

# Deer browsing and soil disturbance induce cascading effects on plant communities: a multilevel path analysis

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**Abstract.** Understanding how large herbivores shape plant diversity patterns is an important challenge in community ecology, especially because many ungulate populations in the northern hemisphere have recently expanded. Because species within plant communities can exhibit strong interactions (e.g., competition, facilitation), selective foraging by large herbivores is likely not only to affect the abundance of palatable species, but also to induce cascading effects across entire plant communities. To investigate these possibilities, we first tested the effects of deer browsing and soil disturbance on herbaceous plant diversity patterns in boreal forest, using standard analyses of variance. Second, we evaluated direct and indirect effects of deer browsing and soil disturbance on the small-scale richness of herbaceous taxa using a multilevel path analysis approach. The first set of analyses showed that deer browsing and soil disturbance influenced herb richness. Path analyses revealed that deer browsing and soil disturbance influenced richness via complex chains of interactions, involving dominant (i.e., the most abundant) browsing-tolerant (DBT) taxa and white birch (*Betula papyrifera*), a species highly preferred by white-tailed deer (*Odocoileus virginianus*). We found no evidence that an increase of white birch in fenced quadrats was the direct cause of a decrease in herb richness. However, we found strong evidence that a higher abundance of DBT taxa (i.e., graminoids and *Cirsium arvense*), both in fenced and unfenced quadrats, increased herb layer richness. We propose an empirical model in which competitive interactions between white birch and DBT taxa regulate the strength of facilitative relationships between the abundance of DBT taxa and herb richness. In this model, deer browsing and the intensity of soil disturbance initiate a complex chain of cascading effects in boreal plant communities by controlling the abundance of white birch.

**Key words:** Anticosti Island, Gulf of St. Lawrence, Canada; browsing tolerance; cascading effects; competition; deer browsing; facilitation; indirect effects; multilevel path analysis; *Odocoileus virginianus*; plant diversity; plant–herbivore relationships; white-tailed deer.

## INTRODUCTION

Large herbivores can affect the vegetation physiology of many terrestrial ecosystems (van de Koppel et al. 1997, Côté et al. 2004), particularly in northern hemisphere forests (Horsley et al. 2003) where ungulate populations and their browsing on vegetation have recently increased (Rooney and Waller 2003). In forests, sustained overbrowsing reduces plant cover and diversity, alters nutrient and carbon cycling, and redirects succession to shift future overstory composition (Côté et al. 2004). In temperate and boreal forests, the direct effects of deer browsing on plant tissues can largely explain the decline in distribution and abundance of several palatable forest species (Brandner et al. 1990, Potvin et al. 2003), including common (*Trillium*

*grandiflorum*; Augustine and Frelich 1998) and endangered herbs (e.g., *Panax quinquefolius*; McGraw and Furedi 2005). High-density deer populations also commonly cause tree diversity to decline (Gill and Beardall 2001, Kuiters and Slim 2002, Horsley et al. 2003). However, few studies have evaluated the browsing impacts of large herbivores on the maintenance of diversity patterns in boreal plant communities (Gill and Beardall 2001). Mechanical site preparation (MSP) is another common disturbance used to create favorable microsite conditions for post-harvest tree seedling establishment in boreal forest. Without considering the effect of herbivores, increasing intensity of MSP was found to increase the negative impacts on boreal plant diversity (Newmaster et al. 2007; but see Haeussler et al. 1999, 2004, Peltzer et al. 2000). Although deer browsing and MSP often occur in the same sites, it is unclear whether their effects on plant diversity patterns are independent, additive, or compensatory.

Understanding the mechanisms by which large herbivores and soil disturbance influence the organiza-

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tion of plant communities is challenging for many reasons. First, the removal of palatable plant species by herbivores can induce complex effects in multispecies assemblages if these plants have strong interspecific relationships. Second, common statistical methods such as (M)ANOVA and multiple regression have limited power to detect these complex chains of interactions. Such analyses estimate coefficients that represent the direct effects of each predictor on dependent variable(s), but cannot fully assess any interdependencies among predictors. Third, experiments aimed at controlling the intensity of deer browsing, soil disturbance, and the strength of interactions among plants are more difficult to design as more species are involved. These limitations can be largely overcome with structural equation models and path analyses. These methods allow for (1) partitioning of direct and indirect effects, (2) testing complex hypotheses about relationships among system components, and (3) evaluating alternate mechanistic hypotheses about the ecological processes that generates data structure (Shipley 2002, Grace 2006).

Although the identification and magnitude of processes controlling plant species diversity have been among the most studied topics in community ecology over the last 40 years (e.g., Grime 1973, Connell 1978, Petraitis et al. 1989, Tilman and Pacala 1993, Grace 1999), a universal explanation has not yet been reached (see Bruno et al. 2003, Lortie et al. 2004, Michalet et al. 2006). Processes considered important in the regulation of species diversity include: competition (Grace and Tilman 1990, Goldberg and Barton 1992), facilitation (Hacker and Bertness 1999, Choler et al. 2001), herbivory (Pacala and Crawley 1992, Collins et al. 1998), abiotic disturbances (Grime 1974, Petraitis et al. 1989), site productivity (Abrams 1995, Mittelbach et al. 2001), and recruitment (Hubbell et al. 1999). Experimental studies have shown that these processes often do not act in isolation, but rather in concert (Gough and Grace 1998). For example, Callaway et al. (2005) demonstrated that fencing subalpine meadows shifted the relationship between unpalatable dominant plants and the number of species per unit area (species density), from positive in unfenced quadrats to negative in fenced quadrats. Numerous processes shape small-scale species diversity, both directly and indirectly, but their relative importance and interactions are still poorly known in several ecosystems.

