

Vegetation recovery following fire and harvest disturbance in central Labrador — a landscape perspective

Brian R. Miranda, Brian R. Sturtevant, Isabelle Schmelzer, Frédérik Doyon, and Peter Wolter

Abstract: Understanding vegetation recovery patterns following wildfire and logging disturbance is essential for long-term planning in sustainable forestry. Plot-scale studies indicate differences in revegetation rates and postdisturbance composition in Labrador, Canada, following fire in comparison with harvest but do not necessarily capture the full range of relevant landscape variability. Using a satellite-based land cover classification that distinguishes forest, woodland, shrub, lichen, and bare ground, we applied partial least-squared regression (PLS) to derive empirical models of vegetation dynamics following fire and harvest. Forest recovery rates were found to be generally slow and sensitive to predisturbance land condition and site quality (potential productivity). We found that, although disturbance type was not specifically retained in the model, estimated rates of vegetation recovery were faster for a typical harvest compared with a typical fire (i.e., 50% recovery at 14 years versus 33 years, respectively). Indeed, the model predicts important regeneration delay following fire that appears sensitive to both site quality and area burned. Understanding factors affecting broad-scale vegetation recovery relationships can help guide future sustainable forestry and wildlife habitat initiatives in the region, in part by parameterizing landscape simulation models used for strategic decision support.

Key words: Canada, disturbance patch attributes, land cover, partial least-squared regression (PLS), site productivity.

Résumé : Il est essentiel de comprendre les schémas de rétablissement de la végétation à la suite d'un feu de forêt ou d'une perturbation causée par l'exploitation forestière pour planifier à long terme dans un contexte de foresterie durable. Des études à l'échelle de la parcelle au Labrador, Canada, montrent que le taux de revégétalisation et la composition diffèrent après une perturbation selon qu'elle ait été causée par le feu ou la coupe. Cependant, ces études ne détectent pas nécessairement toute l'amplitude de la variabilité pertinente du paysage. À l'aide d'une classification de la couverture du sol, établie sur la base de données satellitaires et capable de distinguer la forêt, les terrains boisés, les arbustes, les lichens et le sol nu, nous avons appliqué l'analyse de régression partielle par les moindres carrés pour dériver des modèles de dynamique de la végétation à la suite d'un feu ou d'une coupe. Les taux de rétablissement de la forêt se sont généralement avérés lents et sensibles à l'état du terrain avant la perturbation ainsi qu'à la qualité de la station (productivité potentielle). Bien que le type de perturbation n'ait pas été spécifiquement considéré dans le modèle, nous avons trouvé que les taux estimés de rétablissement de la végétation étaient plus rapides dans le cas d'une récolte typique comparativement à un feu typique (c.-à-d. 50 % de rétablissement respectivement à 14 ans versus 33 ans). En effet, à la suite d'un feu le modèle prédit un important décalage de la régénération qui semble sensible tant à la qualité de la station qu'à la superficie brûlée. La connaissance des facteurs qui influencent le rétablissement de la végétation à grande échelle peut aider à orienter la foresterie durable dans l'avenir et les initiatives concernant l'habitat de la faune dans la région, en partie en paramétrant les modèles de simulation du paysage utilisés comme outils d'aide à la prise de décisions stratégiques. [Traduit par la Rédaction]

Mots-clés : Canada, attributs des parcelles perturbées, couverture du sol, régression partielle par les moindres carrés, productivité de la station.

Introduction

There is a growing awareness that natural disturbances are an integral component of functioning ecosystems and, as such, need to be accounted for when planning future timber supply and biodiversity objectives (Bergeron et al. 2001; Doblas-Miranda et al. 2009). Understanding the rates of vegetation recovery and successional pathways following different disturbance types is therefore fundamental to effective forest ecosystem management. Recent

interest in emulation silviculture and ecosystem forest management (Gauthier et al. 2009) — where natural disturbances such as fire are used as models for silvicultural prescriptions and harvesting patterns — has spurred research investigating the similarities and differences between postfire and postharvest vegetation recovery (McRae et al. 2001). Yet there are also very strong regional disparities in fire regimes, behavior, and consequent vegetative response across a large biome such as the North American boreal forest (Bergeron et al. 2002; Senici et al. 2010), making extrapolation

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tion of vegetative recovery patterns across regions problematic (McRae et al. 2001). Understanding local sources of variability contributing to trends of vegetation recovery within the context of a regional disturbance regime is therefore essential to inform emulation silviculture and related efforts to enhance resilience within systems commonly impacted by natural disturbances (Puettmann et al. 2012).

Rates of vegetation recovery following disturbance clearly affect long-term landscape structure and function of forests at high latitudes (Dunford et al. 2006; Foster 1985; Gordon and Shugart 1989), which remain a frontier of commercial forest harvest activities (Burton et al. 2003). In central Labrador, the rate and type of vegetation recovery following fire and harvesting disturbance are important sources of uncertainty affecting sustainable forestry (Doyon et al. 2011). Both fire and harvest disturbance are also known to have long-term influence over habitat quality for threatened woodland caribou (*Rangifer tarandus caribou* (Gmelin, 1788)) (Dunford et al. 2006) and may influence fruit-bearing shrubs — affecting ecosystem services for indigenous peoples and other inhabitants in the region (Forsyth et al. 2003). Understanding the factors affecting forest revegetation patterns in response to natural fire disturbance and the more novel harvest disturbance in this region are therefore essential for sustainable use of multiple ecosystem services reflecting important economic, social, and cultural values in the region.

The majority of postdisturbance vegetation studies are based on data collected at plot scales that are, by necessity, a subset of conditions affecting variation in recovery patterns within real landscapes. Sampling the full variability of conditions using plots is especially challenging for wildfires, which can have very high heterogeneity in site conditions and disturbance impacts both within and among individual fire events (Perera and Buse 2014; Turner et al. 1999). Spatially continuous data sets derived from remote sensing and other inventory methods provide opportunities to evaluate postdisturbance vegetation trends across a much wider range of variability than could be achieved through plot-scale analysis alone (Lentile et al. 2006).

