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Review

Managing Understory Vegetation for Maintaining Productivity in Black Spruce Forests: A Synthesis within a Multi-Scale Research Model

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Abstract: Sustainable management of boreal ecosystems involves the establishment of vigorous tree regeneration after harvest. However, two groups of understory plants influence regeneration success in eastern boreal Canada. Ericaceous shrubs are recognized to rapidly dominate susceptible boreal sites after harvest. Such dominance reduces recruitment and causes stagnant conifer growth, lasting decades on some sites. Additionally, peat accumulation due to *Sphagnum* growth after harvest forces the roots of regenerating conifers out of the relatively nutrient rich and warm mineral soil into the relatively nutrient poor and cool organic layer, with drastic effects on growth. Shifts from once productive black spruce forests to ericaceous heaths or paludified forests affect forest productivity and biodiversity. Under natural disturbance dynamics, fires severe enough to substantially reduce the organic layer thickness and affect ground cover species are required to establish a productive regeneration layer on such sites. We succinctly review how understory vegetation influences black spruce ecosystem dynamics in eastern boreal Canada, and present a multi-scale research model to understand, limit the loss and restore productive and diverse ecosystems in this region. Our model integrates knowledge of plant-level mechanisms in the development of silvicultural tools to sustain productivity. Fundamental knowledge is integrated at stand, landscape, regional and provincial levels to understand the distribution and dynamics of ericaceous shrubs and paludification processes and to support tactical and strategic forest management. The model can be adapted and applied to other natural resource management problems, in other biomes.

Keywords: *Kalmia angustifolia*; *Rhododendron groenlandicum*; *Sphagnum*; silviculture; mechanical site preparation; tactical and strategic forest management

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1. Introduction

The sustainable management of boreal ecosystems requires the establishment of vigorous forest regeneration after harvest [1]. Moreover, the recent paradigm shift towards ecosystem-based management calls for the development of harvesting techniques that maintain the functions and structure of forest ecosystems [2,3]. The boreal forest of northeastern Canada is characterized by relatively dense stands mainly composed of boreal softwood species (black spruce, *Picea mariana* (Mill.) B.S.P.; balsam fir, *Abies balsamea* (L.) Mill.; and jack pine, *Pinus banksiana* Lamb.) and intolerant hardwoods (mainly white birch, *Betula papyrifera* Marsh.; and trembling aspen, *Populus tremuloides* Michx.). Fire and insect outbreaks are the major natural disturbances driving the forest succession in this region [4]. Because of these characteristics, careful logging around advance growth [5] or variants of the selection method [6] are seen as effective approaches to regenerate these sites, while maintaining essential ecosystem functions.

Despite the use of these harvesting approaches, some regenerating stands of the boreal forest present low juvenile growth after major disturbances, which compromise sustainable and ecosystem-based forest management objectives. Two examples are of particular relevance to the context of boreal ecosystems of northeastern Canada. Both are related to the strong influence that understory vegetation can exert on stand dynamics [7].

First, the presence in the shrub layer of certain species from the Ericaceae family can slow forest succession to a point where ecosystem retrogression is induced [8]. Indeed, some ericaceous species induce a “growth check” on regenerating conifers that can last several decades [9]. Such shifts from productive forest stands to ericaceous heaths have been documented in various ecosystems in Europe [10,11] and in western Canada [12]. In northeastern Canada, rapid dominance by the ericaceous shrubs *Kalmia angustifolia* L. and/or *Rhododendron groenlandicum* (Oeder) Kron & Judd, followed by long-lasting site domination, constitutes another well-documented example of this phenomenon [13,14] (Figure 1).

Figure 1. Site dominance by ericaceous shrubs, such as *Kalmia angustifolia* and *Rhododendron groenlandicum*, after harvest has a significant impact for forest succession, ecosystem structure and functioning.