In this study, we first assessed whether white-tailed deer (*Odocoileus virginianus*, Zimmermann) browsing interacts with soil mechanical disturbance to influence plant species diversity in boreal forest communities. Second, we quantified the causal relationships among: (1) the intensity of disturbance caused by simultaneous deer browsing and soil disturbance, (2) the dominance of the dominant browsing-tolerant (DBT) taxa and white birch (*Betula papyrifera*), and (3) herb richness (i.e., the number of herbaceous taxa per quadrat). We used multilevel path analysis models to test the following

hypotheses: (1) deer browsing and soil disturbance directly affect the abundance of white birch and DBT taxa; (2) deer browsing and soil disturbance indirectly influence competitive relationships between DBT taxa and white birch; (3) deer browsing and soil disturbance directly affect herb richness; (4) deer browsing and soil disturbance indirectly influence herb richness through their effects on the abundance of white birch; and (5) both types of disturbance and competition directly influence herb richness. Further, we used exploratory path analysis to propose a new model that best explain the causal patterns in our data.

## METHODS

### Study site

The experiment was carried out on Anticosti Island (7943 km<sup>2</sup>) in the Gulf of St. Lawrence, Québec, Canada (49°06'–49°95' N, 61°67'–64°52' W). Climatic, topographic, and site conditions are described in Beguin et al. (2009). Anticosti Island's forests belong to the boreal zone and are part of the eastern balsam fir–white birch bioclimatic region (Saucier et al. 2003), where the main tree species are balsam fir (*Abies balsamea* (L.) P. Mill.), white spruce (*Picea glauca* (Moench) Voss), black spruce (*Picea mariana* (Mill.) B.S.P.), and white birch. Before cutting, the study area was covered by stands dominated by balsam fir (61% ± 20% of basal area, mean ± SD) and white spruce (28% ± 22%), whereas white birch and trembling aspen were a minor component. After the introduction of ~200 white-tailed deer in the late 19th century, the deer population increased rapidly to peak in the 1930s (Potvin et al. 2003). Since that time, population size has remained high (>15 deer/km<sup>2</sup>) and probably fluctuates as a function of winter severity and large-scale vegetation dynamics. The current population density is estimated at >20 individuals/km<sup>2</sup> (Potvin and Breton 2005), but local densities can be higher. Although the island has a short (~100 years) evolutionary history of browsing (sensu Milchunas et al. 1988), the impacts of deer browsing on the physiognomy, composition, and dynamics of vegetation are apparent (Potvin et al. 2003, Casabon and Pothier 2008). In particular, Casabon and Pothier (2008) showed that after clear-cutting, early-successional plant communities are dominated by white birch in fenced areas, and by DBT species in unfenced areas (e.g., grasses and Canada thistle (*Cirsium arvense*)).

### Experimental design

The experiment was conducted in two sites 10 km apart, both dominated by balsam fir, that were harvested in autumn 1998 (site 1) and autumn 1999 (site 2). In both sites, we applied a clearcut, where circular groups of trees were left unharvested within the cutover matrix to improve seed supply and tree regeneration establishment in adjacent clearcut areas. To investigate the joint effects of soil disturbance and deer browsing on ground vegetation in clearcut areas,

we experimentally manipulated the intensity of forest floor disturbance and deer browsing. First, we randomly applied two mechanical site preparations (MSP) of varying intensity (a single-pass scarification, and a double-pass scarification with the second pass perpendicular to the first) plus one control (undisturbed). We used a disk trencher mounted on a crawler tractor to create a range of soil disturbance intensities around each circular group of trees. Each of the three intensities of forest floor disturbance was applied to a radial segment covering a 60° angle from the center of the seed-tree group and 100 m from the edge of the group (Fig. 1). Second, we set up a pair of fenced and unfenced 4-m<sup>2</sup> sampling quadrats, 10 m apart, at 30 m from the forest edge and within each radial segment where the soil disturbance treatment was applied (Fig. 1). Hence, the experimental set up is a split-split plot design in which sites are in main plots, soil disturbance treatment is in subplots, and fencing treatment is in sub-subplots. Initially, 63 pairs of fenced and unfenced quadrats were set up around 21 tree groups (12 in site 1 and 9 in site 2). However, the fence of 17% of all fenced quadrats was damaged at the time of survey and evidence of browsing was apparent. Therefore, we excluded these quadrats (and their paired unfenced quadrats) from analyses (Table 1).