Fine-scaled studies of postdisturbance succession in Labrador arrive at three consistent conclusions: (i) postfire vegetation recovery is generally slow relative to other regions of the boreal forest (Foster 1983; Simon and Schwab 2005a); (ii) postfire vegetation recovery is slow relative to postharvest vegetation recovery (Elson et al. 2007; Hebert and Weladji 2013; Simon and Schwab 2005b); and (iii) successional pathways differ between both disturbance types (Elson et al. 2007; Simon and Schwab 2005b). These results are generally consistent with studies elsewhere in the boreal forest, though regional differences in vegetation recovery rates and successional pathways are also the norm (McRae et al. 2001). Discrepancies among Labrador studies appear largely in the details — in particular, the specific rates of vegetation recovery and dominant successional pathways that are likely landscape context dependent. Different successional responses following harvest and fire have been attributed to the following: direct impact on the seedling substrate (Johnstone and Chapin 2006; Nguyen-Xuan et al. 2000); increased successional paludification, resulting in the long-term reduction in site productivity (Simard et al. 2007); and advance regeneration during harvest activities (Elson et al. 2007).

Accordingly, our study addresses the influence of landscape context and specific disturbance attributes by examining temporal patterns of vegetation recovery following disturbance at the landscape scale, encompassing broad ranges of site and disturbance attributes. We developed empirical models to quantify patterns of vegetation recovery following fire and harvest disturbance using forest disturbance records and remotely sensed land cover classifications. We hypothesized that vegetation recovery patterns evaluated at the scale of disturbance events would fundamentally differ following fire and harvest, and that covariates including forest site quality (potential productivity), predistur-

bance condition and indicators of disturbance severity would influence the recovery process differently for the two disturbance types. Resulting vegetation recovery drivers are discussed in the context of sustainable forestry, caribou habitat, and as validation for landscape disturbance and succession models used to aid the management of forests as complex systems.

Methods

Study area

The study area is defined by Newfoundland and Labrador's Management District 19a in Labrador, Canada (~2.0 million ha; Fig. 1). This forest management district straddles the boundary between a closed-canopy Boreal Shield ecozone at the lower elevations (generally <300 m) and an open-canopy Taiga Shield ecozone at higher elevations (210–650 m) (Ecological Stratification Working Group 1995). Forest composition is strongly dominated by black spruce (*Picea mariana* Mill. BSP) and, to a lesser extent, balsam fir (*Abies balsamea* L.) (Forsyth et al. 2003). Closed-canopy spruce and fir stands are the dominant forest types and are embedded within a diverse mosaic of open sphagnum forest, lichen woodlands, mixed hardwoods (*Betula papyrifera* Marsh., *Populus tremuloides* Michx.), black spruce bogs, lakes, and open wetlands, with less closed-canopy forest in the Taiga Shield ecozone than in the Boreal Shield ecozone. Topography is characterized by moderate relief underlain by glacial moraines and drumlins (Roberts et al. 2006). Climate is primarily continental, though moderated by Lake Melville, with long harsh winters, heavy snow accumulation, annual precipitation averaging between 900 and 1100 mm (Roberts et al. 2006), and mean annual temperature of approximately 0 °C (Banfield 1981).

Fire is the dominant natural disturbance in this landscape, and the contemporary fire regime has been estimated from provincial fire records (D. Jennings, Newfoundland and Labrador Department of Natural Resources, unpublished data) to have a mean fire return interval of 352 years, with a mean fire size of 1146 ha (Sturtevant et al. 2009). The fire return interval is relatively long compared with other regions of the North American boreal forests (50–200 years) (Heinselman 1981; Senici et al. 2010) but shorter than the rotation in more coastal southeastern Labrador (500 years) (Foster 1983) and the North Atlantic region as a whole (455 years) (Boulanger et al. 2014). Harvesting remains a novel disturbance in central Labrador. Commercial harvesting in this district was limited to a few thousand hectares harvested between 1969 and the present day (Hillyard 2003), and the district contains correspondingly few roads (Sturtevant et al. 2007). Commercial salvage logging following fire is uncommon due to the lack of access roads, though local firewood collection does occur. Likewise, some limited planting of disturbed areas has occurred, including jack pine (*Pinus banksiana* Lamb.) and black spruce. The region is currently under treaty negotiations regarding land title and aboriginal rights between the Innu Nation and the Canadian and provincial governments. Two central items of concern to local indigenous and nonindigenous communities have been identified: sufficient timber supply to support a local sawmill and therefore boost the local economy, and the viability of a threatened woodland caribou population important to the cultural well-being of the region (Schmelzer et al. 2004).

