combination that includes human disturbances (PE∩HD∩C and PE∩HD∩ND). However, the sum of all fractions containing the HD∩ND combination remains lower than the sum of all fractions including the PE∩ND combination (Table II, lower section). These results show that human disturbances are a secondary, yet important, cause of landscape heterogeneity, despite their relatively recent appearance in the study area.

Discussion

Previous studies that defined ecological gradients of a territory and quantified the contribution of several sets of explanatory variables to landscape vegetation heterogeneity were mainly conducted in areas characterized by a strong altitudinal gradient (Whittaker, 1967; Romme & Knight, 1981; Ohmann & Spies, 1998; Cushman & Wallin, 2002). In our study area, gradients are more numerous and are characterized by various directions: from south to north (latitudinal gradient), west to east (longitudinal gradient), and southeast to northwest (latitudinal-oblique gradient). There is a synchronicity between changes in vegetation and changes in sets of explanatory variables (climate, natural disturbances, physical environment, human disturbances) along all of these gradients, as revealed by the high proportion of the total vegetation variation explained primarily by the combinations of these sets. The landscape heterogeneity is therefore structured (organized), because the spatial pattern of the forest mosaic reflects the relationship between vegetation and environmental characteristics (Legendre, Borcard & Peres-Neto, 2005; Wagner & Fortin, 2005; Dray *et al.*, 2012; Legendre & Legendre, 2012). Not all parts of the forest mosaic are equivalent. Landscapes are composed of different types of habitats, and each has its own ecological processes. Structured heterogeneity has been observed regardless of the theme used to describe the vegetation. Hubbell's (2001, neutral theory) and Hutchinson's (1957, niche theory) concepts are more similar than one might expect (Gravel *et al.*, 2006, continuum hypothesis) Therefore, toposequences showing the spatial organization (vegetation and explanatory variables) of a

TABLE III. R^2_{adj} for each vegetation theme in relation to 4 sets of explanatory variables (climate [C], natural disturbances [ND], physical environment [PE], and human disturbances [HD]).

	Vegetation theme		
R^2_{adj} (%)	Tree species	Forest types	Potential vegetation–successional stages
C	26.7	36.5	23.4
ND	45.3	46.3	49.4
PE	26.8	43.5	20.2
HD	18.5	21.7	16.6

territory are relevant (Blouin & Berger, 2005). In the study area, ecological gradients vary according to vegetation themes, which determine the framework of the discussion.

Heterogeneity of tree species and potential vegetation–successional stages: the latitudinal gradient

The characterization (organization, structure) of landscape heterogeneity is similar for these 2 themes. Their ecological gradients and variation partitioning are closely related. The latitudinal gradient is dominant (Figures 3 and 5), and natural disturbances explain the largest fractions of vegetation variation (Figure 4). Specificity of tree species in relation to latitudinal gradient is well known (*e.g.*, Damman, 1979; Ohmann & Spies, 1998). Specificity of potential vegetation–successional stages in regard to a latitudinal gradient has been noted in works concerning ecological classification (*e.g.*, Powell, 2000; Saucier *et al.*, 2009). In the study area, the abundance of the 3 types of potential vegetation (*Abies balsamea–Betula papyrifera* [Ms2], *Abies balsamea–Picea mariana* [Rs2], and *Picea mariana* [Re2]) shows a decrease from the south towards the north (Grondin *et al.*, 2014).

Three elements explain the high proportion of variation assigned to natural disturbances regarding the themes of tree species and potential vegetation–successional stages. First, natural disturbances are characterized by substantial unique variation, mainly caused by large portions of the study area having been affected by a uniform abundance of insect outbreaks or fires. For example, the central portion of the study area has numerous stands originating from the 1921 fire period. The areas affected by these landscape-scale processes are more uniformly distributed than those affected by gradual changes caused by other sets of explanatory variables, for example variation in relief from hilly to undulated or flat along a specific ecological gradient (Appendix 3e). The high unique variation of the natural disturbance set reveals the relative independence of this set from changes in vegetation and other sets of explanatory variables. The finding that natural disturbances are the major driver of landscape heterogeneity, without necessarily having links with other sets, concurs with many other studies (Heinselman, 1973; Payette, 1992; Ali *et al.*, 2008; de Lafontaine & Payette, 2011).

Second, natural disturbances overlap other natural sets to a large extent. For all vegetation themes, the fractions of variation associated with combinations involving natural disturbances (especially combined with physical environment or with physical environment and climate) are much higher than the fraction associated with natural disturbances as the unique source of variation. These results concur with those of several authors who have emphasized natural disturbances and physical environment in explaining intra-regional heterogeneity. When larger territories are considered, climate is inserted into the most important combination of explanatory variables (*e.g.*, Peet, 1978). The predominance of combinations of natural disturbances with climate (*e.g.*, Ohmann & Spies, 1998; Parisien & Sirois, 2003; Bouchard, Pothier & Gauthier, 2008) and physical environment (*e.g.*, Rowe & Scotter, 1973; Zackrisson, 1977; Peet, 1978; Hemstrom & Franklin, 1982) is the basis of the integrated concept promoted in this study (second hypothesis).

Third, a proportion of variation explained by natural disturbances is attributable to the combination of this set with human disturbances. Although the fraction of landscape vegetation heterogeneity explained by human disturbances (HDt) is smaller than that of natural sets of explanatory variables (Ct, NDt, PEt), 2 combinations involving natural and human disturbances explain a relatively high proportion of variation (HD∩ND, HD∩ND∩C). Variation partitioning clearly demonstrates that human disturbances are a secondary, yet important, cause of landscape heterogeneity, despite their relatively recent appearance in the landscape (third hypothesis). Over time, the combination of human disturbances with natural sets of explanatory variables could become more important than the combination of natural sets alone, as is the case in Europe (*e.g.*, Bradshaw & Hannon, 1992) and in the Canadian temperate forest (*e.g.*, Boucher *et al.*, 2009). At that point, the study area would be more strongly affected by human disturbances and, perhaps, climatic conditions (Périé *et al.*, 2014).

Heterogeneity of forest types: the latitudinal-oblique gradient

The landscape heterogeneity of the forest types theme is mainly associated with the latitudinal-oblique gradient. Natural disturbances and climate remain the most important sets of explanatory variables, but the role of physical environment is more significant than in other themes. This phenomenon is illustrated in Figure 5, where the distribution of *Abies balsamea* as a forest type is closely related to that of physical environment, particularly elevation (GEle, Figure 3). Specificity of forest types according to their site characteristics has been reported in numerous phyto-sociological studies (*e.g.*, Damman, 1964; Gauvin & Bouchard, 1983). This interpretation is close to the Hutchinsonian view of ecosystems and niche control of the spatial distribution of the vegetation. The unique fraction associated with natural disturbances is relatively small here. This indicates that, for this theme, the changes in natural

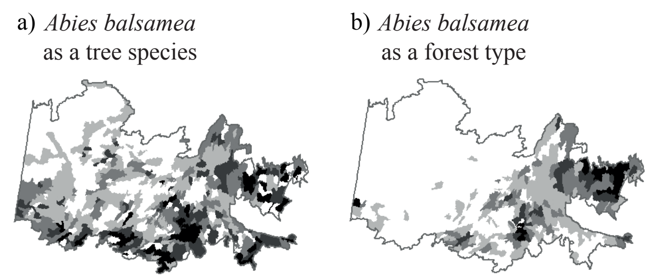

Figure 5. Vegetation heterogeneity according to vegetation themes. The tree species theme follows a latitudinal gradient in close association with the distribution of elements composing this theme, such as *Abies balsamea* as a tree species (AbbaS, a). The forest types theme follows a latitudinal-oblique gradient in close association with the distribution of elements composing this theme, such as the *Abies balsamea* forest type (AbbaF, b). On each map, the abundance of the variable is proportional to the darkness of the shade of grey.

disturbances along ecological gradients are mostly synchronous with those of other sets.

The vegetation variation explained by the unique fraction of the physical environment is generally small, except in the forest types theme, where it is moderate. This indicates that the same physical environment may be affected by a variety of processes related to natural disturbances. For example, thick till may be associated with various types of potential vegetation regardless of location in the territory. In such situations, vegetation appears randomly distributed. However, this phenomenon is not considered to be important in the study area (Grimm, 1984; McCune & Allen, 1985; Messaoud, Bergeron & Leduc, 2007).

Climate as a sub-dominant driver

In this study, the fraction of vegetation variation explained by climate alone is very small, because changes of this set along ecological gradients are always accompanied by changes in other sets. Climate in combination with other sets of explanatory variables ranks close to combinations involving natural disturbances, which suggests that climate could be considered a subdominant set. This subdominance is mainly defined by 3 combinations (2 triple and the quadruple) involving climate. The combination of climate and natural disturbances, often favoured by paleoecologists (*e.g.*, Payette *et al.*, 1989), and the double combination of physical environment and climate, which is typical of regions dominated by late-successional species and low fire frequency (*e.g.*, Swanson *et al.*, 1988), explain a low proportion of variation. These sets become more important when considered in a triple or quadruple combination. Climate would likely be the most important factor in territories that are much larger than our study area, such as the total area covered by boreal and temperate forest in the province of Quebec (Grondin, Noël & Hotte, 2007).

Conclusion

This study explored the role of 4 sets of explanatory variables (drivers) in explaining the landscape heterogeneity of the boreal forest. We established a link between gradient analysis, which has a long history in vegetation science (Whittaker, 1967), and more recent developments concerning numerical ecology (RDA and partial RDA; Borcard, Legendre & Drapeau, 1992; Legendre, Borcard & Peres-Neto, 2005; Dray *et al.*, 2012; Legendre & Legendre, 2012). We used 3 vegetation themes (n = 36 response variables) and 4 sets of factors (n = 44 explanatory variables), including human disturbances, to provide a complete description of ecological gradients and their overlap for a large portion of the Canadian boreal forest (175 000 km^2). Although fire is the main disturbance controlling the forest dynamics in boreal forest (Heinselman, 1973; Rowe & Scotter, 1973; Payette, 1992), the overall heterogeneity, defined by the links between environmental variables and vegetation, is caused by the integration of several sets of explanatory variables (drivers). Our findings show the variability of vegetation themes in regard to sets of explanatory variables, the integration of drivers, and the significant role of human disturbances in explaining landscape heterogeneity. We consider it likely that the processes characterizing the study area resemble those at work in numerous landscapes across the biomes of the world. The structured nature of landscape heterogeneity justifies the subdivision of the study area into relatively homogeneous landscape units for finer-scale analysis (Grondin *et al.*, 2014; Grondin, 2014), as well as for development of regional strategies regarding biological diversity, conservation, forest management, and the effects of global climate change.

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Supplementary material

APPENDIX I. Definition of response variables by theme (Y-matrix)

APPENDIX II. Definition of explanatory variables by set (X-matrix)

APPENDIX III. Overlap of vegetation themes and sets of explanatory variables

APPENDIX IV. Variables forming the parsimonious X-matrices developed for each vegetation theme (X-PE.pars, X-ND.pars, X-C.pars, X-ND.pars)

Appendix I

Definition of response variables by theme (Y-matrix)

This appendix provides more information on the response variables used in this study and gathered in a Y-matrix (Legendre & Legendre 2012). The Y-matrix contains response variables for 3 vegetation themes (total m = 36 variables): tree species (m = 10), forest types (m = 14), and potential vegetation–successional stages (m = 12) (Appendix I, Table I). Most of the variables describe a relative proportion of forest inventory plots (tree species, potential vegetation–successional stages) or a relative proportion of area (forest types).

1.1 THE FIRST THEME: TREE SPECIES

The description of the first theme (tree species) is based on forest inventory plots (n = 53 635) conducted by the Ministère des Ressources naturelles du Québec (MRN) from 1970 to 2000 (Bard *et al.* 1975, 1983; Letarte *et al.* 1995) (Appendix II, Figure 1). Each plot is circular (radius of 11.28 m), has an area of 400 m^2 and was measured only once (temporary plots). Within each plot, each living tree with a diameter at breast height (dbh) larger than 9 cm was measured and tallied (2-cm classes). The tree species theme describes the relative proportion of 10 tree species in each ecological district based on forest inventory plots. First, each forest inventory plot was characterized by the relative proportion of basal area occupied by each species. Second, the mean relative proportion of basal area was defined for each tree species using all plots within a specific ecological district.

1.2 THE SECOND THEME: FOREST TYPES

The description of the second theme (forest types) is based on forest cover maps (scale of 1:20 000) developed during the 1980s. Initially, the forest maps were created through photointerpretation of black and white aerial photographs (scale of 1:15 840). Each forest map was accompanied by a database containing a reference number, with a description of each stand delineated on the map. The description includes information on forest type, density, height, age, disturbance type (*e.g.*, light insect outbreaks) and surface area. Subsequently, the forest map database was integrated into a geospatial database named SIFORT-2 (Pelletier *et al.* 1996; Pelletier, Dumont & Bédard, 2007). The geospatial reference of the database lies on a spatial grid of rectangular polygons called tesserae. Each tessera represents a segment of 15 seconds of latitude and 15 seconds of longitude (geographic coordinates), and covers a 14-ha area. Integration of forest information with geospatial references (latitude, longitude) was obtained by superimposing the center of each tessera onto a forest map in order to note the reference number of the forest stand and its attributes (forest type, density, etc.). This procedure was extended to all tesserae and maps (scale 1:20 000) covering the study area. A synthesis of all forest stands delineated on the forest maps led to the definition of 14 main forest types. This synthesis was based on the total area occupied by each forest type and its geographical distribution. Less-represented forest types with similar distributions were agglomerated with more abundant forest types. To characterize each of the 606 ecological districts of the study area according to the 14 main forest types, we determined the relative proportion of area covered by each forest type using all tesserae associated to a specific forest type.