#### Data collection

Vascular plants were surveyed in July 2006 to estimate the horizontal cover of each species in 12 classes (cover: <1%, 1–5%, nine classes of 10% intervals up to 95%, and 96–100%). The median value of each cover class was used in analyses. Nonvascular plant and lichen species (relative percent cover < 5%) were not considered in this study. Most vascular plants were identified to the species level, but the absence of reproductive organs and/or heavy damage on vegetative tissues caused by deer browsing constrained some identifications to a higher taxonomic level (Appendix A). To avoid potential duplication in taxon identification, which would increase Type 1 error in the analyses, we conservatively rescaled the taxonomic classification in our initial survey to the broadest level common to both taxa, when a risk of potential duplication existed (e.g., *Vaccinium myrtilloides* and *Vaccinium* sp. became *Vaccinium* sp. for both types/plants).

#### Classification of dominant taxa

We distinguished the dominant taxa in fenced and unfenced quadrats over the entire survey to evaluate the competitive interactions between these taxa, and their respective effects on herb diversity. In fenced quadrats, white birch was the dominant species based on its frequency and abundance (Appendix A). White birch is a pioneer, shade-intolerant species (Safford et al. 1990), highly browsed by white-tailed deer on Anticosti Island (Casabon and Pothier 2008). The dense regeneration of white birch seedlings, in conjunction with the rapid

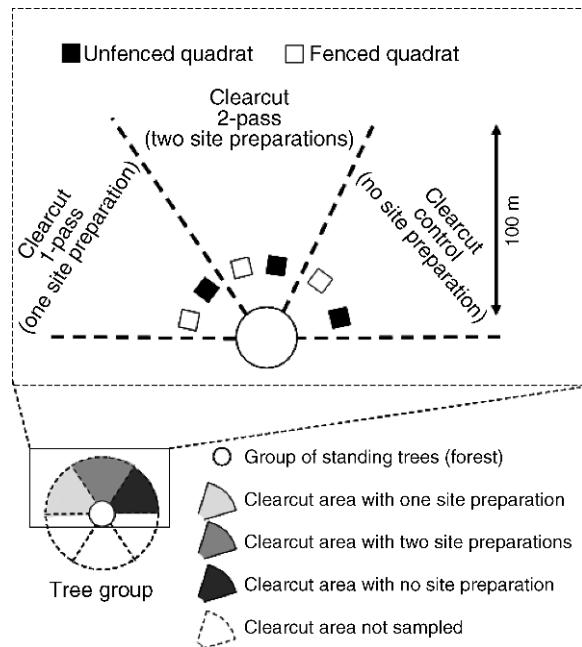


FIG. 1. Experimental design showing the location of the three different intensities of soil disturbance (control, low intensity; single preparation or 1-pass, intermediate; two preparations or 2-pass, high intensity) around one of the 21 tree groups. The upper panel shows the organization of sampling quadrats (open squares, fenced; solid squares, unfenced) located within each level of soil disturbance intensity. The study was conducted on Anticosti Island, Gulf of St. Lawrence, Canada.

development of a dense surface-root system and lateral branches, can negatively impact the development of neighboring species (Perala and Alm 1990). Given these life history traits, the effect of white birch on small-scale herb richness during early stages of forest succession is expected to be negative, mainly through competition. In unfenced quadrats, however, grasses and Canada thistle equally dominated the cutovers in both sites according to their frequency and abundance (Appendix A). Exploratory analysis did not reveal any signs of competition between dominant grasses and Canada thistle at the scale of the 4-m<sup>2</sup> sampling quadrats. Thus, we combined them into a single variable called DBT taxa. In our survey, the grass species in unfenced and fenced quadrats were dominated by *Schizachne purpurascens* and *Cinna latifolia* (J. Beguin, *personal observations*). These grasses and Canada thistle are tolerant of deer browsing (Casabon and Pothier 2008), although their effects on neighboring herbaceous species in a context of deer overabundance are mostly unknown. Given the lack of empirical evidence about their competitive or facilitative effects on herbaceous species in our system, we tested the hypothesis that the relationship between DBT taxa and herb richness was neutral.

TABLE 1. Number of 4-m<sup>2</sup> vegetation quadrats as a function of three levels of soil disturbance intensity, site, and the presence or absence of a fence preventing deer browsing for the experiment on Anticosti Island, Gulf of St. Lawrence, Canada.

Soil disturbance	Site 1		Site 2		Total
	Fenced	Unfenced	Fenced	Unfenced	
Control	10	10	7	7	34
1-pass	11	11	7	7	36
2-pass	11	11	6	6	34
Total	32	32	20	20	104

Note: Soil disturbance is low (control), intermediate (single preparation, 1-pass), or high (two preparations, 2-pass).

Statistical analyses

*Indicators of plant communities.*—We first estimated the effect of fencing and soil disturbance treatments on cumulative richness (the number of distinct taxa present in all quadrats) and on quadrat richness (the number of taxa in every quadrat). These two estimates of richness help to assess the spatial extent at which disturbance treatments can impact taxon diversity. For each site, we estimated the cumulative richness for every plant group (woody, herbaceous, or both) and for each of the six treatment combinations, using taxon accumulation curves (Gotelli and Entsminger 2009). No interaction between sites and treatments was detected on cumulative richness for each plant group, so we pooled the two sites and estimated the mean cumulative richness and the 95% confidence intervals, calculated from 10 000 randomly selected subsets of data, for each of the six treatments and for each plant group. Hereafter, the term *cumulative herb richness* refers to the number of distinct herbaceous taxa present in all quadrats belonging to the same combination of fencing and soil disturbance intensity. We used a  $\chi^2$  test to determine if cumulative richness in each plant group differed among treatments, based on equivalent sampling effort. If we found a difference ( $P < 0.05$ ), we used pairwise  $Z$  test comparisons to locate differences between treatments.