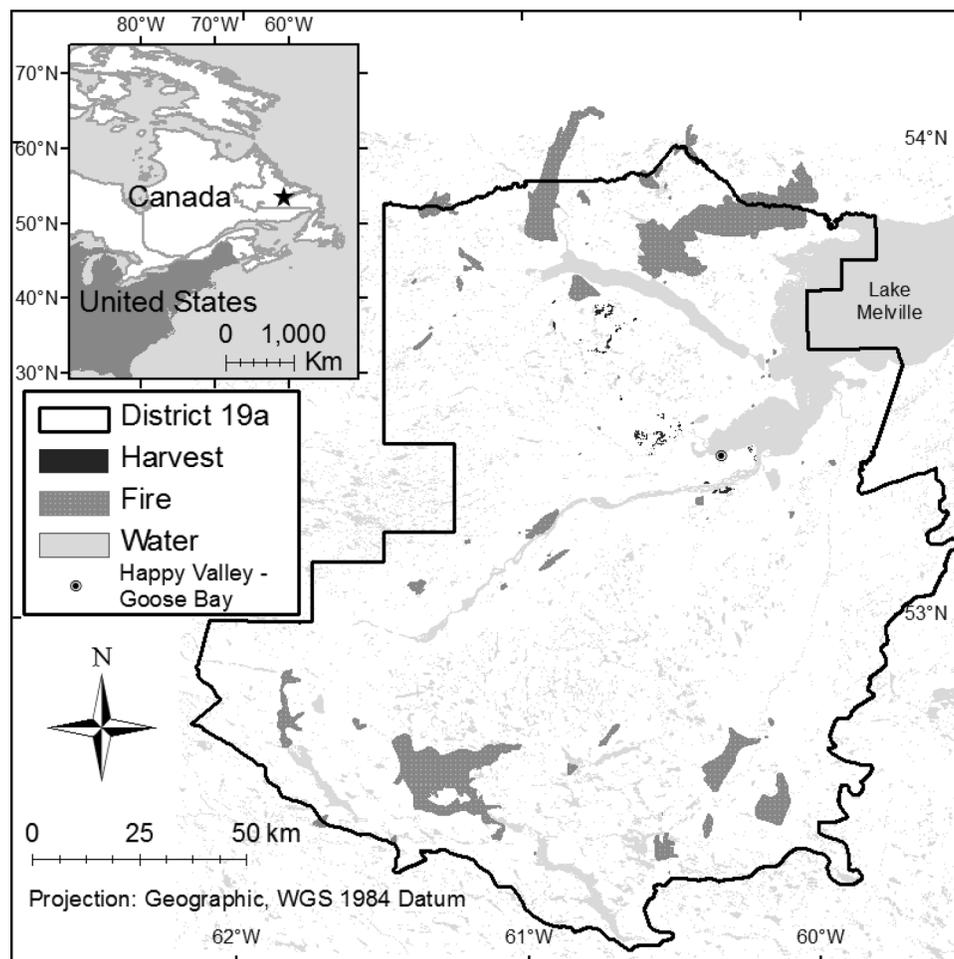
Data preparation

We constructed a database of fire and harvest records that included proportions of land cover types and attributes of the disturbance events. Disturbance attributes included the proportions of predisturbance land classes and site productivity classes, disturbance size, shape indices, and time since disturbance.

Land cover classification

Land cover data were extracted from a 30 m resolution classified data set derived from Landsat imagery (2005, 2006, and 2010

Fig. 1. Study area location map, identifying Management District 19a in Labrador, Canada. The map is unprojected with latitude and longitude coordinates, using the WGS 1984 Datum.



images). The data set is an intermediate version of the Ecological Land Classification (ELC) presented by [Schmelzer and Senecal \(2013\)](#) (Table 1; see Supplementary material¹ for details on how this data set was created and how the version we used differs from the final version). For the intermediate version we used, the accuracy assessment reported for the ELC showing 84% overall accuracy (see Supplementary material¹) cannot be assumed to be completely representative of the intermediate data set in our evaluation; however, the high accuracy of the final ELC gives us confidence that the data are generally reliable. The classification used for our analysis comprised of eight land cover classes (Table 2). The proportions of the 2005–2010 ELC classes in each disturbance polygon served as the dependent variables in our partial least-squared (PLS) regression analysis (details below).

Predisturbance land class

The land class conditions prior to disturbance were estimated from the Global Forest Inventory (GFI) data ([NL DNR and NCC 2012](#)), which was digitized at the stand level from aerial photos (1:20 000 and 1:50 000) taken between 1966 and 1976 (Table 1). We classified the stands into three predisturbance land condition classes: Productive Forest (PF; forest land capable of producing a commercial stand, including recent burn and cutover), Non-Productive Forest (NP; hardwood and softwood scrub incapable of producing a commercial stand), and Non-Forest (NF; all other

classes). The three condition classes were numerically coded and converted from polygons to a 30 m raster to match the resolution of the ELC data set.

Site productivity

Site productivity classes were determined from the provincial forest stand inventory data (Newfoundland and Labrador Department of Natural Resources, unpublished data), with classes of Good-High, Medium, and Poor. The site index values effectively represent differences in local environmental variables such as soils, climate, and topography. The site classes were determined from air photo-interpreted stand site-index values, consistent with height-age curves from [Page and van Nostrand \(1973\)](#), with minimum class thresholds of 10.7 m and 13.7 m for Medium and Good-High, respectively, and Poor below those thresholds. Areas that were absent from the stand data had an “Unknown” productivity class. These Unknown areas are typically NF or NP, as the stand inventory targets the commercially viable forest lands, and likely to be less productive than the Poor class.

Disturbance polygons and attributes

Dated fire polygons representing past burn perimeters were acquired from both the GFI and provincial records from the Newfoundland and Labrador Division of Forestry (D. Jennings and S. Payne, personal communication), which includes fires recorded

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2015-0516>.

Table 1. Data sources and time periods.

Data set name	Time period of data used	Source
Ecological Land Classification (ELC) ^a	2005–2010	Schmelzer and Senecal (2013)
Global Forest Inventory (GFI)	1966–1976	NL DNR and NCC (2012)
Provincial forest stand inventory	ca. 1990	NL DNR (unpublished)
Provincial fire records	1976–2008	D. Jennings and S. Payne (NL Division of Forestry; unpublished)
Provincial harvest records	1976–2005	D. Jennings (NL Division of Forestry; unpublished)

^aAnalysis used an intermediate version of the ELC data set (see Supplementary material¹).

Table 2. Cover type classes in the Ecological Land Classification and their relative abundance (proportion) in the study area (District 19a).

Cover type	Description	Landscape proportion
Forest No Lichen	Forest (including all deciduous forests) with relatively closed canopy, no lichens	0.62
Forest with Lichen	Coniferous trees with widely ranging crown closure; forest is patchy and open areas can contain lichens	0.12
Lichen Woodland	Open coniferous forest (<35% crown closure) with a predominant lichen understory	0.01
Lichen–Shrub Woodland	Trees, shrubs, and lichens in similar proportions	0.03
Alpine	Areas >650 m in elevation, including rock–lichen tundra and shrub–lichen tundra; trees present only in protected enclaves	0.00
Water	Open water	0.11
Wetland	Land with water table at surface, with a mixture of low and tall shrub; also misclassified regenerating burns	0.09
Burn	Recent and partially regenerated burns	0.02

Note: Wetland and Burn were pooled into a “Disturbed” class within disturbance polygons due to classification confusion (see Supplementary material¹).

in the Canadian Large Fire database (Stocks et al. 2002), with records between 1954 and 2008. Fire records in the North American boreal forest are known to have substantial georegistration errors due to inconsistent cartographic standards for fire monitoring (Rommel and Perera 2009), which were evident in portions of these data sets when compared with other reference layers. We therefore adjusted the location and orientation (but not the shape) of each fire perimeter polygon using the burn class in the land cover classification as an independent reference set (see details on the spatial adjustment process in the Supplementary material¹). To standardize the resolution of detail among the various fire data sources, mapped water bodies were overlaid and clipped out from all fire polygons, and the clipped polygons were then converted to 30 m rasters and back to polygons. These two standardization steps ensured that fire polygons consistently represented the shape and extent of the burned area in a similar manner, regardless of original source.