1.3 THE THIRD THEME: POTENTIAL VEGETATION–SUCCESSIONAL STAGES

The description of the third theme (potential vegetation–successional stages) is based on forest inventory plots (n = 53 635) produced since the 1970s and complemented by 7000 recent ecological (1980–2000) inventory plots (Blouin & Berger, 2005; Saucier *et al.*, 1994). To develop the Y-matrix in regard to this theme, we first characterized each plot according to its potential vegetation and successional stage on the basis of forest species. To standardize the information noted in forest inventory plots over several years, each plot was subjected to a similar key to that presented in Appendix I, Figure 1. Such keys are also presented in *Guides de reconnaissance des types écologiques* produced for the entire study area (*e.g.*, Blouin & Berger, 2005). The successional stages have also been defined on the basis of vegetation, and specifically the shade tolerance of species. Ultimately, the potential vegetation and successional stages are characterized on the basis of vegetation. Secondly, using all plots within a specific ecological district, the relative proportion of each combination of potential vegetation–successional stage was calculated.

Three potential vegetation types were considered: *Abies balsamea–Betula papyrifera* (Ms2), *Abies balsamea–Picea mariana* (Rs2) and *Picea mariana* (Re2). Four successional stages were also identified: early-successional (S2), intermediate (S3), facies (S4), and late-successional (S5) forest types. Plots dominated by species of early stage succession belong to S2, while those dominated by late successional species form the S5 stage. Stage S1, characterizing recently burned or cut stands, is not considered because this vegetation type was not sampled. The stands of various successional stages can recover after a disturbance, developing a forest composition similar to that of its predecessor (*e.g.*, cyclic dynamics of *Pinus banksiana* stands), or evolve until they reach the late-successional stage (*e.g.*, successional dynamics of *Betula papyrifera* stands evolving towards *Abies balsamea* stands) (Cogbill, 1985; Foster and King, 1986; De Grandpré, Morissette & Gauthier, 2000; Gauthier *et al.*, 2000; Couillard, Payette & Grondin, 2012). The proportion of successional stages belonging to the same potential vegetation type varies by region. For example, *Pinus banksiana* forest stands (S2) are an important successional stage of *Picea mariana* potential vegetation (Re2) in the central portion of our study area, where many fires are centered on the year 1921. These forest stands are less common in the northern portion composed of older landscapes (fires centered on 1851) (Grondin *et al.*, 2014).

The *Abies balsamea–Betula papyrifera* potential vegetation type (Ms2) is associated with rich soils, especially thick till or thick mesic clay. The forest dynamics of this potential vegetation type are mainly characterized by successional dynamics of stands of *Betula papyrifera* (S2 stage), *Betula papyrifera–Abies balsamea* (S3), *Abies balsamea–Betula papyrifera* (S4), and *Abies balsamea* (S5). The floristic understory generally consists of *Acer spicatum* and *Dryopteris spinulosa*. Early-successional forest stands (S2, S3) dominate the landscape for the first 100–150 y after a fire and are then replaced by late-successional species (S4, S5) (Bergeron & Dubuc, 1989; Bergeron & Dansereau, 1993; Bergeron & Charron, 1994; Bergeron, 2000; Lesieur, Gauthier & Bergeron, 2002; Gauthier *et al.*, 2010; Couillard *et al.*, 2012). In our study area, the high frequency of fires makes pure *Abies balsamea* stands (S5) rare.

The *Abies balsamea–Picea mariana* potential vegetation type (Rs2) differs from the previous type by the absence of both *Picea glauca* and rich undergrowth species (*e.g.*, *Acer spicatum*) and by the common presence of *Pinus banksiana* and *Picea mariana*. In forest stands with a forest floor receiving abundant light, ericaceous species (*e.g.*, *Kalmia angustifolia*) and other shrubs (*e.g.*, *Nemopanthus mucronata*) are well-represented. This potential vegetation type's topographic position, soil richness, and possibly fire regime, are midway between Ms2 (previous section) and Re2 (next section). Early-successional stands (S2-S3) are dominated by *Betula papyrifera*, *Populus tremuloides*, and *Pinus banksiana*, while those at the late-successional stage (S4-S5) are dominated by *Abies balsamea* and *Picea mariana* (Carleton & Maycock, 1978; Gerardin, 1980; De Grandpré, Morissette & Gauthier, 2000; Bouchard, Pothier & Gauthier, 2008; Gauthier *et al.*, 2010). We have also included in the Rs2 potential vegetation the stands dominated, in their early-successional stages, by *Populus tremuloides*. These stands are mainly observed on the clay deposits that characterize the western part of the study area (Abitibi). These sites are classified within the *Picea mariana* and *Populus tremuloides* potential vegetation (ME1 codification for mixed forest with *Picea mariana*) according to the ecological classification of the MRN. Considering that the late-successional stage is composed of *Picea mariana* and *Abies balsamea*, the same species that comprise Rs2, potential vegetation ME1 can be refered to as Rs2 given a synthetic view of the study area.

The *Picea mariana* potential vegetation type (Re2) generally occurs on flat or undulating topography. Soils are poorer than those of previous potential vegetation types.

A-soils can be well-drained and are composed of till, sand, or rock (*Picea mariana* and mosses) (Re2 according to the MRN forest classification). In these situations, undergrowth vegetation is dominated by mosses and ericaceous shrubs, including *Kalmia angustifolia* and *Ledum groenlandicum*. This potential vegetation type is mainly characterized by the following types of forest stands: *Pinus banksiana* (S2 stage), *Pinus banksiana–Picea mariana* (S3), *Picea mariana–Pinus banksiana* (S4), and *Picea mariana* (S5). Early-successional stands (S2, S3) dominate the landscape for the first 100–150 y after a fire and are then replaced by late-successional stands (Dix & Swan, 1971; Cogbill, 1985; Foster, 1985; Bergeron & Dansereau, 1993; Harper *et al.*, 2002; Harvey *et al.*, 2002; Lesieur, Gauthier & Bergeron, 2002; Lecomte & Bergeron, 2005). In some situations, fires can initiate a cyclic dynamic of *Pinus banksiana* stands (Harper *et al.*, 2002). This dynamic is more frequent on coarse deposits, where fire frequency is higher than on other surficial deposits (De Grandpré, Morissette & Gauthier, 2000). Finally, some old *Picea mariana* stands, located in landscapes without *Pinus banksiana*, are replaced by young *Picea mariana* stands according to recurrent dynamics characteristic of eastern Quebec (Gauthier *et al.*, 2010), which are also found in the study area. Moreover, as time since the last fire increases, late-successional stands (*Picea mariana*) located in relatively flat areas can be subject to paludification and decreased productivity, thereby opening the forest cover. The severity of fires in these ecosystems is the main factor affecting forest dynamics. Intense fires lead to the formation of relatively dense and productive stands. Low-intensity fires do not favour the regeneration of *Picea mariana*, so previously well-drained sites may be altered to host *Picea mariana*–lichen stands, with previously poorly-drained stands supporting *Picea mariana*–sphagnum stands (Lecomte & Bergeron, 2005; Lecomte *et al.*, 2006; Simard *et al.*, 2007).

B-soils can be hydric and formed essentially of peat (*Picea mariana* and sphagnum) (Re3 according to the MRN forest classification). In these situations, undergrowth vegetation is dominated by *Sphagnum* species and ericaceous shrubs, including *Ledum groenlandicum* and *Chamaedaphne calyculata*. Forest cover is mainly characterized by *Larix laricina* (stage S2), *Picea mariana–Larix laricina* (S3), *Picea mariana–Larix laricina* (S4), and *Picea mariana* (S5). Early-successional stands (S2, S3) dominate the landscape for the first 100–150 y before being replaced by late-successional stands (Carleton & Maycock, 1978; Cogbill, 1985; Gauthier, De Grandpré & Bergeron, 2000; Lecomte & Bergeron, 2005). Regardless of fire severity, these ecosystems retain a thick layer of organic material (more than 40 cm, edaphic paludification; Simard *et al.*, 2007) and exhibit low productivity.

1.4 Grouping and description of the response variables (Y-matrix, the 3 themes)

To synthesize the great number of response variables (Figure 2, Appendix I, Table I), a *k*-means grouping was performed on all the canonical axes of the RDA related to vegetation variables (the 3 themes) (R Development Core Team, 2010 and Vegan package) in order to form

9 groups (Appendix I, Figure 3). Each of these groups is associated with one of the 3 ecological gradients characterizing the study area (latitudinal, latitudinal-oblique, or longitudinal). Gradients were determined according to the spatial distribution of response variables (maps) and their position on the ordination diagrams (Figure 3 and Appendix III, Figure I). The gradients can be considered as the synthesis of each map describing a group.

-Four groups are closely related to the latitudinal gradient: AcruS (*Acer rubrum*), BepaF (*Betula papyrifera*), AbbaS (*Abies balsamea*), and PimaF (*Picea mariana*). The first 3 mainly characterize the southern portion of the study area. The AcruS group is restricted to the southern border of the study area. The BepaF group is well-represented in the entire southern portion. The AbbaS group has a wider distribution in the south. The PimaF group characterizes the northern portion of the study area.

-Two groups express the latitudinal-oblique gradient. The PimaAbba group (*Picea mariana–Abies balsamea*) is distributed mainly in the southeastern portion of the study area. At the opposite end of the gradient, the Wetland group becomes increasingly abundant in landscapes dominated by undulating or flat topography. Wetlands dominate the northwestern portion of the study area.

-Three groups characterize the longitudinal gradient and all are more abundant in the western portion of the study area. The PotrF group (*Populus tremuloides*) is confined to the southwestern portion of the study area, with a small extension into the southeastern portion. The PotrPimaF group (*Populus tremuloides–Picea mariana*) is more widely distributed. The PibaF group (*Pinus banksiana*) is abundant in the central and north-central portions of the study area.

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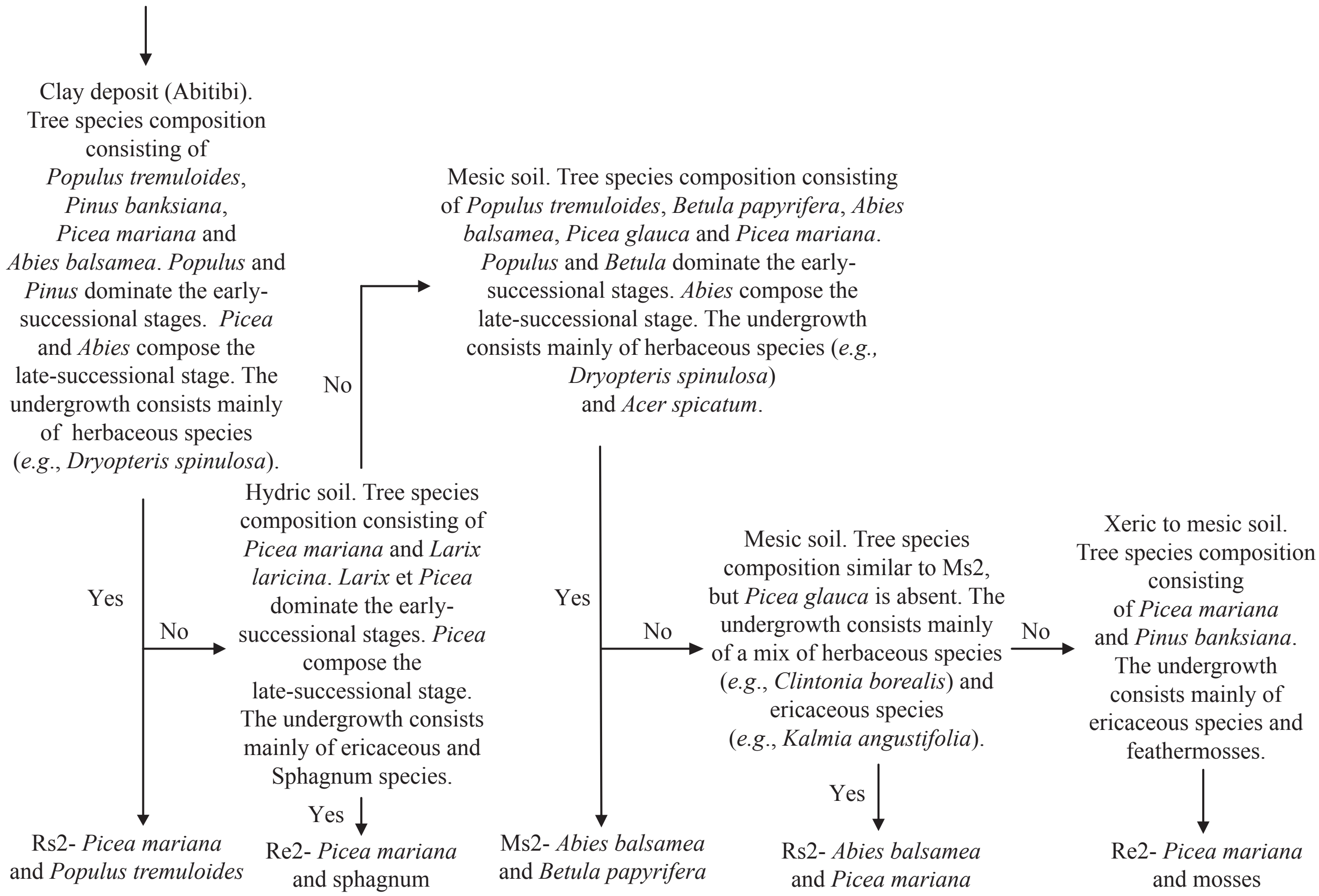
APPENDIX I, TABLE I. Response variables and their groups.