To evaluate the effects of disturbance treatments on quadrat richness for each plant group, we used the maximum likelihood method to estimate the effects of soil disturbance and fencing treatment on the number of taxa per quadrat with a log-linear mixed model:

$$Y_{ijkl} \sim \text{Poisson}(\mu_{ijkl})$$

$$\log(\mu_{ijkl}) = \mu + S_j + F_i + S_j \times F_i + \theta_l + \tau_{k(l)} + S_j \times \theta_l \times \tau_{k(l)}$$

where  $Y_{ijkl}$  is the response value in the  $i$ th level of  $F$ , the  $j$ th level of  $S$ , the  $k$ th level of  $\tau$ , and  $l$ th level of  $\theta$ ;  $\mu_{ijkl}$  is the variance of  $Y_{ijk}$ ;  $\mu$  is the constant general mean effect;  $S_j$  is the fixed effect of soil disturbance  $j$  ( $j = 0, 1, 2$  for control, 1-pass, and 2-pass, respectively);  $F_i$  is the fixed effect of fencing treatment  $i$  ( $i = 0, 1$  for unfenced and fenced, respectively);  $S_j \times F_i$  is the interaction between soil disturbance  $j$  and fencing  $i$ ;  $\theta_l$  is the random

effect of the  $l$ th site ( $l = 1, 2$ );  $\tau_{k(l)}$  is the random effect of the  $k$ th tree group ( $k = 1, 2, \dots, 12$ ) within the  $l$ th site; and  $S_j \times \theta_l \times \tau_{k(l)}$  is the random effect of the interaction between soil disturbance  $j$ , seed group  $k$ , and site  $l$ . Gaussian distributions were assumed for random variables. Hereafter, we define “herb richness” as the number of distinct herbaceous taxa in each single quadrat.

We used a linear mixed model to evaluate simple and interaction effects of disturbance treatments on horizontal cover for each plant group using

$$Y_{ijkl} \sim \text{Normal}(\mu_{ijkl}, \sigma^2)$$

$$\mu_{ijkl} = \mu + S_j + F_i + S_j \times F_i + \theta_l + \tau_{k(l)} + S_j \times \theta_l \times \tau_{k(l)}.$$

We also used presence/absence data to evaluate how the degree of similarity in floristic composition between fenced and unfenced quadrats differed depending on soil treatment. For this purpose, we calculated the Sørensen floristic similarity index (SFSI) for each pair of fenced/unfenced quadrats within each plant group. With an ANOVA, we tested the hypothesis that floristic similarity between fenced and unfenced quadrats decreases as soil disturbance intensity increases, using the following linear mixed model:

$$Y_{jkl} \sim \text{Normal}(\mu_{jkl}, \sigma^2)$$

$$\mu_{jkl} = \mu + S_j + \theta_l + \tau_{k(l)} + S_j \times \theta_l \times \tau_{k(l)}.$$

We used generalized linear mixed models (GLMM) when the probability distribution associated with a dependent variable was Poisson. Otherwise, linear mixed models (LMM) were used, after square-root transformation of the dependent variable, to meet assumptions of homogeneity of variance and the normal distribution of residuals. Analyses were performed with SAS using MIXED and GLIMMIX procedures (SAS Institute 2008).

*Confirmatory multilevel path analysis.*—Next we assessed causal relationships among deer browsing, soil disturbance, the abundance of white birch, the abundance of DBT taxa, and herb richness in each quadrat. Structural equation modeling (SEM) and path analysis are two statistical approaches aimed at testing the

structural or causal nature of the relationship between variables, in an approach analogous to the hypothetico-deductive experimental method (Thomas et al. 2007). Both approaches have their advantages and limitations. SEM using frequentist methods allows testing of the effects of latent variables, contrary to path analysis, but requires multivariate normality of dependent variables, linear relationships between variables, and simple hierarchical structure in the data, whereas path analysis with d-sep (directional separation) tests is flexible regarding these assumptions. Because our data structure precluded the use of standard SEM, we used path analysis with d-sep tests. However, as in most in situ experiments in natural systems, not all variables could be measured; thus any causal mechanism can be further decomposed into a more detailed causal mechanism. Therefore the terms “causality,” “direct cause,” or “indirect cause” can be meaningful only in relative terms in the context of the other variables that make up the causal explanation in the path diagram (Shipley 2002:27).

Path diagrams include variables or vertices (boxes) and directed edges (lines and arrows) that describe which variables are causally related ( $A \rightarrow B$  or  $B \rightarrow A$ ). Directed acyclic graphs (DAG) are a special case of path diagrams when there are no feedback relationships (directed cyclic graph with feedback:  $A \rightarrow B \rightarrow C \rightarrow A$ ); see Shipley (2002). If the causal process generating the data follows the process proposed by the model, then the constraints in the model will be mirrored in the data (Thomas et al. 2007). Alternatively, if the constraints in the model do not agree with the generating process, then the patterns of covariation predicted by the model will show significant lack of fit to the data, allowing us to reject the model (Thomas et al. 2007).