Harvest cut-block perimeters based on air photo interpretation were also provided by the Newfoundland and Labrador Division of Forestry (D. Jennings, personal communication), with the harvest cut-blocks dating between 1974 and 2005. These primarily clear-cut harvests occurred prior to the recent transition to a short-wood system with greater retention of residuals and riparian buffers (C. Coady, Newfoundland and Labrador Department of Natural Resources, personal communication). No spatial adjustments were applied to the harvest polygons due to the perceived mapping accuracy. The same standardization steps (clipped out water bodies and raster conversion) were applied to the harvest data as described above for the fire polygons. Although other studies have used agglomerations of harvest patches created over several years as the unit of analysis (Madoui et al. 2015), we chose to treat each harvest polygon as a separate event. Using separate harvest polygons maintained adequate sample sizes, as well as facilitated the evaluation of the influence of both local conditions (i.e., site productivity and predisturbance condition) and disturbance size as potential drivers of the vegetation response. The harvest data also included records of applied planting treatments, which would be expected to influence the vegetation recovery process. Although planting is rare in this landscape and generally applied to aid reforestation efforts rather than establishing plantations, we used the records of planting after disturbance as a component of our vegetation models. We limited analysis of both fire and harvest data records to those ≥ 5 ha, excluded distur-

bances occurring in the relatively developed areas of Happy Valley–Goose Bay, Sheshatsiu, and North West River (using census block boundaries). Our analysis assumed that each disturbance polygon was independent of all other polygons, so we also excluded polygons that overlapped in space or time. To use the GFI land classes to represent conditions prior to disturbance, we limited disturbance records to those occurring after the period of GFI data collection (i.e., after 1976). Final sample sizes for harvest and fire polygons were 85 and 36, respectively. To our knowledge, the area was not substantially affected by major wind or insect disturbances during the study period (1954–2008). We did not consider disturbance severity as a factor because neither disturbance database included information on disturbance severity within or among events. However, we acknowledge that within- and between-event variation in severity was likely high for fire disturbance relative to consistent harvest practices.

The proportions of cover types, excluding water and wetland cover, were estimated within the boundaries of each fire and harvest polygon using the land cover classifications (see Table 2 for classes). We defined the time since disturbance by subtracting the recorded year of disturbance from imagery dates (either 2005 or 2010 depending on location) of the land cover classifications. We similarly estimated the proportions of the four site productivity classes (Good–High (Prop_G), Medium (Prop_M), Poor (Prop_P), and Unknown (Prop_U)), the proportions of the three predisturbance land classes (NF (Prop_NF), NP (Prop_NP), and PF (Prop_PF)), and the proportion planted (Prop_Plant) after disturbance for each disturbance polygon. Disturbance shape attributes could potentially serve as surrogates for fire severity, assuming wind-driven, fast-spreading fires (typically the most severe) are generally more elongated and regular in shape than slower, less severe fires (Gutsell and Johnson 2007). Although not related to severity of harvests, disturbance shapes may also influence the resulting interspersed of disturbed and undisturbed cells (patch edge) affecting later forest establishment (Turner et al. 1998). We therefore estimated two attributes reflecting disturbance polygon shape using the formulae from Fragstats (v. 3.3; McGarigal and Marks 1995): SHAPE that defines the relative irregularity of the polygon as the ratio between its area and its perimeter, and CIRCLE that measures the relative elongation of the polygon, where 0 represents a perfect circle and 1 represents a linear feature.

Table 3. Area-weighted mean parameter values and weighted standard deviations for the combined mean values, ordered by variable loading (importance) for the fitted PLS model.

Variable	Description	Combined (n = 121)		
		Mean	Standard deviation	Variable loading
AGE	Years since disturbance	16	5	0.991
AREA	Area (ha) of disturbance event	12 461	11 408	0.021
Prop_PF	Proportion of area in previously productive forests (PF) prior to disturbance	0.62	0.22	0.012
Prop_PLANT	Proportion of area planted between disturbance event and imagery date	0.0029	0.0363	0.005
Prop_P	Proportion of area in a poor (P) site productivity class	0.23	0.09	0.002
Prop_NF	Proportion of area in the nonforest (NF) class prior to disturbance	0.015	0.013	0.001
Prop_M	Proportion of area in a medium (M) site productivity class	0.34	0.15	N/A
Prop_G	Proportion of area in a good (G) site productivity class	0.044	0.081	N/A
Prop_U	Proportion of area in an unknown (U) site productivity class	0.38	0.15	N/A
Prop_NP	Proportion of area in the nonproductive (NP) forest class prior to disturbance	0.36	0.22	N/A
SHAPE	Patch shape metric (McGarigal and Marks 1995)	6.4	2.0	N/A
CIRCLE	Patch shape metric (McGarigal and Marks 1995)	0.67	0.07	N/A

Note: Mean and standard deviation for AREA were calculated from the log₁₀-transformed area distribution. Information for NF, NP and PF is from NL DNR and NCC (2012). Loadings represent the relative importance of the predictor variables in modeling the response variables and are reported here as the sums of predictor variable loadings across all included latent variables (components), weighted by the proportion of variance explained by each component. A single loading was calculated for each predictor variable for each component across all multiple forms of a variable (i.e., AGE) in the regression model. Each variable could have a 0 to 1 value for each component, so sums across variables can exceed 1.0. Variables that were dropped from the final model are denoted with a loading of “N/A”.