Theme	Response variables		Group	Vegetation variable
	Code	Description		
Species [a]	BepaS	Basal area for *Betula papyrifera*	GAcruS	BealF
	BealS	Basal area for *Betula alleghaniensis*		PotrAbbaF
	PiglS	Basal area for *Picea glauca*		BealS
	PimaS	Basal area for *Picea mariana*		AcruS
	AcruS	Basal area for *Acer rubrum*		ThocS
	PotrS	Basal area for *Populus tremuloides*		
	PibaS	Basal area for *Pinus banksiana*	GBepaF	BepaF
	AbbaS	Basal area for *Abies balsamea*		BepaAbbaF
	SaspS	Basal area for *Salix* spp.		BepaPimaF
	ThocS	Basal area for *Thuja occidentalis*		BepaS
				PiglS
Forest				Ms2S4
types [b]	Alru	Area for *Alnus rugosa* shrub communities		Ms2S5
	BepaF	Area for *Betula papyrifera*		Ms2S3
	BepaAbbaF	Area for *Betula papyrifera* and *Abies balsamea*		
	BepaPimaF	Area for *Betula papyrifera* and *Picea mariana*	GAbbaS	AbbaS
	BealF	Area for *Betula alleghaniensis*		Rs2S5
	Wetland	Area for non-forested wetlands	GPimaAbbaF	PimaAbbaF
	Heathland	Area for heathlands		AbbaF
	PimaF	Area for *Picea mariana*		
	PimaAbbaF	Area for *Picea mariana* and *Abies balsamea*	GPotrF	PotrF
	PibaF	Area for *Pinus banksiana*		PotrS
	AbbaF	Area for *Abies balsamea*		Ms2S2
	PotrF	Area for *Populus tremuloides*		
	PotrPimaF	Area for *Populus tremuloides* and *Picea mariana*	GPotrPimaF	Alru
	PotrAbbaF	Area for *Populus tremuloides* and *Abies balsamea*		Heathland
				PotrPimaF
Potential				SaspS
vegetation–				Rs2S2
successional				Rs2S4
stages [c]	Ms2S2	Plots for *Abies balsamea–Betula papyrifera* early successional stage		Rs2S3
	Ms2S3	Plots for *Abies balsamea–Betula papyrifera* intermediate stage		
	Ms2S4	Plots for *Abies balsamea–Betula papyrifera* facies stage	GPibaF	PibaF
	Ms2S5	Plots for *Abies balsamea–Betula papyrifera* late successional stage		PibaS
	Re2S2	Plots for *Picea mariana* early successional stage		Re2S4
	Re2S3	Plots for *Picea mariana* intermediate stage		Re2S3
	Re2S4	Plots for *Picea mariana* facies stage	GWetland	Wetland
	Re2S5	Plots for *Picea mariana* late successional stage		
	Rs2S2	Plots for *Abies balsamea–Picea mariana* early successional stage	GPimaF	PimaF
	Rs2S3	Plots for *Abies balsamea–Picea mariana* intermediate stage		PimaS
	Rs2S4	Plots for *Abies balsamea–Picea mariana* facies stage		Re2S2
	Rs2S5	Plots for *Abies balsamea–Picea mariana* late successional stage		Re2S5

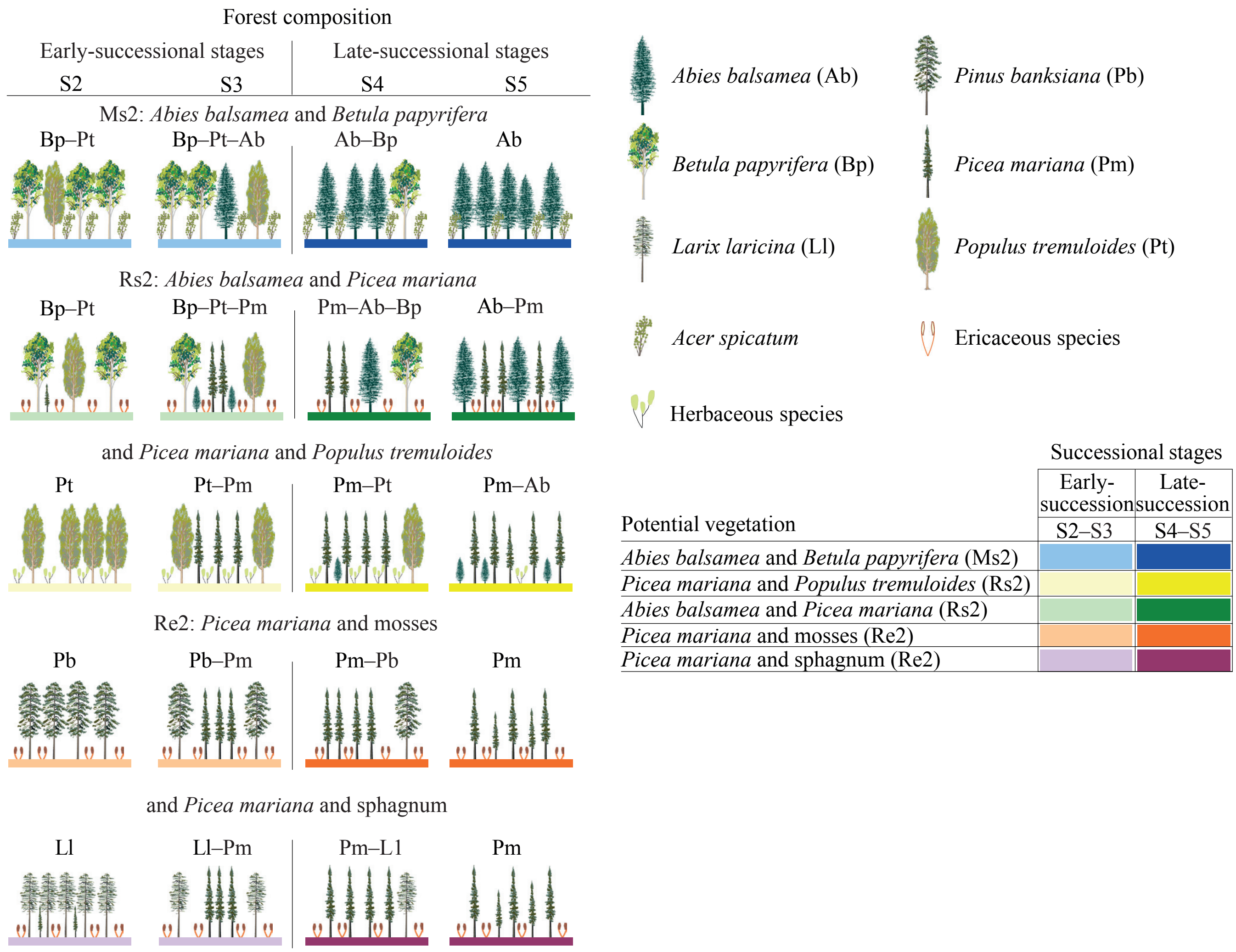
[a] Source: forest inventory plots.

[b] Source: forest maps developed during the 1980s and integrated in the SIFORT-2 geobase.

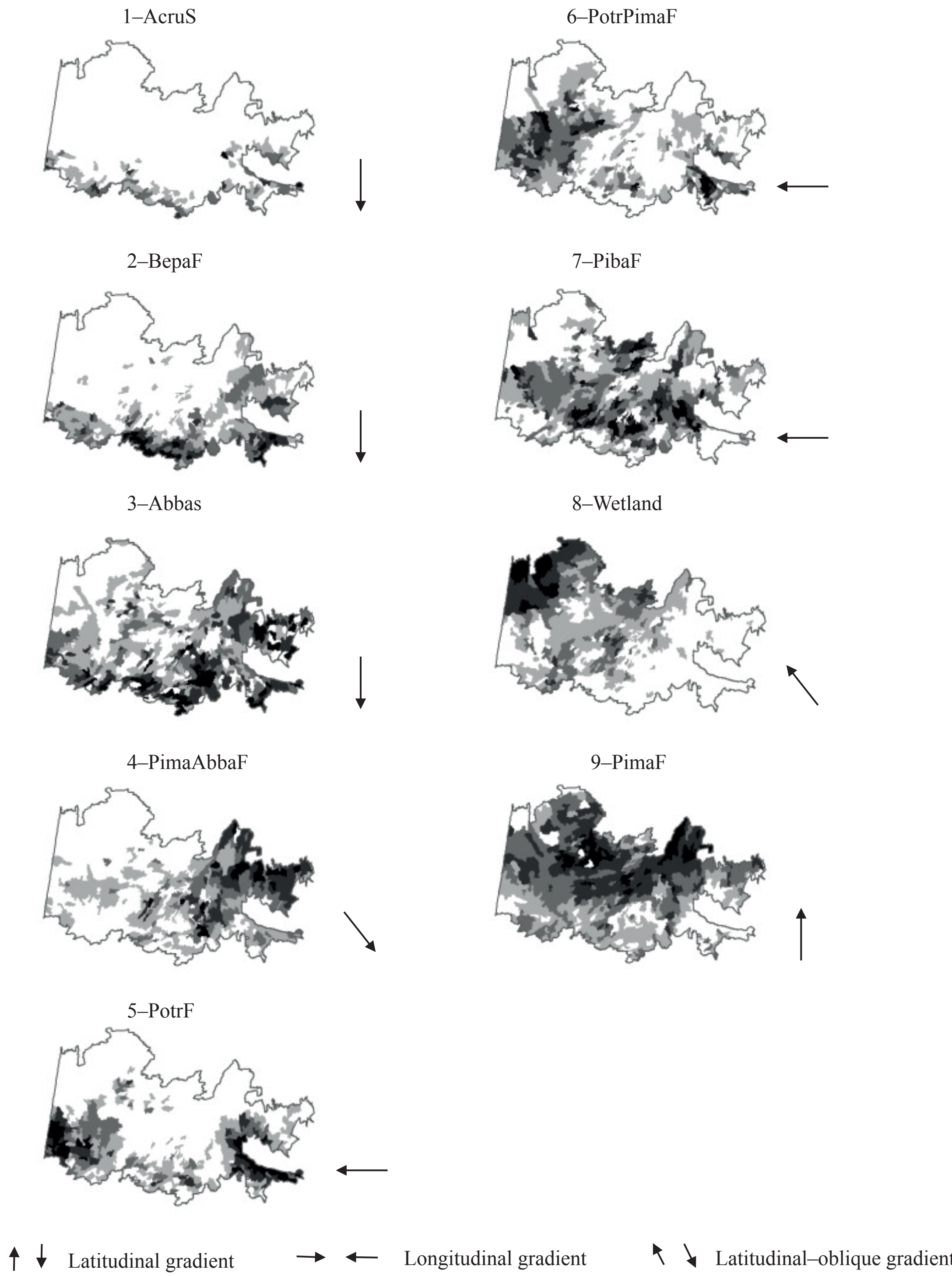
[c] Source: forest inventory and ecological plots.



APPENDIX I, FIGURE 1. Synthetic key for the identification of potential vegetation types considered in this study.



APPENDIX I, FIGURE 2. Description of potential vegetation types and their successional stages.



Appendix I, FIGURE 3. Groups of vegetation variables (1-AcruS to 9-PimaF) presented according to the variable used to name the group. The darker the shade of gray, the greater the abundance of the variable. An estimate of the ecological gradients is shown near the maps. The meaning of groups of variables is presented in Appendix I, Table I.

Appendix II

Definition of the explanatory variables by set (X-matrix)

This appendix provides additional information on the explanatory variables used in this study and gathered in a X-matrix (Legendre & Legendre, 2012). The X-matrix contains 4 sets of explanatory variables (total m = 44 variables): climate (m = 8), natural disturbances (m = 12), physical environment (m = 16), and human disturbances (m = 8) (Appendix II, Table I). Most of the variables describe a relative proportion of area or a relative proportion of forest inventory plots (Appendix II, Figure 1).

2.1 The first set: climate

The climate (C) of each of the 606 ecological districts was characterized using the BioSIM simulator designed by the Canadian Forest Service (Régnière, 1996; Régnière & St-Amant, 2007; Régnière, Saint-Amant & Béchard, 2014). Climatic variables were estimated for the center of each ecological district for the 1961–1990 period, based on observations from 37 meteorological stations throughout the study area (Appendix II, Figure 2). Data from 4 weather stations closest to each sampling location were used to define the climate, after compensating for differences in latitude, longitude and elevation using the BioSIM system. The choice of 4 stations is based on the mean absolute error obtained when this large a number of stations is considered and our goal of preserving a local description of the climatic variables for each ecological districts. Climate was calculated for the 1961–1990 period from 30 y of Environment Canada's daily weather data (Régnière, Saint-Amant & Béchard, 2014). Some variables describe the temperature regime (Gdd, Ef, Dwfc, Dwf, Mat, Appendix II, Table I), and others, rainfall (Ari, Vpd, Preci). The annual number of growing degree-days (Gdd) is the year sum of average daily temperatures, cumulative for the days on which the average temperature was >5 °C. The aridity index (Ari) corresponds to the sum of the monthly water deficits based on the difference between monthly precipitation and Thornthwaite potential evapotranspiration. The vapor pressure deficit (Vpd) is the difference (deficit) between the amount of moisture in the air and how much moisture the air can hold when it is saturated. This variable is expressed in millibars (mbar).