Directional separation tests (d-sep) can be used to test if the hypothetical causal structure defined by a DAG corresponds to the patterns of dependence or independence in the data (Shipley 2002). Briefly, d-sep tests allow one to deduce probabilistic partial independence and dependence relationships between variables that are predicted by a path analysis diagram. Using the same logic as in experimental manipulations, where researchers experimentally fix some variables to constant values in order to prevent them from changing randomly with the response variable, d-sep tests allow the deduction of relationships of dependence and independence among variables in a path diagram, but using statistical control rather than physical control. For example, testing a path diagram where  $X \rightarrow Y \rightarrow Z$  is equivalent to testing the independence relationship (d-sep test) between  $X$  and  $Z$  when  $Y$  is held constant. In path diagrams involving several variables, there are generally several d-sep tests to describe dependence and independence relationships among variables and these tests are not necessarily mutually independent in finite samples (Shipley 2000). However, Pearl (1988) demonstrated that the minimum list of d-sep statements contained in the *basis set* (the set

of d-sep tests that are mutually independent) is sufficient to predict the entire set of d-sep statements in a causal graph. The basis set associated with a path diagram can easily be obtained by listing each of the  $k$  pairs of variables ( $X_i, X_j$ ) in the graph that do not have an arrow between them and by conditioning each  $k$  pairs ( $X_i, X_j$ ) by the set of other variables  $\{Z\}$  that are direct causes of  $X_i$  or  $X_j$  (for more details, see Shipley 2009). The hypothesized causal structure implied in a path diagram can be tested using Shipley's  $C$  test, where  $C = -2 \sum \ln(p_i)$ , where  $p_i$  is the probability that the pair ( $X_i, X_j$ ) in the basis set is statistically independent conditional on the variable(s)  $Z$ . If all  $k$  independence relationships defined by the basis set are true, then the  $C$  statistic will follow a  $\chi^2$  distribution with  $2k$  degrees of freedom (Shipley 2000). Therefore, the hypothesized causal structure is rejected if the  $C$  statistic is greater than the critical  $\chi^2$  value with  $2k$  df.

In our study, causal relationships among variables were assessed with a confirmatory path analysis, using d-sep tests in a generalized multilevel context (Shipley 2009). Generalized multilevel path analysis is a generalization of Shipley's d-sep test allowing one to fit generalized linear mixed models (GLMM) to test the d-sep claim of independence in a path analysis model. In addition to GLMM, we used generalized additive mixed models (GAMM) with cubic regression splines to take into account nonlinear relationships between variables. However, the use of GAMM and GLMM with non-normal distributions is at the frontier of frequentist statistical approaches, so  $P$  values close to the 5% borderline must be interpreted with caution (Zuur et al. 2009:329). We used both GAMM and GLMM to ensure a higher confidence in their interpretation. GAMM were run in R (R Development Core Team 2008) using the “mgcv” package (Wood 2006); GLMM were run using the GLIMMIX procedure in SAS (SAS Institute 2008).

Based on existing disturbance models and our knowledge of ecosystem dynamics on Anticosti Island, we proposed two sets of competing hypotheses to explain the responses of vegetation to the disturbances caused by soil disturbance and browsing. The first set of hypotheses (Hypotheses 1 and 2) evaluated the response of white birch and DBT taxa to deer browsing, soil disturbance, and their possible interaction. The second set of hypotheses (Hypotheses 3, 4, and 5) was built on the results of the first two hypotheses and evaluated different mechanisms by which disturbances, the abundance of white birch, and DBT taxa influenced herb richness. The rationale for the five hypotheses is described as follows.

*Hypothesis 1.*—Both white birch and DBT taxa are influenced directly by disturbances, with white birch cover increasing with soil disturbance intensity (Prévost 1997) and decreasing in unfenced quadrats because of deer browsing (Casabon and Pothier 2008), whereas cover of DBT taxa could be influenced by disruption of belowground interactions and soil conditions created by

soil disturbance. However, the abundance of white birch is independent of the abundance of DBT taxa.

*Hypothesis 2.*—Deer browsing and soil disturbance are indirect causes of the dominance of DBT taxa in unfenced areas. The indirect effects are mediated by direct effects on white birch. In fenced quadrats and with increasing soil disturbance, an increase in white birch cover reduces the abundance of DBT taxa through competition. In unfenced quadrats, severe browsing limits the development of white birch, providing competitive release to DBT taxa.

*Hypothesis 3.*—The main causal processes affecting herb richness are deer browsing and the intensity of soil disturbance (with a possible interaction effect), which prevent species recruitment and increase species loss. Herb richness is independent of the abundance of white birch or DBT.

*Hypothesis 4.*—Soil disturbance and deer browsing are indirect causes of the abundance of DBT taxa and the richness of herbaceous taxa. In fenced quadrats, increased abundance of white birch reduces the abundance of DBT taxa and herb richness because of competition. In unfenced quadrats, competition by white birch on associated species is relaxed and herb richness increases accordingly.