Analysis

We used PLS regression (Geladi and Kowalski 1986) to construct a suite of models to predict the proportions of the ELC cover types from the attributes of a disturbance event. Predictor variables were the proportions of each of the four site productivity classes, and the three predisturbance land classes, event size (log₁₀ (ha)), SHAPE index, CIRCLE index, proportion planted after disturbance, and time since disturbance (two forms: AGE and AGE²). We applied the centered log-ratio transformation (Wang et al. 2010) because the response variables (proportions of each polygon in each cover type) were compositional and constrained to sum to one (Aitchison 1982). Zero values were replaced with a small value (0.005) using the multiplicative replacement method of Martín-Fernández et al. (2003). We used the package “compositions” (v. 1.40, van den Boogaart and Tolosana-Delgado 2008) to apply the centered log-ratio transformation and the package “pls” (v. 2.4–3, Mevik and Wehrens 2007) to implement the PLS regression, within the statistical software R (v. 3.1.0, R Development Core Team 2010).

PLS regression is not compromised by including highly correlated predictor variables (such as proportions of site productivity classes and predisturbance land condition classes) and is well suited for exploratory analysis with many predictor variables (Norgaard et al. 2000). We therefore evaluated alternative models including all potential predictors. Performance of models was compared using the “leave-one-out” cross-validation results of the PLS regression, with the best model identified by the lowest model root mean square error (RMSE). The model RMSE was calculated using the back-transformed predicted residual sum of squares, averaged across all response variables. We used the xPLS method of Wolter et al. (2012) to remove weak predictor variables from the full model prior to evaluation. This backwards step-wise approach started with a full saturated model and removed individual variables sequentially as long as the overall RMSE improved (i.e., decreased). In each step, the number of latent variables was determined by the minimum overall RMSE value for each model. If removal of a variable resulted in lower RMSE, then that variable was dropped from all subsequent models. The process continued until the removal of any remaining variable did not reduce RMSE. This method of variable reduction is conservative in retaining variables with no change to RMSE, but as noted above, retaining extra variables is not detrimental to the PLS regression analysis. A single PLS model was fit for harvest and fire disturbances combined using a categorical dummy variable to indicate

Table 4. Area-weighted mean parameter values and weighted standard deviation for harvest and fire events used for effects displays and reforestation plots.

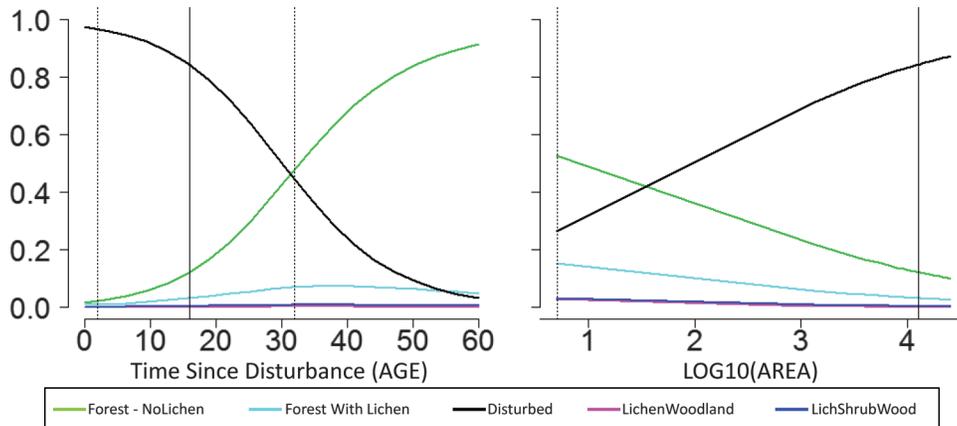
Variable	Harvest (n = 85)		Fire (n = 36)	
	Mean	Standard deviation	Mean	Standard deviation
AGE (years)	10	6	16	5
AREA (ha)	71	77	16 362	10 443
Prop_PF	0.99	0.02	0.60	0.21
Prop_PLANT	0.040	0.154	0.0010	0.0085
Prop_P	0.071	0.111	0.24	0.08
Prop_NF	0.00050	0.00226	0.016	0.013

Note: For additional information and the definitions of abbreviations, see Note under Table 3.

disturbance type. Alternative models were constructed to evaluate whether the spatially adjusted fire polygons improved model results. From the models with the best performance, we used the PLS regression component loadings to identify the predictor variables that had the strongest influence on the response variables. We also plotted effect displays (Fox 2003) for the response variables and the retained predictors to facilitate model interpretation and comparison. Effect displays demonstrate the predicted model results as one variable changes in value while all others are held constant (Fox 2003). The effect displays used area-weighted mean values as the constants (see Table 3). The area-weighted mean values across all disturbances represent a typical disturbance, regardless of cause, and effect displays using these values give us a picture of general vegetation dynamics after a generic disturbance. We also compiled area-weighted mean values for each disturbance type, which were used to represent “typical harvests” and “typical fires” in the construction of effect displays (Table 4).

Focusing on the cover type differences in response to the time since disturbance (AGE) variable, we extracted information regarding the rates of cover type change through time predicted by the model. We evaluated the relative rates of revegetation by focusing on the combined abundance of the two cover types (burn and wetland) representing a disturbed condition (i.e., disturbed is the inverse of vegetated (Table 2)). From the fitted PLS model, we determined the predicted proportion of disturbed land immediately following a disturbance (AGE = 0). We then calculated at

Fig. 2. Effects displays for the fitted PLS regression model using the combined area-weighted mean values (Table 3) for the AGE and AREA predictors. Predicted proportions of the cover type classes are plotted across a range of values for a single variable, and all other variables are held constant at the mean value. The solid vertical line in each plot represents the fixed mean value used in estimates for all other variables, and the dashed vertical lines represent the range of values represented in the combined data set. The “disturbed” class is the combination of the “burn” and “wetland” classes.



what AGE the proportion of disturbed land was estimated to be half the original proportion, essentially the “half-life” of the disturbed land following disturbance in the terminology of exponential decay. Although the decline of the disturbed class may not precisely fit a negative exponential function, the principle of using half-life as a relative indicator of the rate of decline still applies. This analysis allowed us to control for the residual vegetation remaining immediately after disturbance and does not require any assumption about the condition of the “disturbed” cells prior to disturbance.