Paludification is a second mechanism by which regenerating boreal forest stands are halted or limited through peat accumulation (mainly *Sphagnum*) initiated directly over a formerly mesic mineral soil [15] (Figure 2). Through this process, rooting zone temperatures, organic matter decomposition rates, microbial activity, and soil nutrient availability are reduced [16]. The alteration of these production factors leads to a decline in forest productivity [17], with significant impacts on forest management sustainability.

Many studies have investigated the influence of understory vegetation (either ericaceous shrubs or *Sphagnum* species) on black spruce stand regeneration in northeastern Canada [16,18]. We have contributed to part of this literature by investigating the problem at various scales. Over time, our research efforts have been integrated within a multi-scale research model, where results from one scale are used into higher levels of research activities, and each level is associated with specific outcomes related to forest management.

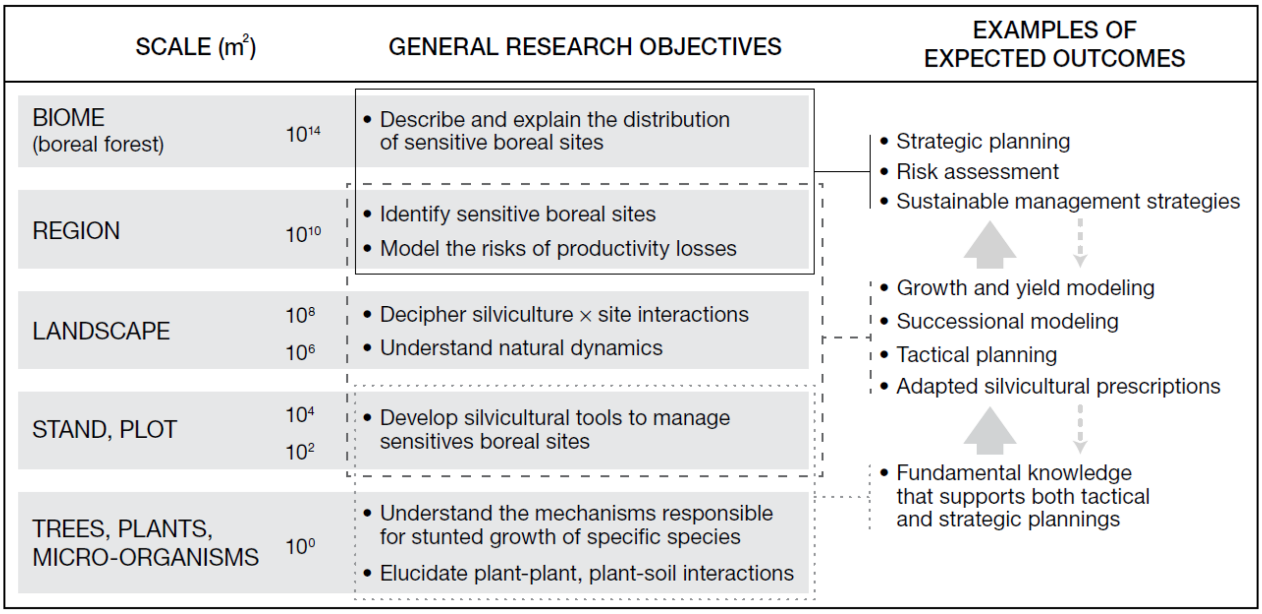
Figure 2. Paludification reduces rooting zone temperatures, organic matter decomposition rates, microbial activity and soil nutrient availability and ultimately leads to a decline in forest productivity.

Our objectives are to describe the research model we have implemented regarding boreal site productivity as affected by ericaceous shrubs dominance and peat accumulation. We aim at providing tangible examples of research activities related to forest management, summarizing key results obtained at the various scales of investigation, as well as enhancing some of the practical outcomes from our research model. We suggest that this research model is well adapted for large-scale ecological experiments with objectives and outcomes at various scales [19], and that it can be adapted and applied to other natural resource management problems, in other biomes. We did not aim at extensively reviewing the literature pertaining to ericaceous dominance and paludification of boreal sites, as other reviews have already been published on the subject [13,16].