*Hypothesis 5.*—Deer browsing and soil disturbance have both direct and indirect effects on herb richness, by increasing species loss (direct) and by increasing competition through white birch abundance (indirect). This hypothesis differs from the fourth hypothesis in that herb richness does not increase in unfenced quadrats because deer browsing increases species loss.

Note that for each hypothesis, disturbance treatments are organized in a randomized experiment and test the effects of  $X_1 \times X_2$  (interaction between Deer and Soil). The analysis of the effect of  $X_1$  (Deer) and  $X_2$  (Soil) on any dependent variable (e.g., DBT taxa) must follow the standard approach of two-way ANOVA: (1) if the interaction term is significant ( $P < 0.05$ ), single effects are not analyzed for statistical significance; (2) if the interaction is nonsignificant and at least one single effect is significant, single effects (Deer, Soil) are analyzed for significance; (3) if neither the interaction term nor single effects are significant, the global effect of disturbance treatments on any dependent variable can be evaluated by estimating an orthogonal contrast ( $X_i$ ;  $t$  is treatments).

*Exploratory multilevel path analysis.*—Finally, we performed an exploratory analysis to identify a set of candidate path models able to mirror dependence and independence relationships among variables, but without directly testing an a priori causal structure. This a posteriori method is useful and efficient to clarify the full causal structure(s) between variables in a system when empirical evidence and theoretical support are insufficient. To this end, we successively applied two algorithms: the undirected dependency graph algorithm (Spirtes and Glymour 1991, Shipley 2002:246) and the

orientation algorithm using unshielded colliders (Shipley 2002:256). The first algorithm allows the retention only of pairs of variables that share a direct dependence in the causal explanation. Briefly, this algorithm tests the statistical dependence of each possible pair of variables after conditioning on any other observed variable or set of variables in the path model. If the association of two variables  $X$  and  $Y$  remains significant ( $P < 0.05$ ) after conditioning on any other observed variable, a dependence relationship between  $X$  and  $Y$  is retained; otherwise, no direct relationship (or edge) between  $X$  and  $Y$  exists. The second algorithm allows orientation of the direction of the relationship between variables that have previously been found to be dependent. According to d-sep test properties, if a variable  $Y$  in a path model has arrows pointing into it from both directions (e.g.,  $X \rightarrow Y \leftarrow Z$ ), variables  $X$  and  $Z$  will never be d-separated once conditioned on  $Y$  ( $Y$  is called a unshielded collider in this case). However, in the path  $X \rightarrow Y \rightarrow Z$ ,  $X$  and  $Z$  are d-separated once conditioned on  $Y$  ( $Y$  is called a definite non-collider in this case). It is therefore possible to detect colliders from non-collider variables in an undirected acyclic graph using d-sep tests and ultimately to orient the direction of relationships between dependent variables. A thorough description of these algorithms is beyond the scope of this study (for more details, see Shipley 2002). This process generated one exploratory DAG with our data because white birch and DBT taxa are definite non-colliders.

## RESULTS

### *Direct effects of fencing and soil disturbance on indicators of plant communities*

We observed no differences in mean cumulative richness among the six disturbance treatments when we considered woody species only ( $\chi^2_{k=5} = 6.0$ ;  $P = 0.3$ ; Appendix B), and all taxa together ( $\chi^2_{k=5} = 8.0$ ;  $P = 0.2$ ; Appendix B). However, cumulative herb richness differed among the six treatments ( $\chi^2_{k=5} = 15.3$ ;  $P = 0.009$ ; Appendix B) and was 39% higher in fenced quadrats compared to unfenced quadrats, within unscarified areas ( $Z = 3.65$ ,  $P = 0.0005$ ; Fig. 2). In fenced quadrats, cumulative herb richness decreased linearly with increasing soil disturbance intensity and was 32% higher in the unscarified control than in the double-pass scarified areas ( $Z = 2.47$ ,  $P = 0.02$ ; Fig. 2). For quadrat richness, we failed to detect any significant effect of fencing and soil disturbance intensity on richness for woody taxa and for all taxa together (all  $P$  values  $> 0.05$ ; Appendix B). However, similar to cumulative herb richness, the effect of fencing interacted with the intensity of soil disturbance to influence herb richness ( $F_{2,49} = 3.19$ ,  $P = 0.05$ ). Herb richness was 18% higher in fenced than in unfenced quadrats within unscarified areas and tended to decrease in fenced quadrats with increasing soil disturbance.

We did not detect any effect of soil disturbance intensity on Sørensen floristic similarity indices

(Appendix B), which were  $56.1 \pm 7.9$  (mean and 95% CI) for woody plants,  $53.3 \pm 3.8$  for herbaceous plants, and  $58.9 \pm 3.1$  for all plant groups, nor did it influence horizontal cover for all plant groups (Appendix B). However, mean horizontal cover was higher in fenced vs. unfenced quadrats for all taxa (fenced,  $196\% \pm 18\%$  (mean and 95% CI); unfenced,  $135\% \pm 18\%$ ), woody plants (fenced,  $64\% \pm 9\%$ ; unfenced,  $20\% \pm 9\%$ ), and herbaceous plants (fenced,  $120\% \pm 20\%$ ; unfenced,  $103\% \pm 20\%$ ), respectively.