We estimated the rates of forest regeneration for generic disturbances and for typical harvests and fires by focusing on the initially disturbed portion of the disturbances and the forest cover that replaced it through time, using the fitted PLS models with area-weighted mean attributes (Table 4). The Forest No Lichen and Forest with Lichen cover types were pooled as a single “forest” class for this analysis (excluding woodlands). We first determined the proportions of disturbed land (P_{D0}) and existing forest cover (P_{F0}) predicted by the PLS model for a typical event immediately following disturbance (AGE = 0). We then calculated the proportion of the disturbed land subsequently filled by forest cover types ($P_{Refor(a)}$) at any age (a) as

$$P_{Refor(a)} = \frac{P_{F(a)} - P_{F0}}{P_{D0}}$$

where $P_{F(a)}$ is the proportion of forest cover at AGE = a . This equation accounts for the residual forest cover (P_{F0}) left within the event perimeter following the disturbance and also scales the result based on the proportion of the disturbance that was initially mapped as disturbed. We refer to this proportion as “reforestation”, that is disturbed land converting to forest cover. These reforestation proportions were then plotted against AGE, from which we estimated the rate of reforestation (slope) by decade, and the number of years required for reforestation to reach 80%. To discern the impact of site quality and predisturbance land class on reforestation, we plotted reforestation proportions against AGE where the relevant site quality or predisturbance land class proportions were set to be either 0% or 100%. The reforestation predictions used the area-weighted mean values (Table 3) for all variables, except the site quality or predisturbance land class being evaluated.

Results

The fitted model (following variable reduction) had a model RMSE value (using the back-transformed predicted residual sum of squares, averaged across all response variables) of 0.23 and a R^2 value of 0.68. The xPLS process of removing weak predictors resulted in a model containing six predictor variables (Table 3). The time since disturbance (AGE) was clearly the variable with the greatest influence on the predictions of cover type composition, with a variable loading of 0.991. The next highest variable loading was 0.021 for AREA. The categorical disturbance type variable (representing harvest or fire) was among the predictors that were dropped from the model.

Effect displays (Fig. 2; Supplementary Figs. S1–S3¹) isolate the effect of a single model predictor on the response variables while holding other predictors constant. The primary focus of our results is the AGE variable, which predicts changes in composition as a function of time since disturbance for a “typical” disturbance. All effect displays showed the consistent decline of the disturbed class (burn + wetland) with increasing AGE, although at different rates depending on the values of the other predictor variables. The model predictions for a typical fire (Supplementary Fig. S3¹) showed the disturbed land declined by half after 32 years, whereas the model showed only 14 years for the disturbed class to decline by half for the average harvest (Supplementary Fig. S2¹; Table 5).

When looking specifically at the establishment of forest classes (Forest No Lichen and Forest with Lichen) in initially disturbed areas, the rates of reforestation clearly differed between the typical harvest and typical fire disturbances, especially in the first decade (Fig. 3; Table 5). Reforestation rates estimated by our study indicated that 25 years after disturbance about 82% and 30% of the area was reforested within harvest and burn polygons, respectively (Fig. 3). Reforestation was most rapid (3.5%–3.7% year⁻¹) in the first two decades following a typical harvest, whereas a typical fire resulted in a more consistent and slower reforestation (0.5%–1.4% year⁻¹) across multiple decades. Slower reforestation was predicted for events that occur completely in Poor site quality or NF areas (Fig. 3), and conversely, reforestation was more rapid for events completely in PF or completely outside of Poor site quality.

Despite the differences among reforestation rates, the cover types of the regenerating vegetation were consistent for typical harvests and fires. Generally, the Forest No Lichen class dominated the vegetation response, along with small proportions of Forest with Lichen. The effect displays for the predictor variables

Table 5. Summary of the age response of disturbed and forest classes (Disturbed, combination of “Burn” and “Wetland” classes; Forest, combination of “Forest No Lichen” and “Forest with Lichen” classes) for the fitted PLS regression model using the area-weighted mean values for all disturbances, only harvests, and only fires.

Disturbance type	Initial disturbed (%) ^a	Disturbed half-life (years) ^b	Reforestation rate (%·year ⁻¹) ^c by decade			80% reforestation (years) ^d
			1	2	3	
Combined	97.4	31	0.6	1.6	2.8	43
Harvest	77.6	14	3.7	3.5	1.8	24
Fire	97.7	32	0.5	1.4	N/A	44

Note: The age response was calculated using the mean values for all other variables from the respective combined, harvest, or fire data sets (Table 3).

^aAverage percentage of event area in the Disturbed class 0 years after disturbance.

^bAverage number of years for the percent disturbed to fall to half of the Initial Disturbed percentage.

^cThe average rate of forest cover type replacement of disturbed types (Fig. 3), estimated in 10 year increments since disturbance. N/A indicates no data available for the reported decade.

^dThe average number of years for 80% of the Initial Barren to be replaced by forest cover types (Fig. 3). The estimated values for Combined and Fire disturbances (bold) are extrapolated beyond the temporal extent of the analysis data set.

Fig. 3. Reforestation curves estimated from the fitted PLS regression model for typical harvest and fire events (black lines). Additional curves show predicted reforestation when either the site class variable (Prop_P) or the land class variables (Prop_PF or Prop_NF) are set to 0 or 100% and all other attributes are held constant. The y axis represents the proportion of initially disturbed land that is subsequently reforested with AGE (time since disturbance). The dashed vertical lines represent the range of values represented in the corresponding data set. The reforestation curves also are dashed outside of the actual data range.