2. A Multi-Scale Research Model

We propose a multi-scale research model (Figure 3) elaborated to limit productivity and diversity losses in boreal ecosystems of northeastern Canada after site dominance by ericaceous species or paludification. Fundamental investigations of plant-plant and plant-soil interactions are carried out to provide insights into the mechanisms responsible for growth inhibition in conifers and site fertility reduction. This new knowledge is used to develop innovative silvicultural approaches to both prevent either heath formation or paludification and bring back dominated sites to a productive state. We pursue research activities at the landscape level, so that silvicultural efforts might be oriented on the most responsive sites and to improve knowledge on how disturbances and permanent site conditions influence ericaceous and *Sphagnum* species. Along with the regional assessment of the problem, research results obtained at the stand and landscape levels have direct outcomes for tactical forestry planning and growth/yield modeling. Ultimately, regional understanding of either heath formation or paludification in interaction with site characteristics and natural dynamic processes is analyzed at the supra-regional and provincial (or biome) levels to fine-tune the provincial ecological classification system. At this level, biodiversity and productivity issues can be taken into account for strategic planning, *e.g.*, in elaborating the provincial sustainable forest management strategy, or introducing adapted risk management approaches to annual allowable cut calculations.

Figure 3. A multi-scale research model elaborated to limit productivity and diversity loss in boreal ecosystems of northeastern Canada after site dominance by ericaceous species or paludification.



To provide the expected outcomes, research activities at the various scales (plant, stand, landscape, region and province/biome) overlap, so that knowledge gain at one level can be integrated into coarser scales. For example, fundamental knowledge at a fine scale about the relative competitive potential of *Kalmia* in the presence of black spruce is essential to develop adapted mechanical site preparation treatments. Furthermore, knowledge about how these competitive interactions vary with permanent site characteristics will help to manage or limit long-lasting dominance by ericaceous species. As a complement to the work at fine scales, both regional and provincial assessments of regeneration issues are essential for the development of a sustainable management strategy. The following sections further describe how this multi-scale approach is used to develop new knowledge and practical solutions to both the problem of ericaceous dominance (section 3) and of paludification (section 4) in black spruce forests in Québec, Canada.

3. Ericad Dominance

3.1. The Tree and Plant Level

A combination of mechanisms is thought to be responsible for the effects of *Kalmia* and related species on conifer establishment and growth. Peterson [20] was the first to demonstrate that dried leaves of *Kalmia* contain substances that hinder primary root development of black spruce through destruction of epidermal and cortical cells. This led to work by Mallik [21], who showed that *Kalmia* throughfall and *Kalmia* soil leachate significantly reduces the early growth of black spruce seedlings. Here, we describe some of our own contributions that further explored the mechanisms controlling these *Kalmia*-black spruce interactions.

In a field trial in northwestern Québec, we used stable isotopes to investigate direct competition for nutrients and water between *Kalmia* and conifer seedlings [22]. Double-labeled ^{15}N ammonium-nitrate was applied to plots containing both ericaceous shrubs and planted black spruce. We observed that most of the available nutrients were absorbed by the ericaceous shrubs, despite the fact that black spruce seedlings were more effective than either *Kalmia* (or *Vaccinium*) at absorbing N per unit of root biomass. In other words, this experiment demonstrated that *Kalmia* and black spruce compete for soil nutrients and that *Kalmia*'s competitive ability stems from its more extensive root systems compensating for its lower specific absorption efficiency. In another experiment on the same field site, LeBel *et al*. [23] showed that six consecutive years of *Kalmia* removal resulted in a four-fold increase of N mineralization rates in the forest floor. These results illustrate that, besides competing directly for soil nutrients, *Kalmia* also interferes indirectly with black spruce growth by modifying nutrient cycling and energy fluxes in the soil. The authors of that study went on to speculate that condensed tannins, assumed to be higher in *Kalmia* litter, were a source of interference to soil N cycling. We tested this hypothesis in a series of *in vitro*, microcosm and field experiments. For example, Joanisse *et al*. [24] demonstrated that *Kalmia* leaf litter could contain up to 23.5% tannins (dry wt. equivalent) and that these very tannins were responsible for inhibiting the activity of important soil enzymes involved in the cycling of N, P and C. Furthermore, Joanisse *et al*. [25] found that *Kalmia* tannins were efficient at precipitating soil proteins into stable compounds that were recalcitrant to decomposition and mineralization. They also showed that *Kalmia* gained access to the organic-N sequestered as soil tannin-protein complexes via their associated mycorrhizas. Taken collectively, these experiments demonstrated that the production of litter tannins and the preferential association to specialized root symbionts confer a competitive advantage to *Kalmia* in acquiring soil N, with strong implications for forest succession, ecosystem structure and functioning.