2.2 The second set: natural disturbances

Natural disturbances (ND) were described relative to the contemporary history (the last 150 y) of fires and spruce budworm outbreaks. The SIFORT-2 geospatial database provided data for variables describing the relative proportion of each ecological district affected by light insect outbreaks (Sbom), severe insect outbreaks (Sbos), windthrow (Wi), and natural fires (Fia). The number of years of infestation by spruce budworm (Sbon) and the frequency of fires per 100 km^2 (Fif) from 1938 to 1998 were described from archived data concerning natural and human disturbances (anhd) available from the Ministère des Ressources naturelles du Québec (MRN). The forest inventory plots provided information about the period and type of disturbance (fire, spruce budworm outbreaks). In each plot, 3 dominant or codominant trees were selected to calculate age and total height. Selected trees were cored at 1 m above the root collar in order to count the number of annual growth rings. Each plot was ascribed an age based on the oldest tree studied (based on the ring counts of 3 mature trees). These ages were standardized to obtain the age in 2000. Age data shows that natural disturbances were centered on 4 distinct periods: 1851 (origin prior to 1870), 1891 (1871–1900), 1921 (1901–1930) and 1951 (1930 and later). These periods were established by comparing the distribution and abundance of the plots classified by 10-y periods. Similar decades were pooled. This procedure explains why periods do not have the same duration. Each plot was also classified according to type of disturbance, based on 1) forest composition and 2) maps of natural disturbances (fires). Post-fire forest types formed categories (1851f, 1891f, 1921f) different from those following spruce budworm outbreaks (1851o, 1891o, 1921o). All the plots dominated by early-successional species, such as *Pinus banksiana* and *Betula papyrifera*, were associated with fires. By contrast, plots dominated by *Abies balsamea* were classified according to insect outbreaks dynamics. The proportion of plots belonging to the 1951 period and located in the area covered by logging (log1) were added to that of the 1851 period because we estimated that a large proportion of stands associated to the 1951 period originated from logging conducted in old stands (Grondin, 2014). For each of the 606 ecological districts, the relative proportion of plots dating from a specific period and type of origin (*e.g.*, 1921o) was calculated using all plots.

2.3 The third set: physical environment

Physical environment (PE) was described using a MRN database containing information on each ecological district, including the relative proportion of surficial deposits and physiographic variables (*e.g.*, mean altitude) (Saucier *et al.*, 1994; Robitaille & Saucier, 1998).

2.4 The fourth set: human disturbances

Human disturbances (HD) were analyzed mainly on the basis of the SIFORT-1 and SIFORT-2 geospatial databases, which used forest maps from the 1970s and 1980s, respectively. The SIFORT-1 database was developed following the same procedure as that described above for SIFORT 2 (see forest type theme). The relative proportions of the area covered by agriculture, fallow land, logging, and human–induced fires (as well as frequency for this last variable) were calculated from all tesserae in each of the 606 ecological districts. Because of the close correspondence between logging and forests originating from the period centered on 1951, these last forests were considered in the set of human disturbances when located in a logging area (Appendix II, Figure 3, Log1). According to the forest inventory plots (fip), stands dating to the period centered on 1951 are relatively rare (less than 10%), except in the landscapes affected by human activities (Grondin *et al.*, 2014).

2.5 GROUPING AND DESCRIPTION OF THE EXPLANATORY VARIABLES (X-MATRIX, THE 4 SETS)

To synthesize the great number of explanatory variables (Figure 2; Appendix II, Table I), a *k*-means grouping was performed on all the canonical axes of the RDA related to explanatory variables (the 4 sets) (Figure 2; R Development Core Team, 2010 and Vegan package) in order to form 11 groups (Figure 3; Appendix II, Figure 3). Each of these groups occupies a specific portion of the study area and is associated to one of the 3 ecological gradients characterizing the study area (latitudinal, latitudinal-oblique, longitudinal). Gradients were determined according to the spatial distribution of explanatory variables (maps) and their position on the ordination diagrams (Figure 3 and Appendix III, Figure 2). The gradients can be considered as the synthesis of each map describing a group (Appendix II, Figure 3).

-Three groups are closely related to the physical environment set of explanatory variables: Ele, D_7, and D_4ga. The first 2 groups have an opposite distribution along the latitudinal-oblique gradient. The third group is restricted to the western position of the study area and is related to the longitudinal gradient.

-Four groups describe the diversity of the natural disturbances. Two of these, Sbom and 1851f, are strongly related to the latitudinal gradient. Sbom characterizes the southern portion of the study area and 1851f, the northern portion. Groups 1921f and 1891f are mainly observed in the central portion. 1921f is more abundant in the western portion of the study area and 1891f in the western-central portion; both groups belong mainly to the latitudinal gradient.

-Two groups are associated to climate. The first, Gdd, includes the variables characterizing the latitudinal gradient. The second, Ari, is composed of variables associated with the longitudinal gradient.

-Two groups also describe human disturbances. The first, Log1, characterizes the human activities that occurred in the southern portion of the study area and is associated with the latitudinal gradient. The second, Hf1, relates to the variables characterizing mainly the southwestern portion of the study area and, to a lesser extent, the southeastern portion. The longitudinal gradient is associated with this group.

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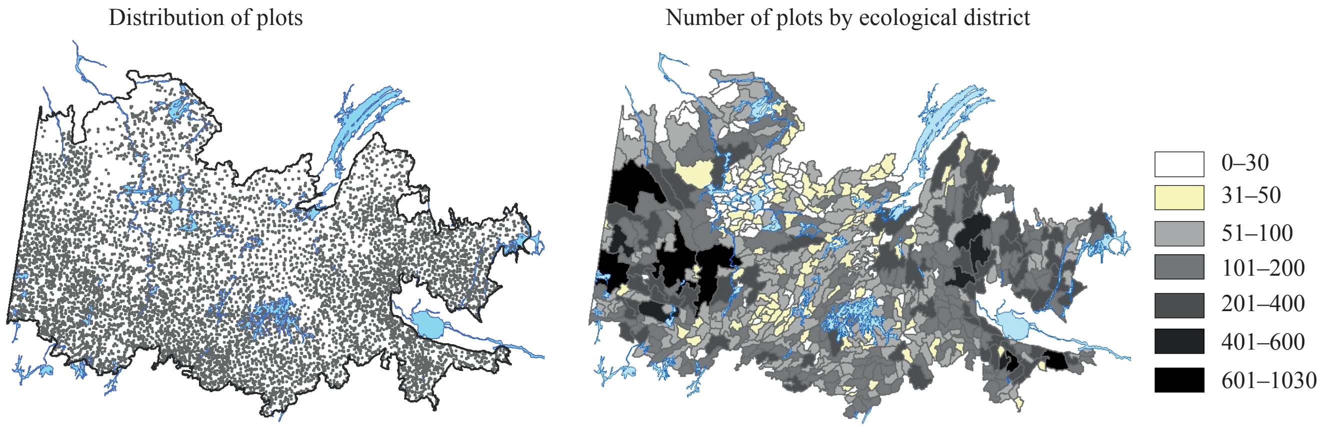
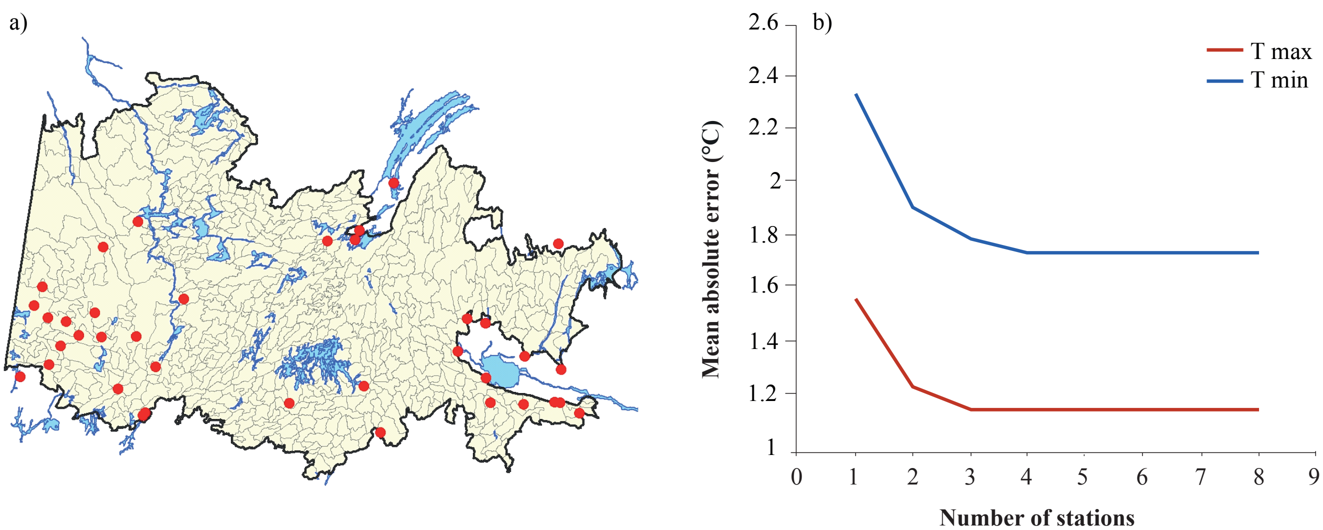
APPENDIX II, TABLE I. Explanatory variables and their groups. Data sources: anhd: archival data of natural and human disturbances; bios: BioSIM software; ded: database of ecological districts; fip: forest inventory plots; gs1: geospatial database Sifort-1; gs2: geospatial database Sifort-2; sfl: shape files of lakes.

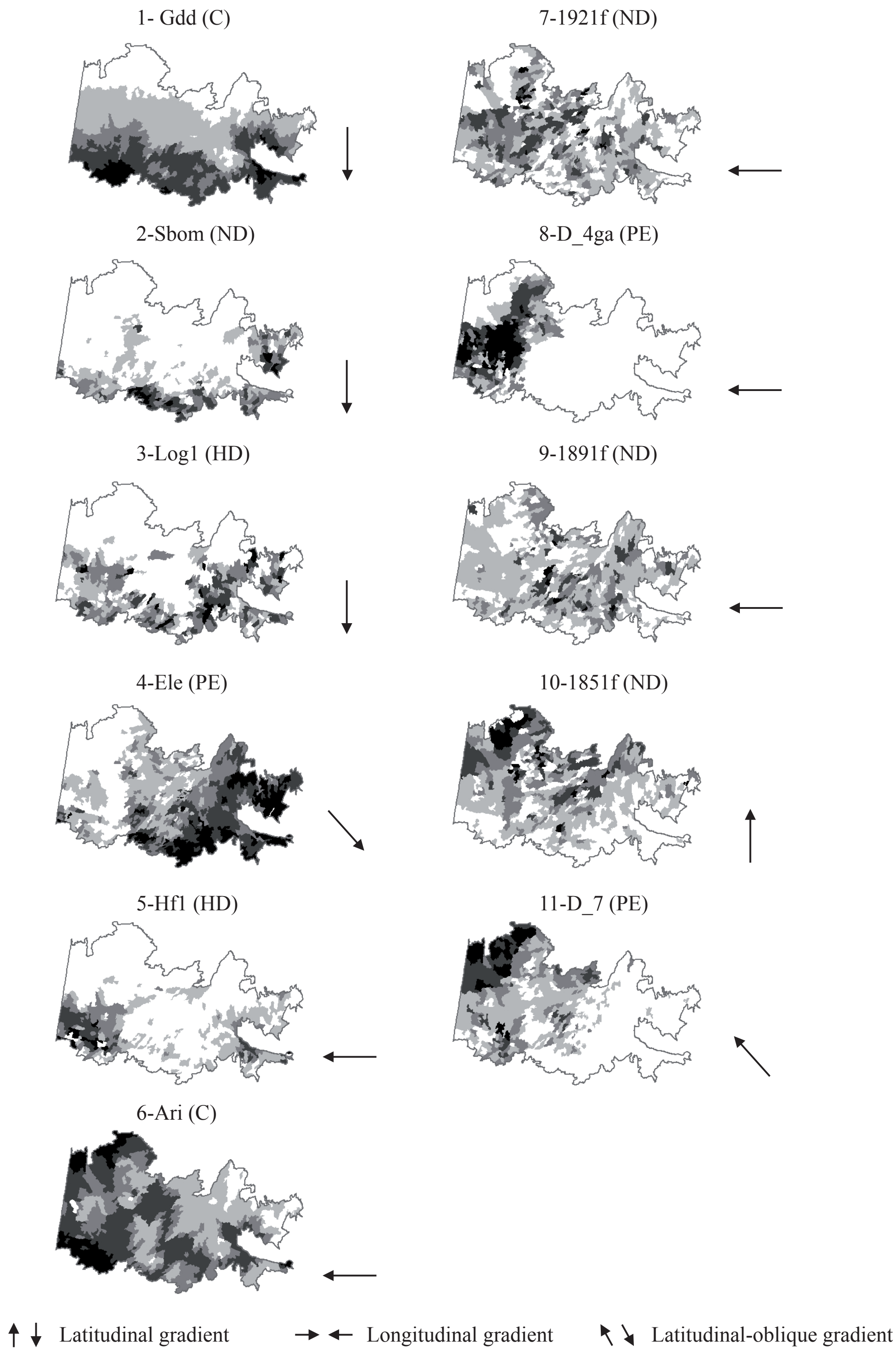
	Explanatory variables			
Set	Code	Description and data source	Group	Explanatory variables
Physical environment	Malt	Mean altitude (m) (ded)	GGdd	Dwfc
	Ele	Absolute difference of topographic elevation (m) (ded)		Mat
	D_wa	Relative proportion of area covered by water (ded)		Gdd
	D_4ga	Area covered by glaciolacustrine fine-textured (clay) surficial deposits (ded)		Dwf
	D_4gs	Area covered by glaciolacustrine coarse-textured (sand) surficial deposits (ded)		Ef
	D_2a	Area covered by juxtaglacial deposits (ded)	GSbom	Sbon
	D_2b	Area covered by proglacial deposits (ded)		Sbom
	D_7	Area covered by organic deposits (ded)		1921o
	S_a	Area covered by slopes below 4% (ded)		Sbos
	S_b	Area covered by slopes ranging from 4 to 8% (ded)	GLog1	Log2
	S_c	Area covered by slopes ranging from 9 to 15% (ded)		1951
	S_d	Area covered by slopes over 15% (ded)		Log1
	D_1a	Area covered by thick till (more than 1 m) (ded)		Hf2
	D_1ar	Area covered by thin till (less than 1 m) (ded)	GEle	D_r
	D_r	Area covered by rock (ded)		L_100 km^2
	L_100 km^2	Mean number of lakes per 100 km^2 (sfl)		D_1a
Natural disturbances	1851o	Plots originating from spruce budworm outbreaks before 1870 (fip)		D_2a
	1851f	Plots originating from fires before 1870 (fip)		D_2b
	1891o	Plots originating from spruce budworm outbreaks between 1870 and 1900 (fip)		D_1ar
	1891f	Plots originating from fires between 1870 and 1900 (fip)		Ele
	1921o	Plots originating from spruce budworm outbreaks between 1901 and 1930 (fip)		S_b
	1921f	Plots originating from fires between 1901 and 1930 (fip)		S_c
	Fia	Area covered by natural fires (gs2)		S_d
	Wi	Area covered by windthrow (gs2)		Malt
	Sbom	Area covered by light spruce budworm outbreaks (gs2)		Preci
	Sbos	Area covered by severe spruce budworm outbreaks (gs2)		1851o
	Fif	Frequency of natural fires per 100 km^2 from 1938 to 1998 (anhd)		1891o
	Sbon	Number of years of infestation by spruce budworm from 1938 to 1998 (anhd)		Fif
Climate	Ari	Aridity index (bios)	GHf1	Ag1
	Gdd	Annual number of growing degree-days (bios)		Fa1
	Vpd	Vapor pressure deficit (total daily deficit [in mbar] from June to August) (bios)		Ag2
	Ef	Early frost (Julian day corresponding to the first frost) (bios)		Hf1
	Dwfc	Number of consecutive days without freezing (bios)	GAri	Vpd
	Dwf	Total number of days without freezing (bios)		Ari
	Preci	Rainfall during the growing season (mm) (bios)	G1921f	1921f
	Mat	Annual average temperature (bios)	GD_4ga	D_4gs
Human disturbances	Ag1	Area covered by agriculture during the 1970s (gs1)		D_4ga
	Ag2	Area covered by agriculture during the 1980s (gs2)	G1891f	D_wa
	Log1	Area covered by logging during the 1970s (gs1)		1891f
	Log2	Area covered by logging during the 1980s (gs2)	G1851f	1851f
	Hf1	Frequency of human-caused fires per 100 km2 from 1938 to 1998 (anhd)		Wi
	Hf2	Area covered by human-caused fires from 1938 to 1998 (anhd)		Fia
	Fa1	Area covered by fallow land (gs1)	GD_7	S_a
	1951	Relative proportion of stands originating later than 1930 (fip)		D_7