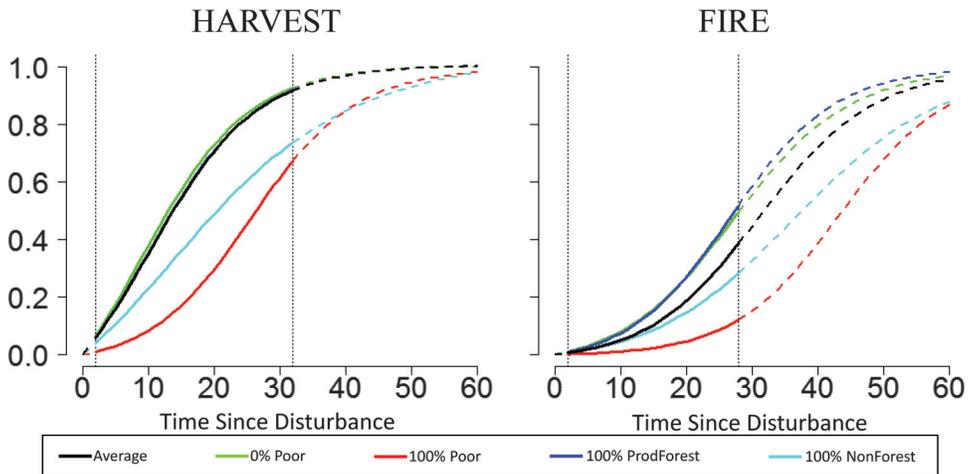
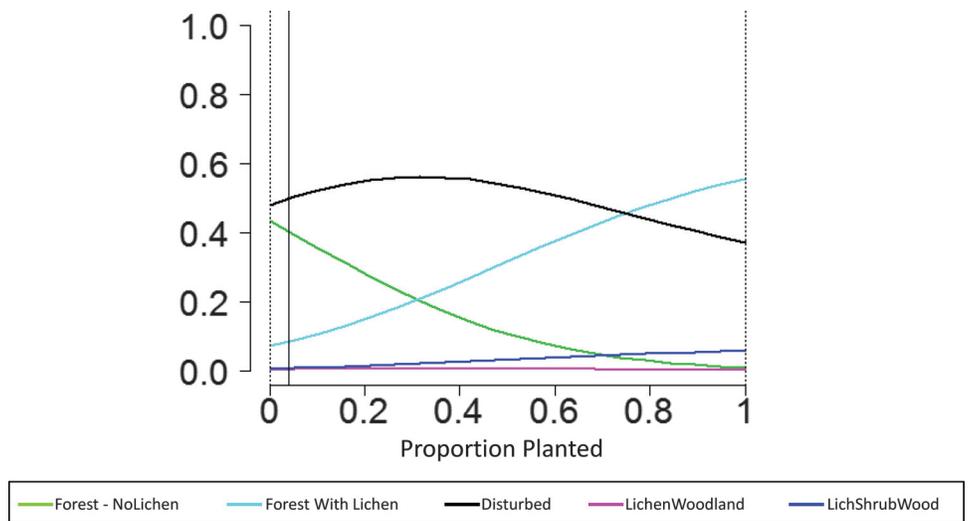


Fig. 4. Effects displays for the fitted PLS regression model using the harvest area-weighted mean values (Table 4) for the PLANT predictor. Predicted proportions of the cover type classes are plotted across a range of values for a single variable, and all other variables are held constant at the mean value. The solid vertical line in each plot represents the fixed mean value used in estimates for all other variables, and the dashed vertical lines represent the range of values represented in the combined data set. The “disturbed” class is the combination of the “burn” and “wetland” classes.



other than AGE demonstrate other factors also influence the predicted cover type. For example, an increase in the proportion of planting (Fig. 4) tended to shift composition away from Forest No Lichen and towards Forest with Lichen and Lichen-Shrub Woodland — a counterintuitive result. More intuitively, the proportion of nonforest prior to disturbance (Supplementary Fig. S1; NONFOR) showed a similar influence (i.e., shift towards Lichen-Shrub Woodland), though its influence was not as strong.

Discussion

Our xPLS regression approach was able to discern useful and credible trends in vegetation recovery with a relatively strong model fit, providing a landscape perspective to more detailed field studies using coarsely defined data. The time window for this analysis was relatively short (32 years), but it was sufficient to capture an informative amount of revegetation following both fire and harvest. As expected, the AGE variable (time since disturbance) was by far the strongest predictor variable, confirming our models were capturing recovery patterns following disturbance. Despite the inherent limitations in the data (including coarse representation of disturbance polygons, a “snapshot” of vegetation representing a single point in time, and a relatively short time span), we found this approach provided useful estimates of forest recovery rates and, by incorporating additional model variables, provided additional insight into drivers of recovery such as disturbance type and site quality.

Based on existing literature on forest recovery in this system, we expected generally slow recovery rates, with recovery after fire slower than after harvest. The revegetation rate in our study (Table 5) was considerably slower than revegetation periods (5–20 years) reported for large fires across Canada by others (Goetz et al. 2006; Gralewicz et al. 2012) but is consistent with Foster's (1983) findings that this region has relatively slow revegetation, with poor initial postfire establishment by conifers, followed by gradual infilling over the course of a century (1985). Likewise, Girard et al. (2008) found that fire reduced the ability of closed canopied forests to self-regenerate at the transition zone between boreal and subarctic (taiga) systems, particularly for latitudes over 51°N. Foster (1983) suggests that incomplete combustion from the low-severity fires common in this landscape produces charred soil conditions that are a poor substrate for seedling establishment (Johnstone and Chapin 2006). We hypothesized that patch shape attributes (CIRCLE, SHAPE) might serve as surrogates for event-scale fire severity. Although these variables were dropped from the model (suggesting little to no influence on recovery patterns), it is likely that they were simply poor surrogates for actual fire severity and unrelated to disturbance severity for harvests. The lack of fire severity data (or high quality indicators of severity) was therefore a significant limitation to this study. Recent advances in development of fire severity maps using change detection methods applied to the Landsat archive (e.g., Miller and Thode 2007) offers one strategy for improving upon our approach and deserves attention in future study. Despite this limitation, our findings of slow revegetation following disturbance are consistent with that expected from a low-severity fire regime in this region (Foster 1983).