Recent greenhouse experiments also investigated how trait plasticity of ericaceous shrubs could explain their dominance after major disturbances, compared to black spruce. Indeed, plasticity of functional traits associated with light and nutrient acquisition may provide a competitive advantage in changing environments [26], such as those found in forest ecosystems before and after harvest. Hébert *et al*. [27] thus submitted *Kalmia*, *Rhododendron* and black spruce plants to combinations of light and nitrogen addition levels during a simulated growing season. Their results showed that the leaf mass per unit of area (LMA) of both ericaceous species was significantly reduced by shading, whereas LMA of black spruce was unchanged in response to light level. The relative high level of plasticity for this trait for ericads suggest that they can positively respond to increased light levels after logging, with increased nitrogen productivity, photosynthesis rate and growth, compared to the non-plastic black spruce.

These fundamental studies that we have conducted for over a decade have strengthened our understanding of plant-plant interactions that drive early stand development on some boreal forest sites subjected to ericaceous shrub dominance. Knowledge of the nutritional and physiological impacts of *Kalmia* and related species on regenerating conifers has supported the development of silvicultural tools for soil and microsite management.

3.2. The Stand/Plot Level

In some ecosystems dominated by ericaceous shrubs, fertilization was effective to overcome planted conifer growth check [28,29]. In boreal Québec, we thus verified if slow-released fertilizer added at the time of planting could alleviate the nutritional issues on various *Kalmia*-dominated sites. Indeed, we measured increased early growth responses after fertilization, compared to unfertilized conditions on many sites [30–33]. Burying slow-release fertilizer near the seedlings at the time of planting was an efficient means of delivering nutrients to the trees while avoiding stimulation of *Kalmia* growth. However, the economic advantages of such treatment in these conditions need to be demonstrated, based on longer term results. Moreover, the initial growth stimulation provided by the fertilizer is short-lived [23]. We have yet to verify if the increased litterfall in fertilized plots will initiate a second wave of fertilizer-induced changes to soil processes, as observed in other ecosystems [34]. Longer term results obtained from another field trial in Newfoundland (Canada) suggest that it may be so, as we measured improved soil fertility 17 years after *Kalmia* control and conifer re-establishment on a *Kalmia* heath [35].

Many authors have identified mechanical soil preparation as a promising silvicultural option to establish tree seedlings on *Kalmia* sites. Soil scarification increases nutrient mineralization through changes in soil temperature and moisture regime and by mixing organic material with mineral horizons [36]. Furthermore, scarification is expected to limit *Kalmia* expansion by creating barriers to rhizome extension [37]. We confirmed the efficacy of mechanical soil preparation on various ericad-dominated sites [30,32,33,38,39]. For example, five years after planting in northeastern Québec, black spruce seedlings in scarified plots exhibit height and diameter gains of near 100% compared to seedlings planted in unscarified plots [32]. Without proper soil preparation, we observe height growth trajectories typical of stunted seedlings that will likely underperform for several decades. Recent results further confirmed that intensive scarification promotes seedling growth over standard, less aggressive site preparation [31]. However, the growth gains associated with intensive treatments need to be balanced against the supplemental investments involved, compared to standard, single-pass treatments [40].