#### Generalized multilevel path analysis

GLMM and GAMM models produced similar results. Some  $P$  values differed slightly when the null hypothesis was tested on single-parameter  $\beta_i$  (GLMM) or spline functions  $f_i$  (GAMM) of continuous variables (Table 2), but conclusions for each causal hypothesis were identical, regardless of the method used (Table 2). Nonlinear relationships of continuous variables probably explain the different  $P$  values obtained with both methods. Indeed, all spline functions in Fig. 3A (edf = 2.374;  $P < 0.0001$ ), Fig. 3B (edf = 2.744;  $P = 0.002$ ), and Fig. 3C (edf = 2.152;  $P < 0.0001$ ) were significant at  $\alpha = 0.05$  and showed departures from linear relationships (edf = 1), where edf is the estimated degrees of freedom associated with each model parameter (Wood 2006).

Hypothesis 1 was rejected but not Hypothesis 2 (Table 2, Fig. 4A, B), indicating that treatments directly affected the abundance of white birch but not the abundance of DBT taxa. Using univariate ANOVA, the percent cover of DBT taxa appeared to be affected only by fencing ( $F_{1,49} = 11.51$ ,  $P = 0.0014$ ) and not by soil disturbance (interaction effect (soil disturbance  $\times$  fencing),  $P = 0.2$ ; single effect (soil disturbance),  $P = 0.8$ ), but the relationship between fencing and abundance of DBT taxa was spurious because it became nonsignificant when we controlled for the abundance of white birch ( $F_{1,48} = 1.57$ ,  $P = 0.22$ ). This result indicates that white birch abundance influenced, at least partly, the abundance of DBT taxa (Fig. 3C;  $R^2 = 0.18$ ,  $P < 0.0001$ ). Hypotheses 3, 4, and 5 failed to explain dependence and partial independence patterns among measured variables (Table 2, Fig. 4C–E), because the observed patterns of data would be unlikely if causal graphs related to Hypotheses 3, 4, and 5 were true, (respective probabilities of  $8.25 \times 10^{-8}$ ,  $5.84 \times 10^{-7}$ , and  $8.38 \times 10^{-7}$ ). These hypotheses predicted an independent relationship between the abundance of DBT taxa and herb richness (Table 2), but this relationship was found to be positive (Fig. 3A;  $R^2 = 0.23$ ,  $P < 0.0001$ ). *Mitella nuda*, *Taraxacum officinale*, and *Fragaria* sp. were positively correlated with the abundance of DBT taxa, in fenced and unfenced quadrats (Appendix C). On the other hand, four taxa (*Galium* sp., *Epilobium palustre*, *Equisetum* sp., and *Rubus pubescens*) were positively correlated with the abundance of DBT taxa only in fenced quadrats, and four distinct taxa (*Dryopteris disjuncta*, *Trientalis borealis*, *Rubus idaeus*, and *Viola*

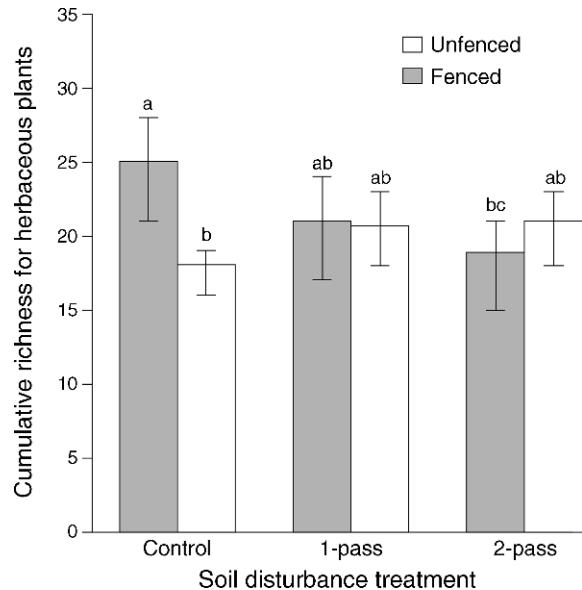


FIG. 2. Cumulative taxon richness of herbaceous plants (mean and 95% CI) seven years after clear-cutting in quadrats that received a combination of soil disturbance intensity and the presence or absence of a fence preventing deer browsing. Bars not sharing a common letter are significantly different at  $\alpha = 0.05$  using a mean comparison  $Z$  test ( $n = 16$ ).

sp.) were positively correlated with DBT taxa only in unfenced quadrats (Appendix C). The exploratory DAG indicated that white birch cover increased with fencing (Fig. 5;  $P < 0.0001$ ) and with increasing soil disturbance (Fig. 5;  $P = 0.02$ ). However, the effect of disturbances on herb richness was only indirect, because when the abundances of white birch and DBT taxa were considered in the analysis, herb richness was not affected directly by fencing, soil disturbance, or their interaction (Fig. 5). The exploratory DAG also revealed that when the abundance of DBT taxa was included in the analysis, the relationship between the abundance of white birch and herb richness became nonsignificant (Fig. 5;  $P = 0.20$ ).