Appendix II, Figure 1. Forest inventory plots established by the Ministère des Ressources naturelles du Québec (MRN) and used to describe some vegetation themes and explanatory variables. These plots were produced between 1970 and 2000 (n = 53 635).



Appendix II, Figure 2. Climate: a) Distribution of the meteorological stations used to describe the climatic explanatory variables across the study area; b) Mean absolute error (°C) according to the number of meteorological stations.



APPENDIX II, FIGURE 3. Groups of explanatory variables (1-Gdd to 11-D_7) presented according to the variable used to name the group. The darker the shade of gray, the greater the abundance of the variable. An estimate of the ecological gradients is shown near the maps. The meaning of groups of variables is presented in Appendix II.

Appendix III

Overlap of vegetation themes and sets of explanatory variables

3.1 GENERAL DESCRIPTION OF THE OVERLAP

This study is composed of 3 main sections: 1) describing the ecological gradients, 2) understanding of the overlap between response and explanatory variables and 3) quantifying the overlap by using variation partitioning. In the main part of the article, sections 1 and 3 have been discussed. The overlap was briefly presented at the end of the second section in Figure 3. This appendix provides more information on the overlap, considered as an important step to interpret the results of the variation partitioning. To characterize the overlap, we defined geographical units for each vegetation theme and each set of explanatory variables and used their location on ordination diagrams to examine the overlap between the 2 types of data (Appendix III, Figures 1 and 2). To define geographical units, separate *k*-means cluster analyses were carried out on raw data from each vegetation theme and each set of explanatory variables. Vegetation data characterizing each ecological district was subjected to Hellinger transformation prior to clustering. More specifically, each of the abundance values of a site was divided by the sum of the abundance values of the entire site, then made the square root of this value . Hellinger minimizes the effect of double-zeros, it flattened the data, attenuated their relative weight. The final number of clusters was based on the Calinski-Harabasz criterion (Borcard, Gillet & Legendre, 2011) and on our knowledge of descriptive and explanatory variables. Calinski-Harabasz criterion is the ratio between the sum of squares between-cluster/sum of squares within-cluster. The ecological districts belonging to each geographical unit were related to the canonical axes of the RDA used to describe the ecological gradients (Figure 2). More specifically, the centroids of each geographical unit were superimposed on ordination diagrams (Appendix III, Figures 1 and 2).

Ordination diagrams make it possible to compare the geographical units of the 3 vegetation themes (Appendix III, Figure 1) with those of the 4 sets of explanatory variables (Appendix III, Figure 2). On both ordination diagrams, axis 1 is vertical and axis 3 is horizontal, to reflect the geographical organization of the territory. Here, axis 3 was given precedence over axis 2, because it best describes the latitudinal-oblique gradient (Grondin *et al.*, 2014). Below are a few key observations regarding the overlap between the vegetation themes and sets of explanatory variables.

1- Geographical unit F1 (Appendix III, Figure 1a) of the forest type theme, located in the southeastern part of the study area, is characterized by a high abundance of the *Betula papyrifera* group (GBepaF) (Appendix III, Figure 1b). Unit F1 has affinities with unit F2 of the same theme and also with units belonging to other themes (PV1-2, S1) (Appendix III, Figure 1b). These affinities are highlighted by the close orthogonal projections of the unit centroids on the vegetation variable vectors (Legendre & Legendre, 2012).

2- The relationship between unit F1 on the first ordination (Appendix III, Figure 1b) and the explanatory variables can be established by analyzing the corresponding portion of the second ordination (Appendix III, Figure 2b), which shows that unit F1 is closely related to 4 explanatory variables: 1) GGdd (climate: highest annual number of growing degree-days), 2) GSbom (natural disturbances: high proportion of area covered by a light spruce budworm outbreak), 3) GEle (physical environment: hilly topography), and 4) GLog1 (high proportion of area affected by logging). There are also links between F1 and some geographical units of explanatory variables, more specifically C1, ND1, HD1, and PE1 (Appendix III, Figure 2b). All these elements characterize the southeastern portion of the study area. The fact that the same position is occupied by vegetation variables and their geographical units on the first ordination, and by explanatory variables and their geographical units on the second ordination, confirms their overlap. A similar description can be made for units F2 to F6.

F2 characterizes the southwestern portion of the study area. It is related to 2 groups of explanatory variables (GHf1 and GAri, Appendix III, Figure 2b) and 2 geographical units (HD2 and C2) (Appendix III, Figure 2b).

F3 is located in the central-eastern portion of the study area (Appendix III, Figure 1a), where the GPimaAbbaF vegetation group is found in abundance (Appendix III, Figure 1b; Appendix I, Figure 2). This portion is linked to some geographical units. PE2, C3, and HD3 have a more southern distribution than HD4, C4, and ND2 (Appendix III, Figure 2).

F4 characterizes the central-western portion of the study area (Appendix III, Figure 1a). Among the geographical units linked to F4, some are more closely related to the western portion. This is the case for 2 groups of environmental variables (G1921f, GD_4GA, Appendix II, Figure III) and 4 geographical units of explanatory variables (PE3, ND4, HD5, PE6, C5, Appendix III, Figure 2). Some geographical units are located in both the western and central portions of the study area (PE5, HD6, ND3, Appendix III, Figure 2).

F5 belongs to the northeastern portion of the study area (Appendix III, Figure 1a), associated with the G1851f group of explanatory variables (fires of the 1851 period) (Appendix III, Figure 2b; Appendix II, Figure 3). Geographical units C6 and ND5 are located in a more eastern position than the other units, which show affinities with the central-northern portion of the study area (ND6, HD7, C7, PE4) (Appendix III, Figure 2).

F6 is strongly associated with the northwestern portion of the study area (Appendix III, Figure 1a). Organic soils are abundant (GD_7, Appendix III, Figure 2b; Appendix II, Figure 3). Geographical units PE7, ND7, and C8 are closely related to this study area. C9 is more widely distributed (Appendix III, Figure 2).

The spatial structure of the study area, described on both ordinations (Appendices III, Figure 1 and 2), makes it possible to identify 3 regions closely related to those delineated by Grondin *et al.* (2014):

- R1 is located in the southern part of the territory. Unit F1, described above, belongs to this region.

- R2, in the center, is defined by units such as F3 (Appendix 3a). The *Picea mariana–Abies balsamea* forest type (GPimaAbbaF) is the most abundant (Appendix III, Figure 1b). The F3 geographical unit (Appendix III, Figure 1b) is first closely related to PE2 (physical environment, Appendix III, Figure 2b), characterized by a hilly topography (GEle, Appendix II, Figure 3), second to ND2, where the stands originating from the 1891 period (1891f) are important, third to C3, considered as a relatively mild and wet climate, and fourth to HD3, where much of the area is affected by recent logging (since 1970) (Appendix III, Figure 2).

- R3 corresponds to the northern part of the territory. Unit F5 (Appendix 3a), belonging to this region, is dominated by the *Picea mariana* forest type (PimaF) (Appendix 3ab). It is first closely related to the PE4 physical environment unit (Appendix III, Figure 2b), characterized by an undulated topography (Ele, Appendix II, Figure 3), second to ND5, with abundant old forests (1851f), third to C7, considered as a relatively cold climate, and fourth to HD7, defined by minimal human activities.

In regions R1 and R2, natural (ND) and human disturbances (HD) show some overlap, which is described by two combinations of groups of variables (Appendix III, Figure 2). The first associates light spruce budworm outbreaks (GSbom) and logging activities (GLog1), in close relation to the ND1 and HD1 geographical units. The second combination concerns natural fires of the 1921 period (G1921f) and human-induced fires (GHf1), which are both closely related to the ND4, HD2, and HD5 geographical units, located in the southeastern and southwestern parts of the study area.

3.2 Maps of vegetation themes

Another goal of this appendix is to provide details on the maps of vegetation themes and sets of explanatory variables (Appendix III, Figure 3 and Table I). Each map is accompanied by an estimate of its gradients. For example, climate shows an important latitudinal gradient expressed by the descriptive variables of the thermal regime. The longitudinal gradient (aridity regime) should also be taken into account, due to an obvious increase in aridity and a decrease in rainfall from east to west. The gradients can be considered as the synthesis of each map.

The tree species map is composed of 5 geographical units (S1 to S5). Unit S1 consists mainly of *Betula papyrifera* (BepaS), *Picea mariana* (PimaS), and *Abies balsamea* (AbbaS). *Abies balsamea* (AbbaS) is well-represented and occurs regularly in hardwood and softwood stands as a subdominant or companion species. Although much more scattered, *Picea glauca* (PiglS) regularly accompanies *Abies balsamea* (AbbaS). Temperate species (BealS) are rare and at the northern limit of their distribution. Unit S2 is dominated by two forest species, *Populus tremuloides* (PotrS) and *Picea mariana* (PimaS). *Betula papyrifera* (BepaS), *Pinus banksiana* (PibaS), and *Abies balsamea* (AbbaS) are also well-represented. Unit S3 shows a dominance of *Picea mariana* (PimaS). *Abies balsamea* (AbbaS) and *Betula papyrifera* (BepaS) are other important species in these forest stands. While Unit S4 is also dominated by *Picea mariana* (PimaS), it shows an increase in *Pinus banksiana* (PibaS) and a decrease in *Abies balsamea* (AbbaS) and *Betula papyrifera* (BepaS), which distinguish it from unit S3. Finally, unit S5 is characterized by high proportions of *Picea mariana* (PimaS), with other components being sparse.

The forest types are distributed according to 6 geographical units (F1 to F6). Unit F1 consists mainly of forests dominated by *Betula papyrifera* (BepaF, BepaPimaF, BepaAbbaF). *Picea mariana* forest stands (PimaF) are relatively abundant. *Betula alleghaniensis* stands (BealF) are very poorly represented and are at their northern limit of distribution. Unit F2 is characterized by abundant *Populus tremuloides* stands (PotrF, PotrPimaF); *Picea mariana* stands are also well-represented. Although scarce, *Alnus rugosa* (Alnu) and well-drained areas of non-forest vegetation (heathland) reach their highest levels of cover. Unit F3 shows a marked decrease in hardwood and mixed stands to the benefit of *Picea mariana* forest stands (PimaF). *Picea mariana* and *Abies balsamea* stands (PimaAbbaF) and *Abies balsamea* stands (AbbaF) are well-represented and reach their maximum cover in the study area. *Pinus banksiana* stands (PibaF) are abundant locally. Three ecosystems dominate unit F4: *Picea mariana* stands (PimaF), *Pinus banksiana* stands (PibaF), and non-forested peatlands (Wetland). *Pinus banksiana* stands (PibaF) reach their maximum cover. F5 is dominated by *Picea mariana* stands (PimaF), with *Pinus banksiana* (PibaF) and wetlands also being well-represented. Finally, F6 is dominated by non-forested peatlands (Wetland) and *Picea mariana* stands (PimaF).