Mechanical scarification also favors the establishment of early-succession species absent from control plots [32]. A shift in species dominance after scarification is expected to influence the quality of future litter inputs and further modify soil processes [35]. With these silvicultural trials, we also showed that the recalcitrant ericad-humus that accumulates in control plots has significant effects on soil temperature, reducing the quantity of energy absorbed by the conifer rooting zone [32].

Lorente *et al*. [41] have also demonstrated how scarification reduces *Kalmia*, *Rhododendron* and *Vaccinium* aboveground biomass. Furthermore, these authors have shown that at the stand level, ericaceous shrubs play a key role in driving soil properties, forest regeneration and long-term succession of boreal sites subjected to forest management.

Taken collectively, these results indicate that the regeneration success of *Kalmia* and *Rhododendron* dominated sites is positively related to forest floor disturbance intensity. For tactical planning, they have confirmed mechanical site preparation as the preferred operational approach for the management of such sites in Québec, where provincial regulations prohibit the use of chemical herbicides [42]. Another tactical outcome is related to microsite selection for planting in provincial guidelines, which now integrates ericaceous shrub cover as a key variable to identify proper planting spots. The various silvicultural trials, conducted at the stand level, have, however, indicated that interactions exist between treatments and site characteristics, thus supporting the need for conducting landscape level analyses of the issue.

3.3. The Landscape Level

The relative importance of direct competition and indirect interference by ericaceous shrubs varies with site characteristics [43]. However, the effects of *Kalmia* and associated species on site productivity are difficult to evaluate, because of the complex interactions among ecosystem components. Moreover, it remains unknown if the dominant harvesting approaches used in boreal Québec (e.g., careful logging around advance growth with minimal soil disturbance) stimulate or restrain *Kalmia* dominance; site susceptibility to productivity losses due to ericad dominance remained to be studied. A better understanding of silviculture and site interactions is thus required to fine-tune both tactical (silvicultural prescriptions) and strategic planning (sustainable management).

Based on the mechanistic knowledge acquired at the plant and plot levels, we set up a series of experiments to answer these questions at the landscape level. An experimental design was established in northeastern Québec to test for *Kalmia* and *Rhododendron* effects on natural black spruce regeneration growth and physiology along a gradient of site fertility [44]. Phytometers [45] and control (untreated) plots were established on recently harvested sites, representing three contrasting ecotypes. We assessed growth and physiological parameters of established conifer seedlings during two consecutive growing seasons, along with indices of soil fertility. We observed that black spruce photosynthesis rate and foliar K were higher in plots where *Kalmia* has been eliminated, compared to the control, untreated plots. However, contrary to our hypothesis, the influence of *Kalmia* on forest regeneration physiology was largely independent from site permanent characteristics. Growth monitoring, along with tree ring analysis are undergoing to verify if these physiological effects are transcribed in similar productivity responses. Based on current knowledge, site type characteristics are integrated in tactical forestry planning to guide mechanical soil preparation operations. Annual allowable cut calculations also integrate ericaceous shrubs and site characteristics interactions through the inclusion of adapted regeneration delays to growth curves [46].