Contrary to our expectation, the model did not retain disturbance type as a predictor variable. However, when we looked at the model predictions for disturbances with attributes typical of fires or harvests, we did see the expected difference in recovery rates (Fig. 2), with reforestation faster for a typical harvest than for a typical fire. The differences in both sample sizes and areas between fires and harvests make the combined mean values (Table 3) appear more similar to a typical fire than harvest (Table 4), but these differences would not contribute to the lack of retention of the disturbance type predictor variable. Therefore, a model that doesn't explicitly separate the disturbance types may

still account for the expected differences between them. One way in which the model differentiates between the disturbance types is through the influence of the site quality variables. The apparent delay in recovery following fire may be largely attributed to differences in site quality between typical harvests and fires. Harvests in this landscape are heavily biased towards productive forests and good site quality, whereas fires are essentially randomly located (Table 4). The latter is consistent with Foster's (1983) observation that fire is more common within the dry lichen woodlands that dominate the more abundant poor quality areas. The model estimates that harvests occurring in areas of non-productive forest or with poor site quality would have slower recovery rates closer to what is estimated for fires (Fig. 3). Madoui et al. (2015) also found that, in the boreal forest, the portions of fires that burned in productive forest had similar revegetation rates as harvests and attributed differences in revegetation rates between fires and harvests primarily to the differences in productivity of the lands disturbed by each disturbance type. Elson et al. (2007) and Simon and Schwab (2005b) controlled for edaphic variability by focusing on mesic and subhygric soil drainage conditions underlying moderate to good quality timber production and still found inherent differences in recovery rates between disturbance types. Their results suggest that productivity alone does not entirely explain why our model did not distinguish between fire and harvest disturbances. Other variables included in our analyses may have served as “surrogates” for disturbance type. In particular, the size (AREA) variable generally differentiates fires (large) and harvests (small), though both fires and harvests indicated slower recovery with increasing size. This result is consistent with increasing seed-source limitations with increasing disturbance patch size (Turner et al. 1998) and indicates that the AREA variable is an important ecological predictor of forest recovery, similar to other regions of the boreal forest (Sturtevant et al. 2014). Analysis of the harvests as agglomerations would have averaged harvest conditions across the independent variables on interest, including site productivity and disturbance patch size, the latter serving as a potential surrogate for availability of nearby seed source.

Related to the influence of site quality is the counterintuitive result that the amount of forest without lichen following disturbance is negatively related to the planting effort following the disturbance (Fig. 4). This outcome is likely explained by planting efforts that were focused on areas known by managers to have poor regeneration (i.e., poor site quality). The PLANT variable is probably indicating where managers expected to have poor recovery, so they attempted to improve recovery through planting. Our results indicate that the planting efforts may not have helped the recovery of closed canopy forest but may have helped promote the more open forest – woodland conditions with lichen components.

Our broad-scale analysis, enabled by classified satellite imagery, allowed us to evaluate recovery trends across the full range of landscape variability. Consequently, this analysis was able to identify influential disturbance attributes that have not been included in finer scale studies (e.g., land class prior to disturbance, disturbance size). Some previous studies have indicated compositional differences between recovery following fire and harvests, with fires having more broad-leaved vegetation (Simon and Schwab 2005b). However, the forest classifications in our land cover data set did not distinguish deciduous and conifer forest classes separately, due to the infrequency of the deciduous type, which made it difficult to correctly classify in a supervised classification. Given the relative rarity of the deciduous forest, we suspect that the composition of recovering vegetation is likely sensitive to the surrounding landscape composition and that a more refined forest classification may show a compositional response to disturbances in areas where hardwoods are locally more prevalent.

The extent of long-term forest conversion caused by disturbance remains a fundamental uncertainty facing sustainable forestry initiatives in the region (Doyon et al. 2011). Our models do

not demonstrate long-term conversion of productive forest following either harvest or fire disturbances. As discussed above, there is an apparent delay following fires, but the models estimate most productive forest to be reforested (80% of disturbed area becoming forested) in less than 40 years after fire (Fig. 3).

Along with sustainable harvest considerations, forest recovery responses have implications for other land uses and for woodland caribou. Typical fires in this system create more persistent open canopy conditions than harvest. Such open conditions may supply certain benefits — such as the promotion of berry-producing shrubs and maintenance of woodland caribou habitat — valued by local indigenous cultures. Our results indicate that harvesting done on low productivity sites could result in vegetation responses more comparable with postfire responses, but this remains untested, and it is not clear whether such actions are economically or socially desirable.

A meta-analysis of calf recruitment and range disturbance from Boreal caribou populations across Canada concluded that that total disturbance, defined as wildfires <40 years old and >200 ha in size, and anthropogenic disturbances buffered by 500 m negatively affect rates of caribou recruitment (Environment Canada 2011). The recovery strategy sets out a threshold of disturbed lands at 35% and requires a “dynamic minimum” of 65% undisturbed habitat be maintained over time to ensure a reasonable probability for population viability (Environment Canada 2012). Our results have implications for determining the component of the disturbed area footprint attributed to fires and also to the vegetation recovery times of both wildfires and forest harvesting. Using our threshold of 80% reforested as an “undisturbed” area, typical harvests could transition to an “undisturbed” forest in approximately 24 years, whereas typical fires would be considered disturbed for 44 years (Table 5). Additionally, our results suggest that an accurate accounting of disturbed and undisturbed areas through time should take into account relevant attributes of the disturbed area, including size, site productivity, planting efforts, and forest condition prior to disturbance. For example, both harvests and fires that occur completely on Poor sites would take considerable longer to transition back to an undisturbed state; 38 years and 56 years, respectively (Fig. 3). Our study area comprises only a small portion of one caribou range in Labrador; natural processes and landscape conditions that affect the restoration of natural and anthropogenic disturbance types require further study to allow for more nuanced and comprehensive range planning for caribou conservation in Labrador and elsewhere.

Conclusions

There is increasing recognition that more persistent early successional stages and greater range of variability in vegetation recovery time observed following many natural disturbances can play an important role in the regional biodiversity of predominantly forested areas (Swanson et al. 2010). Understanding forest recovery following disturbance is therefore fundamental to effective sustainable forest management planning. Spatially continuous data sets derived from remote sensing and other inventory methods provide opportunities to estimate postdisturbance vegetation processes, as we have done in this study, across a much wider range of variability than could be achieved through plot-scale analysis alone. Our results demonstrate the interdependence among predisturbance condition, site quality, and disturbance size influencing recovery relationships difficult to quantify using traditional (though complementary) field methods.

Landscape simulation studies are routinely used to evaluate the interactions of succession and disturbance processes and their consequences on future landscape structure and function (Scheller et al. 2007). Yet forest recovery processes within these underlying models are generally simplified and rarely validated (Scheller and Swanson 2015). The results of broad-scale analyses such as those

presented here (along with traditional plot-scale studies) can serve as useful benchmarks for the parameterization and validation of simulated forest recovery processes examined at broad spatial scales.

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