Under the theme of potential vegetation–successional stages (PV1-PV6), the study area is divided into 4 geographical units. Unit PV1-2 contains the most stands belonging to the *Abies balsamea* and *Betula papyrifera* potential vegetation type (Ms2), particularly in the early-successional stage (Ms2S2). Temperate elements are scattered, but can be considered a particularity of this unit; they are represented by *Abies balsamea* and *Betula alleghaniensis* (Ms1), as well as by the *Abies balsamea* and *Thuja occidentalis* (Rs1) potential vegetation types. Unit PV3-4 shows a drastic reduction of forest stands belonging to Ms2. While not dominant, Rs2 potential vegetation is more abundant than elsewhere. All successional stages (S2 to S5) are represented in equal proportions. The Re2 potential vegetation type dominates, especially in the early-successional stage (Re2S2), which is mainly represented by *Pinus banksiana* stands (PibaF) of varying ages and by *Picea mariana* stands (PimaF) of 90 y of age or less. In unit PV5, Ms2 is rare and mostly located in an area protected from frequent fires (sheltered topography). Stands belonging to Rs2 show a slight decrease in area compared to the PV3-4 unit. This favours the Re2 potential vegetation type, represented by stands of early (Re2S2) or late-successional (Re2S5) stages. Finally, unit PV6 is characterized by an increase in late-successional stands belonging to the *Picea mariana* potential vegetation type (Re2S5) and, to a lesser extent, the *Abies balsamea* and *Picea mariana* potential vegetation type (Rs2S5).

3.3 MAPS OF SETS OF EXPLANATORY VARIABLES

The physical environment is described by 7 geographical units (PE1 to PE7). PE1 is marked by the greatest absolute difference between the highest and lowest elevations of an ecological district (Ele, topographic elevation) and steep slopes (S_c and S_d). The topography is hilly and thin till surficial deposits are relatively abundant. In unit PE2, the topography is less accentuated (undulated), with a lower proportion of steep slopes and an increasing proportion of thick till. Unit PE3 continues the gradation of well-expressed topography toward flattened units. The absolute difference in elevation decreases and the proportions of low slopes (S_a), thick till (D_1a), proglacial deposits (D_2b), and organic deposits (D_7) increase. Unit PE4 shows similar changes in physical environment. Low slopes (S_a) increase significantly and the topography is typically undulated. For the first time, organic deposits cover more than 10% of the unit. However, the Gouin Reservoir, which is not a naturally-occurring land feature, represents a large portion of this area. Unit PE5 forms a transition between units dominated by glacial deposits and those formed mainly by glaciolacustrine and organic deposits. The most abundant surficial deposits are glaciolacustrine fine texture (D_4ga), thick till (D_1a), and organic deposits (D_7). In this unit, the presence of rock (D_R) is generally associated with sites washed by the waves of post-glacial lakes. Unit PE6 forms a vast plain of glaciolacustrine deposits (D_4ga) interspersed with organic material (D_7). The topography is typically flat. Unit PE7 corresponds to poorly-drained lowland, clearly dominated by organic deposits (D_7, ombrotrophic peatlands).

The differing characteristics of natural disturbances make it possible to subdivide the study area into 7 geographical units (ND1 to ND7). Unit ND1 is strongly associated with spruce budworm outbreaks. Nearly 20% of this area shows evidence of outbreaks, according to forest maps of the 1980s (Sbom). The mean number of years of infestation during the 1938-1998 period is close to 20 (Sbon). While most stands currently dominated or subdominated by *Abies balsamea* date back to the spruce budworm outbreak that occurred at the beginning of the last century (1921o), some date back to earlier outbreaks (1891o, 1851o). Some stands might have originated from an outbreak in the middle of the last century (1951 period), but we chose to classify all these forest stands with the set of human disturbances, because in the context of our study, it was impossible to distinguish between stands (dominated or subdominated by *Abies balsamea*) associated with insect infestation and those linked to logging. We hypothesize that only a few stands date back to the last mid-century outbreak. Unit ND2 differs from unit ND1 mainly by its fire-dependent forest dynamics. The relative proportion of stands in this unit affected by insect outbreaks (1921o, 1891o, 1851o) is close to 30%, compared to 45% in unit ND1. Many forest stands originate from fires (50%), and slightly more date back to the 1921 period (1921f) than to earlier periods (1891f, 1851f). In unit ND3, stands having reached the facies or late-successional stages (abundance of *Abies balsamea*) and affected by budworm outbreaks (1921o, 1891o, 1851o) characterize only 15% of the forest inventory plots. Furthermore, stands originating from fires of the 1921 period (1921f) are at their optimum. Unit ND4 is similar to ND3, with stands from fires of the 1921 period (1921f) still abundant. Compared to ND3, ND4 shows a decrease in stands from the 1891 period (1891f), and an increase in stands affected by insect outbreaks (1921o). Stands affected by spruce budworm (1921o) characterize the small hills of mixed forest (*Abies balsamea* and hardwood species) dispersed over the vast clay plain. Units ND5, ND6, and ND7 all have a high proportion (more than 30%) of stands that grew after the fires of the 1851 period (1851f). ND5 has some old-growth forests affected by insect outbreaks (old *Abies balsamea* forest stands in the mountains). These stands originate from several outbreaks (1921o, 1891o, and 1851o) on close to 15% of the forest inventory plots. Although the fires of the 1921 period are well-represented, they are less abundant than in unit ND6, where young stands (1921f) are also more abundant than older ones (1851f). We presume that young stands grow mainly on xeric (glaciofluvial deposits) soils and that old stands are more frequent on hydric soils. Finally, ND7 is a favourable area for old-growth forests because of the abundance of organic deposits (D_7). Stands originating from the 1851 fire period (1851f) cover more than 40% of the unit.

The climate of the study area was divided into 9 geographical units (C1 to C9). Unit C1 is characterized by a relatively high mean annual temperature (Mat), a high annual number of growing degree-days (Gdd), a high number of days without frost (Dwf, Dwfc), and abundant rainfall (Preci). Unit C2 has a thermal balance similar to C1. However, since it is located at the southwestern portion of the study area, aridity (Ari) and vapor pressure deficit (Vpd) are relatively high, and rainfall (Preci) is relatively low. Units C3, C4, and C5, forming the central portion of the study area, are colder than the previous ones. Their mean annual temperature (Mat) is between 0 and 1° C, with 1200 to 1300 annual growing degree-days (Gdd) and 90 to 95 consecutive days without freezing (Dwfc). The main differences between units C3, C4, and C5, which characterize the longitudinal gradient, are 1) an increase in aridity index (Ari) and vapor pressure deficit (Vpd), and 2) a decrease in precipitation (Preci). Units C6, C7, C8, and C9, forming the northern portion of the study area, are colder than the others. The mean annual temperature (Mat) is below 0 °C, the annual number of growing degree-days (Gdd) is generally below 1200, and the number of consecutive days without freezing (Dwfc) is less than 90. The main differences between units C6, C7, and C8, which characterize the longitudinal gradient, are an increase in aridity index (Ari) and vapor pressure deficit (Vpd), and a decrease in precipitation (Preci). The longitudinal weather gradient is not observed in unit C9.

Human disturbances define 7 geographical units (HD1 to HD7). HD1 has been affected by logging for at least

70 y (1951, Log1, Log2). The variable 1951 indicates the relative proportion of plots with the oldest tree dating back no further than 1930, when intensive logging began in the study area (meaning that the oldest tree was younger than 70 y old in 2000). In HD1, forest stands originating from the 1951 period are present but not significant (close to 10%). About 15% of the area is affected by logging, both on the first forest maps used (1970 period, SIFORT-1) and on more recent maps (1980 period, SIFORT-2). In unit HD2, on the other hand, agriculture (Ag1, Ag2) and fallow lands define an agro-forest landscape. The frequency of human-induced fire (Hf1) reaches its highest values. The relative proportion of the area affected by human activities during the 1938–1988 period is high (HF2), but the impact of recent logging (Log1, Log2) is minimal (less than 10%). Unit HD3 had the highest rate of forest harvesting in the 1970s (Log1) and 1980s (Log2). Unit HD4 was the most affected by logging prior to 1970, as indicated on maps based on aerial photos dating back to the 1960s. However, some stands harvested during the 1920–1940 period and considered young forests do not appear as logged areas on 1970s maps. Consequently, logging areas are underestimated on the 1970s forest maps. Logging stretched mainly along a series of small forest villages that follow a railway line crossing the unit. Logging and coal-fired steam locomotives were responsible for some human-induced fires (Hf1, Hf2). Unit HD5 is also strongly influenced by human activities, with a long history of logging (Log1, Log2) and numerous human-induced fires (Hf1). The strong effect of human activities in units HD2 and HD5 is reflected in the abundance of human-induced fires that favoured the development of *Populus tremuloides*. Farther north, unit HD6 was logged extensively during the 1980s (Log2). These activities have since moved still further north (HD7).

In order to improve the methodology used in this study, maps of vegetation themes and sets of explanatory variables could have been elaborated using fuzzy clustering (De Cáceres, Font & Oliva, 2010; Borcard, Gillet & Legendre, 2011; Duff, Bell & York, 2013). In the first stages of development, fuzzy classification might enable vegetation patterns to be summarized using the concept of community, while at the same time recognizing that such communities need not be entirely spatially exclusive. Fuzzy methods have been used to represent uncertainty in the delineation of vegetation classes. These methods might show that some ecological districts are intermediate between 2 geographical units.

3.4 Relations between geographical units of sets of explanatory variables and unique variation of the variation partitioning

Maps of vegetation themes and sets of explanatory variables have also been used to understand the significance of the unique variation (Figure 2b), particularly the unique variation associated to natural disturbances. Appendix III, Table I compares the natural disturbances, characterized by 3 distinct sections (south, central, north), and the physical environment. This last set shows a gradual increase or decrease in regard to explanatory variables from the southeastern to the northwestern part of the study area along the latitudinal-oblique gradient.