3.4. The Regional Level

The shift from productive forest stands into *Kalmia* heaths compromises the sustainability of forestry activities. However, several factors limited the accurate assessment of the spatial importance of the issue, at a scale relevant to strategic forest planning. Past and current forest inventories do not include detailed information related to ericaceous species, which forces the need to develop methods to assess ericaceous dominance at the regional scale. Preliminary work demonstrated the ability to map ericaceous dominance on small areas using images from airborne and satellite sensors [47,48]. However, a useful spatial assessment of the issue involves developing a method suitable to map large areas of the biome. Furthermore, given the dynamic nature of ericaceous species dominance during succession, spatial monitoring implies that the current status can only be interpreted in regards to its evolution since the last significant disturbances. These tools should also help in defining the site conditions favoring their dominance on disturbed forest sites. Therefore, we developed a method for mapping ericaceous shrubs from satellite images at the regional scale (*i.e.*, for area larger than ~10,000 km^2 [49]). Our method integrates high resolution satellite imagery (e.g., IKONOS, 1-m resolution) on a small, but representative, portion of the area to train the initial classification procedure. Once the training areas are mapped, they then serve as extended training areas to map medium resolution satellite imagery (e.g., Landsat, 30-m resolution). Discrimination of ericaceous shrub cover from other land cover types is achieved with global mapping accuracy comparable to the one expected for other forestland types; 88% and 79% from IKONOS and Landsat, respectively. Our method is adapted for mapping the spatial distribution of ericaceous shrub cover and is compatible with existing forest stand maps, thus having direct tactical and strategic applications for forest management. For example, it can be used to compare specific areas with their current status, knowing the time since harvest, to assess if there is an increase in ericad dominance. In such a case, the next five-year forest management plans may include more intense silvicultural treatments, like intensive mechanical soil preparation.

The historical assessment of the spatial distribution of ericaceous shrubs at the regional level implies two specific challenges: (1) producing large mosaics from images taken at times relevant to identify the latest major site disturbances; and (2) integrating spatial modeling of favorable or limiting conditions leading to *Kalmia* dominance. Data on temporal vegetation changes, as influenced by logging and natural disturbances [50], will support the implementation of ecosystem-based management. However, regional-based models are limited by the available spatial layers of information. Therefore, relationships at that scale can only be established with spatial environmental, climatic or historical variables, such as slope, degree-days and type of last significant disturbance. These relationships are often inferred and difficult to establish. A regional model to predict ericaceous dominance can thus be built partially from the conclusion of finer scale studies that provide information on the general conditions that lead to a loss of site productivity due to *Kalmia* dominance. Such a model can also be developed by historical inspections of documented sites. Overall, either a current or historical map of the dominance status or a predictive model will allow managers to integrate the risk of site dominance by ericaceous shrubs. These tools under development will be used to adjust annual allowable cut calculations over entire forest management units and prioritize silvicultural investments accordingly.

3.5. The Provincial (or Biome) Level

The maintenance of forest productivity and biodiversity as influenced by ericaceous species is a significant forestry issue in Québec [51], as the boreal forest supports most of the forest management activities in the province. Despite the abundant literature regarding the mechanisms responsible for heath formation and adapted silvicultural approaches, no information was yet available on ericaceous species distribution and dynamics at the provincial level.

Using data from the provincial ecological survey (~20,000 sample plots), we selected the sample plots found in the boreal zone (10,000 sample plots) to calculate a relative index of abundance for each ericaceous species. Canonical multivariate data analyses were done using forest (e.g., percent tree cover by species), soil (e.g., parent material, drainage, slope), geographic (e.g., ecological region) and climatic data (e.g., mean annual temperature and precipitation). Ordination diagrams were used to identify ecological gradients that control ericaceous species distribution at the biome level and point to variables that best explain the occurrence of ericads on any given site.

Patterns of species distribution appearing at the provincial level were otherwise impossible to apprehend at finer spatial scales. Our preliminary interpretations suggest that at this scale, *Kalmia* is intimately associated with fires and jack pine and that *Rhododendron groenlandicum* is associated with flat terrains and poorer drainages; its relative abundance, thus, diminishes from west to east in the province. Species distribution data, along with environmental and perturbation gradients, were used to define ecological units that cover the entire boreal zone within the province, each unit bearing distinct characteristics about their abundance and composition of ericaceous species. Once refined, this information will be available for fine-tuning of the actual provincial ecological classification system. Ultimately, this new ecological information will be available to forest managers and silviculturists to assess the risk of ericad dominance, depending on the region where they conduct forest activities. Thus, this global assessment of ericaceous species distribution will be useful in refining the provincial and regional sustainable management strategies.