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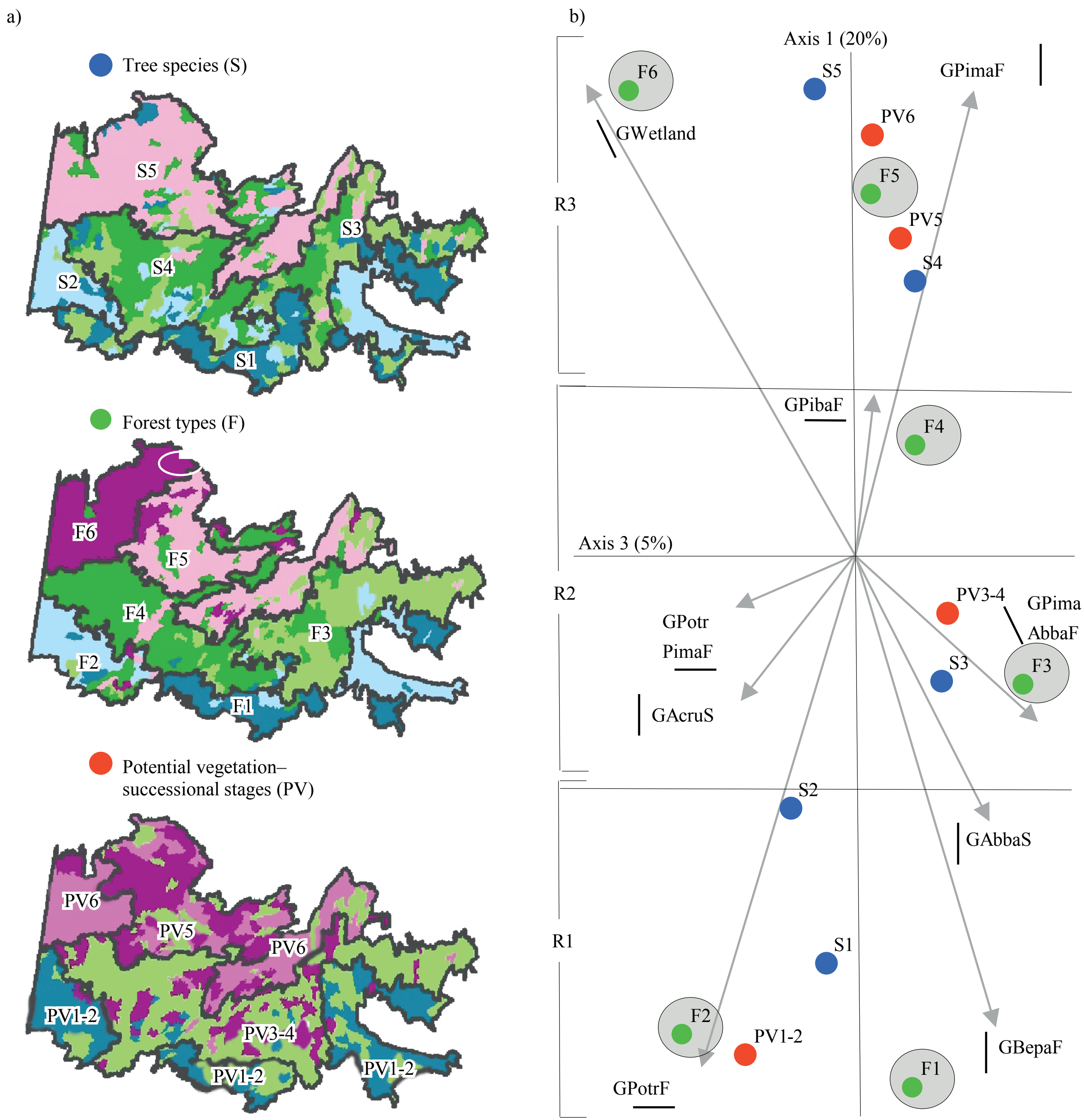
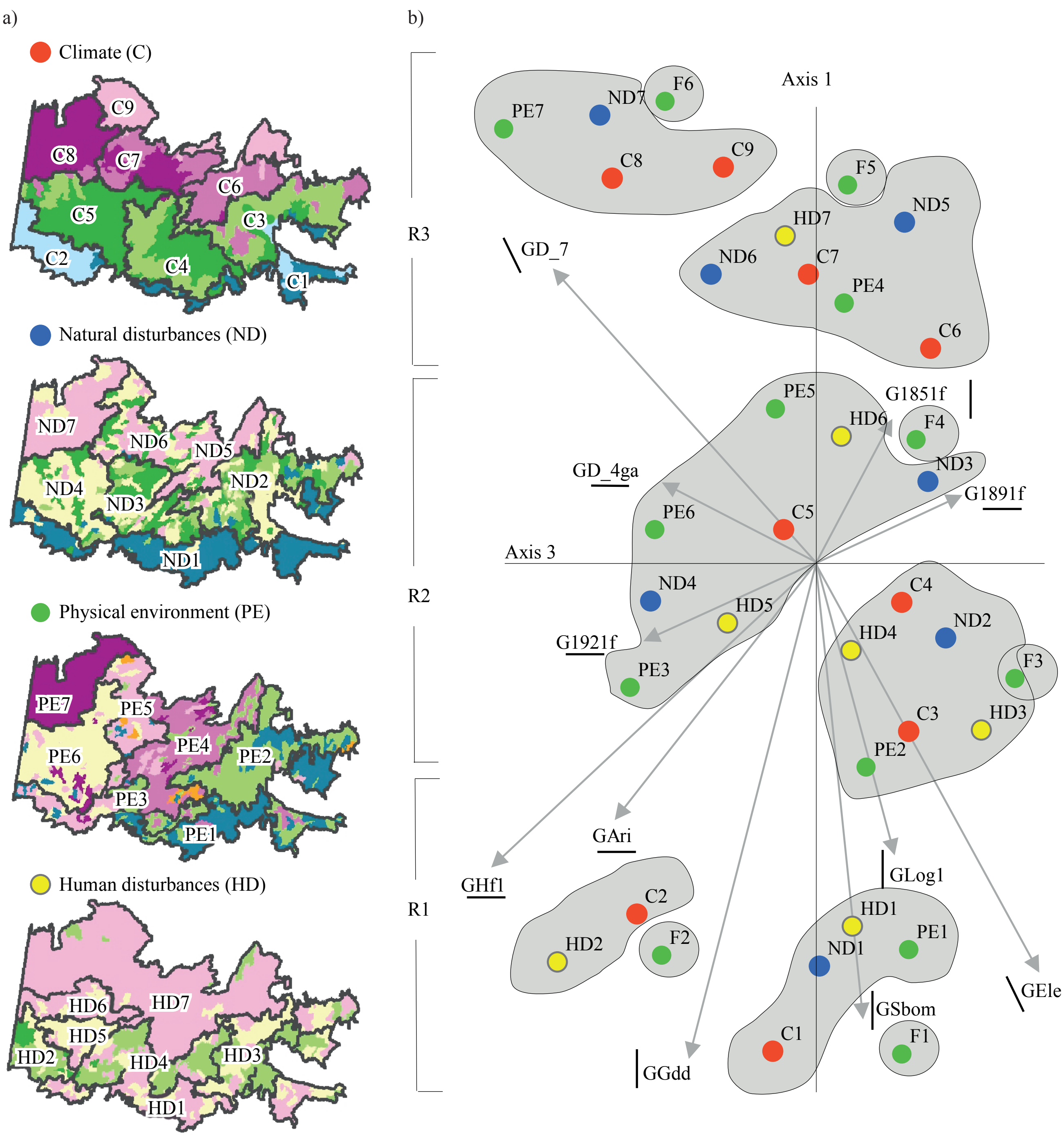
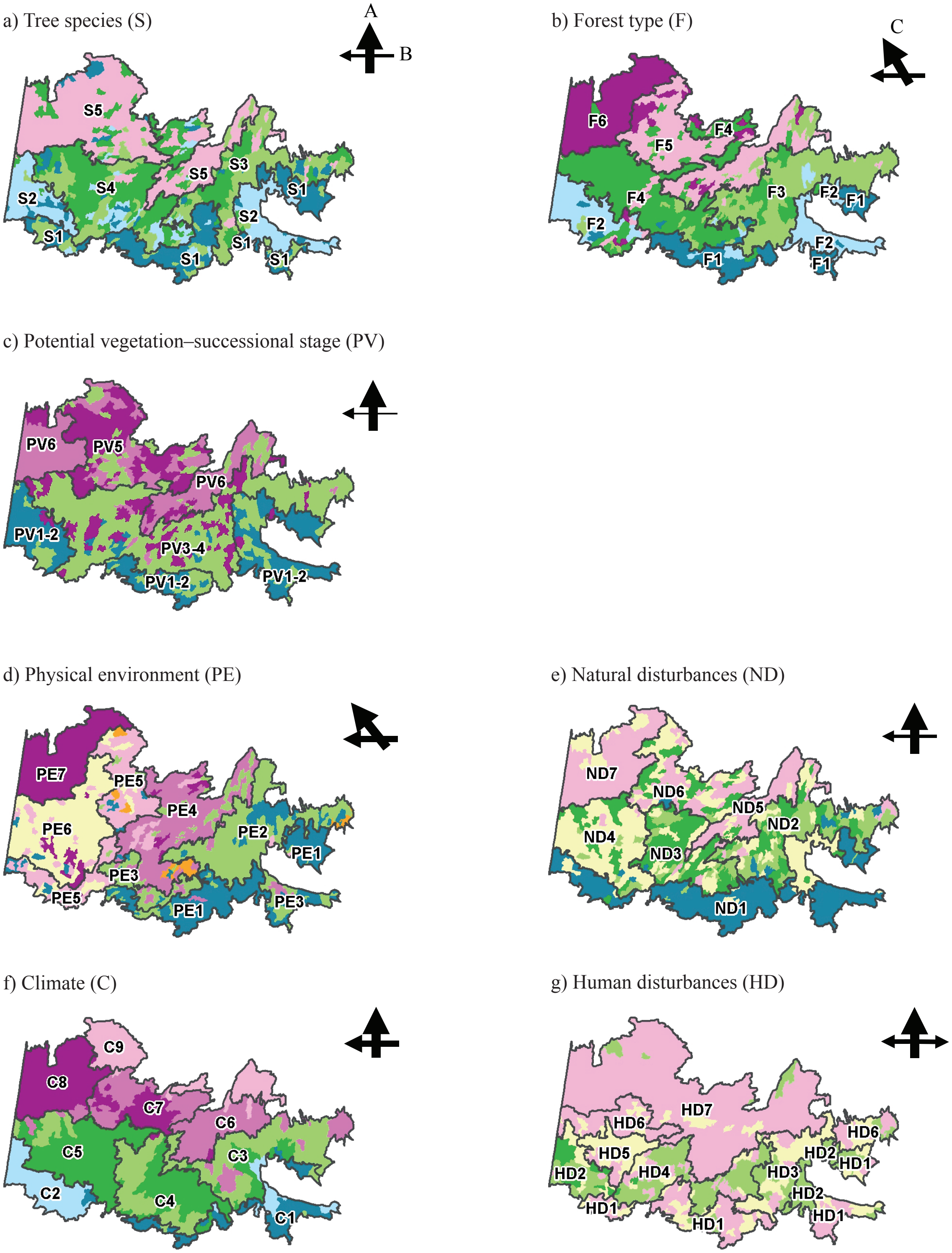


APPENDIX III, FIGURE 1. Landscape heterogeneity of vegetation themes described by a) maps (groups of ecological districts and geographical units) and b) an ordination diagram (groups of vegetation variables [*e.g.,* GPotrF] and geographical units of vegetation themes [*e.g.,* F1]). The ordination is formed by axis 1 and axis 3 of the RDA. Each group of variables is characterized by its ecological gradient as deduced from the distribution of the variables (latitudinal gradient |, latitudinal-oblique gradient \ and longitudinal gradient —). Maps and an ordination diagram are used to define 3 overlapping regions (R1 to R3). The meanings of groups of variables are presented in Table I. The black circle around F1, F3, and F5 indicates that these geographical units will be highlighted in Appendix III, Figure 2 to show the overlap between the vegetation theme and sets of explanatory variables. The maps are presented in Appendix III, Figure 3.



APPENDIX III, FIGURE 2. Landscape heterogeneity of sets of explanatory variables described by a) maps (groups of ecological districts and geographical units) and b) an ordination diagram (groups of explanatory variables [*e.g.,* GGdd], and geographical units of sets of explanatory variables [*e.g.,* PE1]). The ordination is formed by axis 1 and axis 3 of the RDA. Each group of variables is characterized by its ecological gradient as deduced from the distribution of the variables (latitudinal gradient |, latitudinal-oblique gradient \ and longitudinal gradient ─). F1: links between geographical unit F1 of the forest type theme and geographical units of several sets of explanatory variables. F2 to F6: the same as F1, with other specific geographical units of sets of explanatory variables. Maps and the ordination diagram are used to define 3 overlapping regions (R1 to R3). The meanings of groups of variables are presented in Table I. The maps are presented in Appendix III, Figure 3.



APPENDIX III, FIGURE 3. Geographical units of vegetation themes (S: tree species, F: forest types, PV: potential vegetation–successional stages) and sets of explanatory variables (PE: physical environment, C: climate, ND: natural disturbances, HD: human disturbances). An estimate of the ecological gradients is shown near the maps. An estimate of the direction of the ecological gradients is shown near the maps. The thicker the black line, the more important the gradient. A: latitudinal gradient, B: longitudinal gradient, C: latitudinal-oblique gradient.

APPENDIX III, TABLE I. Description of geographical units of vegetation themes (S: tree species, F: forest types, PV: potential vegetation–successional stages) and sets of explanatory variables (PE: physical environment, C: climate, ND: natural disturbances, HD: human disturbances). The geographical units are delineated in Appendix III, Figure 3. The responses variables are defined in Appendix I, Table 1 and explanatory variables in Appendix II, Table I.

		Hardwood tree species					Coniferous tree species				
	Unit	BealS	AcruS	BepaS	PotrS	SaspS	PiglS	PimaS	PibaS	AbbaS	ThocS
Tree species	S1	1.7	0.6	22.0	6.2	0.3	2.9	29.9	6.4	22.1	0.2
	S2	0.7	0.9	15.3	23.3	2.5	2.6	23.3	13.4	10.9	0.5
	S3	0.0	0.0	12.3	3.3	0.1	1.1	53.2	8.0	14.9	0.0
	S4	0.0	0.1	9.5	6.7	0.5	0.7	53.8	18.2	7.1	0.1
	S5	0.0	0.0	3.3	3.3	0.3	0.4	77.3	5.8	5.3	0.1

		Hardwood forest types			Mixedwood forest types				Coniferous forest types				Others		
	Unit	BepaF	BealF	PotrF	PimaF	Bepa AbbaF	Bepa PimaF	Potr AbbaF	Potr PimaF	AbbaF	Pima PibaF	AbbaF	Alru	Wetland	Heathland
Forest types	F1	15.6	1.4	3.1	14.4	11.7	3.1	0.6	20.8	2.5	6.2	2.3	1.3	3.3	0.5
	F2	6.0	0.5	12.8	7.9	2.4	9.6	2.4	17.6	2.0	8.5	1.7	3.6	7.9	2.4
	F3	2.7	0.0	2.0	6.6	3.6	2.5	0.2	31.1	7.0	13.4	5.7	1.0	4.6	1.3
	F4	2.1	0.0	2.1	5.4	1.8	5.2	0.4	28.5	1.8	22.3	0.8	1.7	13.5	0.8
	F5	0.7	0.0	0.9	3.3	0.4	2.2	0.0	47.5	2.3	8.4	0.6	2.2	12.9	1.4
	F6	0.0	0.0	0.1	0.1	0.0	0.6	0.0	27.6	0.4	2.9	0.0	0.9	50.2	1.6