4. Paludification

4.1. The Tree and Plant Level

The nature of the forest soil changes dramatically as paludification proceeds. The tree rooting zone shifts from mineral soil, with a shallow organic layer and a feather moss (*Pleurozium schreberi* (Brid.) Mitt., *Hylocomium splendens* (Hedw.) Schimp., *Ptilium crista-castrensis* (Hedw.) De Not.) dominated field layer, to an inaccessible mineral soil, with a thick organic layer and a *Sphagnum* species dominated field layer. We have investigated how these changing conditions influence tree growth and nutrition. *Sphagnum* species are favourable seedbeds for most tree species [52] due to their ability to provide a constant water supply [52,53]. However, they are not a favourable growth substrate; both field [54,55] and greenhouse [56] studies have shown that black spruce have higher growth rates in *Pleurozium* than in *Sphagnum* (typically *S. capillifolium* (Ehrh.) Hedw. and *S. warnstorfi* Russow). Specifically, living *P. schreberi* and fibric or humic material derived from this species provide a better growth substrate than *Sphagnum* species or their fibric- or humic-derived material. Nitrogen availability plays a key role in these differences, as available N was higher in *P. schreberi* than in

Sphagnum species-derived substrates, and foliar nutrition was correlated with these higher levels. Studies have shown that not only do feather mosses (such as *P. schreberi*) harbour N fixing cyanobacteria [57], but also that black spruce is able to absorb this organic N [58]. Furthermore, *Sphagnum* species have particularly slow decomposition rates [59,60], which are not fully explained by their high C:N, but are probably a function of various secondary metabolites that limit microbial breakdown of their cell walls [61]. This fundamental knowledge raised questions that needed to be addressed at a coarser scale of analysis: what are the drivers of paludification at the site level, and what are the best techniques to manage paludified stands?

4.2. The Stand/Plot Level

At the stand level, we thus studied how paludification is influenced by processes linked to stand and forest floor attributes, and their interactions. We also examined the impact of fire severity on these processes. We found that stand attributes, particularly composition and structure, have a significant impact on paludification. As the accumulation of organic material is dependent upon a lower rate of decomposition than production, the type of environment created by the stand significantly affects the rate of paludification [62,63]. Stands with a partially mixed composition (particularly trembling aspen) accumulate less organic matter, as the decomposition rate of the litter is faster [64], the soil fauna is dominated by macrofauna [65] and bryophytes are less omnipresent on the forest floor [62]. Similarly, stands with a closed canopy tend to be dominated by feather mosses [66], which have a lower photosynthetic compensation point than *Sphagnum* species [67]. Our studies showed a positive feedback loop in the paludification process: as stands open up through natural self-thinning, *Sphagnum* species dominate and replace feather mosses [66], stimulating the accumulation of the organic layer via their slow decomposition rate [59,60] and their faster growth rate [68]. This thick organic layer results in an elevated water table [66], which creates a wet, cold, nutrient poor rooting environment for trees. This, in turn, limits tree growth, maintaining the openness of the stands [17,69]. The low tree cover then helps the growth of heliotrophic *Sphagnum* species. Our studies indicate that on the Clay Belt of Québec and Ontario, a 150,000 km^2 physiographic region, time since fire is the best predictor of paludification [62]. This implies that given enough time in this region, characterized by a flat topography and partially impeded drainage, all stands will paludify [69,70]. However, only on relatively flat areas does this phenomenon proceed rapidly enough to warrant inclusion of this issue in forest management plans.