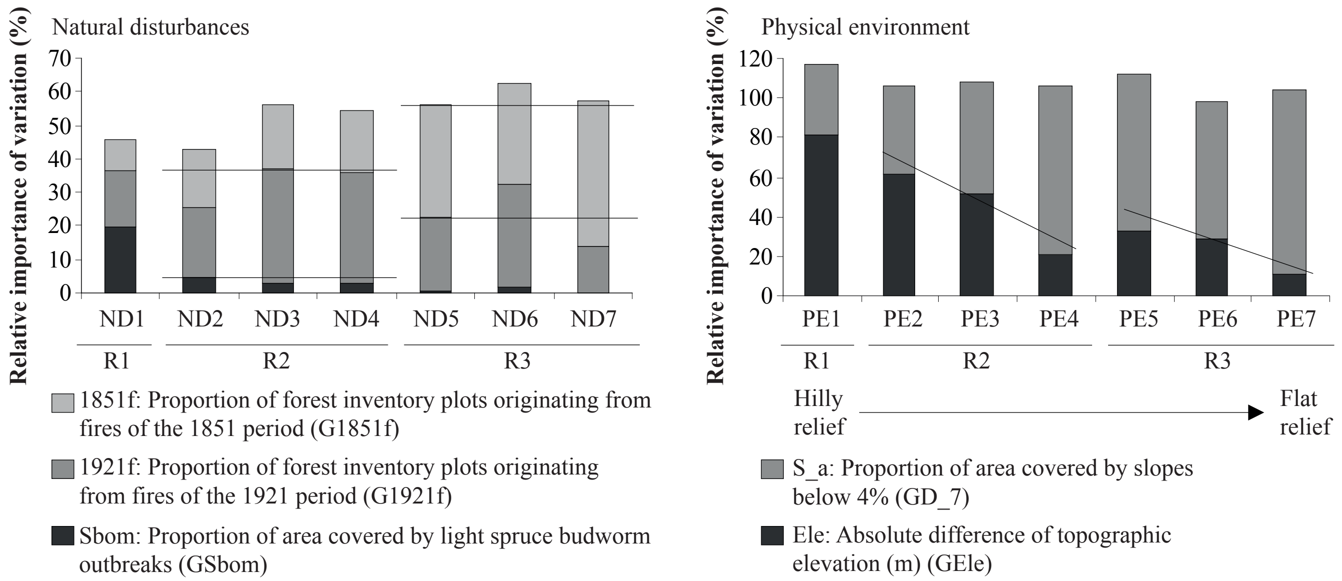
		Ms2 (*Abies–Betula*)					Rs2 (*Abies–Picea*)					Re2 (*Picea mariana*)				
	Unit	Ms2S2	Ms2S3	Ms2S4	Ms2S5	Total	Rs2S2	Rs2S3	Rs2S4	Rs2S5	Total	Re2S2	Re2S3	Re2S4	Re2S5	Total
Potential vegetation–successional stages	PV1–2	21.9	9.6	5.6	4.6	41	8.3	6.8	5.9	8.1	29	13.7	1.5	2.3	1.7	17
	PV3–4	7.5	3.6	3.3	4.4	18	9.9	6.7	6.7	11.0	34	28.1	4.4	5.5	7.9	38
	PV5	2.5	1.0	0.3	0.2	4	9.5	2.8	4.6	7.8	24	36.6	3.4	5.1	21.8	45
	PV6	1.2	0.8	0.7	0.9	3	5.8	3.1	3.3	12.3	24	29.8	2.3	4.4	35.2	36

		Physiography						Surficial deposits									Other
	Unit	Malt	S_a	S_b	S_c	S_d	Ele	D_1a	D_1ar	D_2a	D_2b	D_4ga	D_4gs	D_7	D_wa	D_r	L_100km^2
Physical environment	PE1	454	35	18	24	19	82	32	41	2	8	0	0	1	7	9	1
	PE2	414	45	24	17	11	61	47	23	4	9	0	0	3	7	4	1
	PE3	431	57	18	18	7	52	49	17	4	12	0	1	5	10	1	1
	PE4	401	79	13	6	2	33	46	10	5	5	1	3	14	12	2	1
	PE5	314	70	17	9	3	28	19	13	2	0	26	9	14	9	8	1
	PE6	300	85	11	3	1	21	5	7	1	0	52	5	19	6	4	0
	PE7	242	93	5	1	1	11	2	1	0	0	6	0	63	7	3	1

		Spruce budworm outbreaks						Fires					Other
	Unit	Sbos	Sbon	Sbom	1921o	1891o	1851o	Fia	Fif	1921f	1891f	1851f	Wi
Natural disturbances	ND1	2.3	19.4	19.7	26.2	10.5	10.8	4.0	1.3	16.8	10.9	9.3	0.3
	ND2	0.3	7.7	4.8	8.5	11.4	12.8	4.5	1.5	20.4	19.7	17.6	0.4
	ND3	0.6	5.8	2.9	5.6	6.2	4.3	1.7	0.8	34.0	23.0	19.0	0.9
	ND4	0.5	5.3	3.0	10.8	4.4	6.6	3.8	0.6	33.1	15.4	18.3	0.5
	ND5	0.2	3.3	0.7	3.0	4.3	9.3	3.3	1.8	21.8	13.5	33.5	1.1
	ND6	0.9	3.3	1.6	2.9	3.7	5.6	5.4	1.2	31.0	13.1	30.1	1.6
	ND7	0.1	0.5	0.2	0.7	1.3	4.3	6.0	0.9	13.7	10.9	43.1	0.3

		Aridity regime			Thermal regime						Aridity regime			Thermal regime				
	Unit	Preci	Vpd	Ari	Gdd	Mat	Dwf	Dwfc	Ef	Unit	Preci	Vpd	Ari	Gdd	Mat	Dwf	Dwfc	Ef
Climate	C1	340	1288	1.6	1331	1.2	176	99	248	C6	332	1195	1.2	1167	–0.6	165	90	242
	C2	302	1386	2.1	1349	1.1	175	95	249	C7	313	1251	1.4	1166	–0.5	165	86	242
	C3	331	1232	1.3	1222	0.2	170	94	245	C8	296	1287	1.8	1142	–0.5	165	85	240
	C4	337	1277	1.5	1270	0.5	173	94	247	C9	309	1165	1.5	1069	–1.4	163	85	241
	C5	319	1312	1.6	1258	0.4	173	92	246									

		Logging			Fires		Agriculture				Logging			Fires		Agriculture		
	Unit	1951	Log1	Log2	Hf2	Hf1	Fa1	Ag1	Ag2	Unit	1951	Log1	Log2	Hf2	Hf1	Fa1	Ag1	Ag2
Human disturbances	HD1	9.4	14.8	13.8	12.8	6.8	0.2	0.5	0.3	HD5	12.6	17.1	29.5	7.1	12.8	1.4	1.8	1.2
	HD2	14.6	7.2	8.4	66.6	38.6	3.6	5.7	4.6	HD6	3.3	5.6	27.0	10.0	2.7	0.0	0.0	0.0
	HD3	12.6	26.4	31.3	35.9	3.3	0.0	0.0	0.0	HD7	4.4	0.7	3.9	3.5	0.9	0.0	0.0	0.0
	HD4	20.0	7.7	10.5	64.1	6.4	0.2	0.3	0.2									



APPENDIX III, Figure 4. A substantial proportion of unique variation for natural disturbances in the tree species and potential vegetation–successional stages themes is caused by the independence of natural disturbances from changes in other sets, such as physical environment. For natural disturbances, the proportion of some explanatory variables (*e.g.*, 1921f) is similar in a specific region of overlap (R1 to R3, Appendix III, Figures 1 and 2) and from the eastern part of the study area to the western part. For physical environment, the proportion of some explanatory variables decreases (Ele) or increases (S_a) regularly from the south to the north of the study area and from the eastern part to the western part. Geographical units (ND1 to ND7, PE1 to PE7) are plotted on the ordination diagram of Appendix III, Figures 1 and 2. Geographical units are also presented on maps in Appendix III, Figure 3.

Appendix IV

Vegetation variation partitioning

The vegetation variation partitioning of the explanatory variables corresponds to the third step of this study, the first 2 being the ecological gradients and the description of the overlap between response and explanatory variables. The variation partitioning follows the 6 steps proposed by Borcard, Gillet and Legendre, (2011) as adapted to our study: 1) creation of a separate Y-matrix for each vegetation theme (Y-species, Y-forest types, Y-potential vegetation); 2) Hellinger transformation for each Y-matrix; 3) creation of a separate X-matrix for each of the 4 sets of explanatory variables (X-C, X-ND, X-PE, X-HD); 4) creation of parsimonious X-matrices by running 4 separate RDA-based forward selections, using an adjusted R^2; 5) variation partitioning of each Y-matrix using the 4 parsimonious X-matrices; and 6) tests of significance (by permutations) on all 16 testable fractions of variation obtained from the analysis (15 of these define the explained variation, and 11 are common to 2, 3 or 4 sets of explanatory variables, which means that the variables of these sets are correlated). All testable fractions were considered significant.

Appendix IV, Table I provides more information on the composition of the parsiminious X-matrices used in partitioning vegetation variation. These variables are characterized according to their rank as conferred by a step-by-step selection of all variables (Borcard, Gillet & Legendre, 2011).

- For the set of explanatory variables relating to physical environment, two main variables have an effect on all themes: the absolute difference in topographic elevation (Ele) and the area covered by organic deposits (D_7). These variables are in opposition along the latitudinal-oblique gradient (Appendix II, Figure 3).

- Relative to natural disturbances, 3 explanatory variables have a particularly strong influence: the spruce budworm outbreaks that occurred at the beginning of the last century (in the 1901–1930 period, variable 1921o), the spruce budworm outbreak at the end of the 19^{th} century (before 1870, variable 1851o) and fires of the 1921 period (1921f). The first variable belongs to group GSbom (Appendix II, Figure 3) and is mainly located in the southern portion of the study area. The second variable is included in group GEle and its distribution corresponds to the southern portion of the latitudinal-oblique gradient. The third variable (1921f) occupies the central portion of the study area. It shows a slight dominance in the western portion, compared to the eastern portion. This is the only variable forming the G1921 group.

- The most important climate variables, regardless of the vegetation theme, are annual average temperature (Mat) and vapor pressure deficit (Vpd). The first variable belongs to group Gdd (annual number of growing degree-days). The distribution of these variables is well-adjusted to the latitudinal gradient. The vapor pressure deficit is part of group GAri, which characterizes the longitudinal gradient (Appendix II, Figure 3).

- Three variables related to human disturbances are highlighted in the parsimonious matrices:

frequency of human-induced fires per 100 km^2 during the 1938–1998 period (Hf1), area covered by logging during the 1970 period (Log1), and relative proportion of forest inventory plots affected by logging (1951). The first variable belongs to group GHf1 (Appendix II, Figure 3), which is mainly located in the southwestern portion of the study area, with a small extension into the southeastern portion. The last two variables (Hf1, Log1) form part of the same group (Glog1), which characterizes the latitudinal gradient and reflects the human activities that occurred in the southern portion of the study area.

References

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APPENDIX IV, TABLE I. Variables forming the parsimonious X matrices developed for each vegetation theme (X–PE.pars, X–ND.pars, X–C.pars, X–ND.pars). The variables are presented in order of importance.

Set	Code	Explanatory variable	Forest species	Forest types	Pot. veg.–suc. stages
Physical environment	Malt	Mean altitude (m)	3	3	8
	Ele	Absolute difference of elevation between upper and lower portion of the landscape (m)	1	1	1
	D_wa	Relative proportion of area covered by water	6		
	D_4ga	Area covered by glaciolacustrine fine-textured (clay) surficial deposits	5	8	
	D_4gs	Area covered by glaciolacustrine coarse-textured (sand) surficial deposits	10	7	5
	D_2a	Area covered by juxtaglacial deposits		12	4
	D_2b	Area covered by proglacial deposits	9	4	6
	D_7	Area covered by organic deposits	2	2	3
	S_a	Area covered by slopes below 4%		11	
	S_b	Area covered by slopes ranging from 4 to 8%		10	
	S_c	Area covered by slopes ranging from 9 to 15%		14	
	S_d	Area covered by slopes over 15%	8		9
	D_1a	Area covered by thick till (more than 1 m)	4	5	2
	D_1ar	Area covered by thin till (less than 1 m)	7	9	
	D_r	Area covered by rock		6	10
	L_100km^2	Mean number of lakes per 100 km^2		13	7
Natural disturbances	1851o	Plots originating from spruce budworm outbreaks before 1870	4	4	2
	1851f	Plots originating from fires before 1870	7	10	6
	1891o	Plots originating from spruce budworm outbreaks between 1870 and 1900	2		3
	1891f	Plots originating from fires between 1870 and 1900	3	11	4
	1921o	Plots originating from spruce budworm outbreaks between 1901 and 1930	1	3	1
	1921f	Plots originating from fires between 1901 and 1930	5	5	5
	Fia	Area covered by fires	11	9	8
	Wi	Area covered by windthrow	12	6	9
	Sbom	Area covered by light spruce budworm outbreaks	6	2	7
	Sbos	Area covered by severe spruce budworm outbreaks	9	7	11
	Fif	Number of fires per 100 km^2 during the period 1938–1998	8	8	10
	Sbon	Number of years of infestation by spruce budworm during the period 1938–1998	10	1	
Climate	Ari	Aridity index	6	3	6
	Gdd	Annual number of growing degree–days	5	4	7
	Vpd	Vapor pressure deficit (total daily deficit [in mbar] from months June to August)	4	2	2
	Ef	Early frost (Julian day corresponding to the first frost)	7	7	5
	Dwfc	Number of consecutive days without freezing	3	8	
	Dwf	Total number of days without freezing		6	3
	Preci	Rainfall during the growing season (mm)	2	5	4
	Mat	Mean annual temperature	1	1	1
Human disturbances	Ag1	Area covered by agriculture during the 1970 period	6	7	
	Ag2	Area covered by agriculture during the 1980 period	7		
	Log1	Area covered by logging during the 1970 period	3	1	2
	Log2	Area covered by logging during the 1980 period		4	
	Hf1	Number of human–induced fires during the 1938–1998 period	1	2	1
	Hf2	Area covered by human–induced fires since 1940	4	5	4
	Fa1	Area covered by fallow farmland	5	6	
	1951	Plots originating mainly from logging after 1930	2	3	3