This body of knowledge led to the development of management approaches to limit the productivity losses due to paludification. Stands can be returned to a productive state via significant disturbance of the organic layer [71]. Indeed, our initial studies indicated that high severity fires (near complete combustion of the organic layer [72]), generated dense productive stands [69]. We found that clearcut harvesting and prescribed burning, both of which substantially disturb the organic layer, generated denser, more productive stands than careful logging [55,73,74]. These more disruptive harvest and silvicultural practices (particularly summer clearcut harvesting), controlled competing vegetation, increased the cover of feather mosses and resulted in better conditions in the rooting zone, as a larger proportion of the roots were in the mesic, humic and mineral soil layers [73]. As clearcutting and prescribed burning are not viable options for forest management within the current legislative environment, we are testing other site preparation techniques that could similarly affect the soil. To support the selection of the most appropriate soil preparation techniques, we recently demonstrated the feasibility of using ground penetrating radar as a method to detect organic layer thickness [75].

4.3. The Landscape Level

In addition to the stand level factors, landscape attributes also influence paludification. Slope is a significant factor, both at fine [76] and coarser scales [75]. In these studies, we confirmed that the organic layer accumulates more slowly on steeper slopes than on flat terrains. However, we showed that even sites with significant slopes (from a regional perspective) can also accumulate thick organic layers given enough time. In addition to slope, topographic position influences paludification rates, with more accumulation occurring on plateaus [75,77], resulting in an unusual relationship between elevation and paludification.

Fire severity (estimated as the thickness of the organic layer post-fire) also plays a significant role in paludification rates at the landscape level [62,69,78]. In regions burned by fires that were not severe (thick organic layer remaining post-fire), succession proceeds from stands that are already paludified or partially paludified. Studies indicate that these stands have fewer trees, and these trees grow more slowly than trees in stands established after high severity fires [17,69]. Recent results indicate that the remaining organic layer post-fire is a significant biological legacy that offers a short cut for *Sphagnum* species colonisation, resulting in rapid establishment of species that are typically seen only at the end of succession [79].

Mapping these factors (slope and fire severity) across the region is undergoing and will permit the development of regional paludification maps. These, in turn, will allow the deployment of appropriate management strategies for different states of paludification. For example, sites in depressions that may be paludified are difficult to distinguish from paludified sites on plateaus or slight slopes at the stand level. However, management strategies should be different in these environments, as harvest with significant soil disturbance may be effective on plateaus and slopes, but inefficient in depressions.

4.4. The Regional/Provincial (or Biome) Level

Paludification is essentially a regional phenomenon, although it is wide-spread in specific regions such as the Clay Belt of Québec and Ontario, the James Bay lowlands, central Alaska and the western Siberian plain [80]. However, our research has indicated that even a modest accumulation of organic material (25 cm) affects tree growth [81]. Consequently, considering the significant over-estimation of forest productivity when paludified stands are not managed specifically, province-wide adaptations have been suggested for paludified stands in provincial silvicultural guidelines. Within certain regions across the province, specific site types are targeted for intensive site preparation post-harvest to ensure that productive stands are re-established [82]. While the silvicultural options available are still limited, this first step opens the door for more adaptive management in paludified stands and on sites that are prone to paludification across the province.

5. Conclusions

The achievement of sustainable forest management requires adopting multiple management scales, because multiple ecological scales are involved [83]. Hence, ecosystem-based management must take into account the connection between the various spatial scales, from plants to biome, to preserve biodiversity and ecological processes through time [3]. In this context, and inspired by proponents of multi-scale research activities [19,84], we proposed a multi-scale research model developed for maintaining forest productivity and biodiversity of sensitive boreal sites in Québec (Figure 3). In this model, general research objectives pursued at various scales, from determining microorganisms influence on soil fertility indices up to fine-tuning the provincial ecological classification, are intimately linked, so that new knowledge gained at one scale can be integrated to the next one. Practical outcomes at the fundamental, tactical and strategic levels take advantage of inputs from multiple levels of research activities. We believe that our model can easily be adapted to other contexts and biomes, where natural resources management is based on an understanding of ecosystem processes.

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Conflict of Interest

The authors declare no conflict of interest.

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