#### DISCUSSION

The most salient finding of our study is that the joint impacts of deer browsing and mechanical soil preparation on herb layer richness (i.e., the number of herbaceous taxa per quadrat) are strongly influenced by interspecific interactions among dominant plants. The analysis of these interactions revealed two distinct but related processes. First, we found a strong negative relationship between white birch, a species highly preferred by white-tailed deer, and dominant browsing-tolerant taxa (DBT): grasses and Canada thistle. Second, we found a positive relationship between the abundance of DBT taxa and herb richness. The competitive effect of white birch and the effects of deer browsing and soil disturbance on herb richness were therefore only indirect.

TABLE 2. Tests of conditional independence in the basis sets implied by the path models in Fig. 4A–E, and Fig. 5 for directed acyclic graph (DAG) hypotheses.

D-sep claim of independence	Model in R	$H_0$	Probability distribution
DAG hypothesis 1			
$(X_3, X_4)   \{[X_1, X_2, X_1:X_2]\}$	$X_4 \sim X_1 + X_2 + X_1:X_2 + f_3(X_3) + (1   \theta/\tau/X_2)$	$f_3 = 0$	Normal
DAG hypothesis 2			
$([X_1, X_2, X_1:X_2], X_4)   \{X_3\}$	$X_4 \sim f_3(X_3) + X_t + (1   \theta/\tau/X_2)$	$X_t = 0$	Normal
DAG hypothesis 3			
$([X_1, X_2, X_1:X_2], X_4)   \{X_3\}$	$X_4 \sim f_3(X_3) + X_t + (1   \theta/\tau/X_2)$	$X_t = 0$	Normal
$(X_3, X_5)   \{[X_1, X_2, X_1:X_2]\}$	$X_5 \sim X_1 + X_2 + X_1:X_2 + f_3(X_3) + (1   \theta/\tau/X_2)$	$f_3 = 0$	Poisson
$(X_4, X_5)   \{[X_1, X_2, X_1:X_2], X_3\}$	$X_5 \sim f_3(X_3) + X_1 + X_2 + X_1:X_2 + f_4(X_4) + (1   \theta/\tau/X_2)$	$f_4 = 0$	Poisson
DAG hypothesis 4			
$([X_1, X_2, X_1:X_2], X_4)   \{X_3\}$	$X_4 \sim f_3(X_3) + X_t + (1   \theta/\tau/X_2)$	$X_t = 0$	Normal
$(X_4, X_5)   \{X_3\}$	$X_5 \sim f_3(X_3) + f_4(X_4) + (1   \theta/\tau/X_2)$	$f_4 = 0$	Poisson
$([X_1, X_2, X_1:X_2], X_5)   \{X_3\}$	$X_5 \sim f_3(X_3) + X_t + (1   \theta/\tau/X_2)$	$X_t = 0$	Poisson
DAG hypothesis 5			
$([X_1, X_2, X_1:X_2], X_4)   \{X_3\}$	$X_4 \sim f_3(X_3) + X_t + (1   \theta/\tau/X_2)$	$X_t = 0$	Normal
$(X_4, X_5)   \{[X_1, X_2, X_1:X_2], X_3\}$	$X_5 \sim f_3(X_3) + X_1 + X_2 + X_1:X_2 + f_4(X_4) + (1   \theta/\tau/X_2)$	$f_4 = 0$	Poisson
Exploratory DAG			
$([X_1, X_2, X_1:X_2], X_4)   \{X_3\}$	$X_4 \sim f_3(X_3) + X_t + (1   \theta/\tau/X_2)$	$X_t = 0$	Normal
$(X_3, X_5)   \{X_4\}$	$X_5 \sim f_4(X_4) + f_3(X_3) + (1   \theta/\tau/X_2)$	$f_3 = 0$	Poisson
$([X_1, X_2, X_1:X_2], X_5)   \{X_4\}$	$X_5 \sim f_4(X_4) + X_t + (1   \theta/\tau/X_2)$	$X_t = 0$	Poisson

Notes: Variables in square brackets are experimentally controlled in a randomized experiment. Variables in parentheses (i.e., in the left-hand side of the conditional probability expression) correspond to the pair of variables for which the claim of independence holds. A conditioning set  $\mathbf{Z}$  of other variables is indicated by  $\{ \}$  in the right-hand side of the conditional probability expression. Notation such as  $(X_1, X_2) | \{X_3, X_4\}$  means that variable  $X_1$  and  $X_2$  are independent, conditional on the combined set of variables  $X_3$  and  $X_4$ .  $X_t$  corresponds to the orthogonal contrast for the global effect of disturbance treatments when the effects associated with  $X_1, X_2, X_1$ , and  $X_2$  were not significantly different from zero. Because  $X_1$  and  $X_2$ , respectively, have two and three levels, variable  $X_t$  has six ( $2 \times 3$ ) different levels. Variables are  $X_1$  or “Deer” (presence or absence of a fence preventing deer browsing),  $X_2$  or “Soil” (treatment of soil disturbance),  $X_1X_2$  or “Deer  $\times$  Soil” (interaction between  $X_1$  and  $X_2$ ),  $X_3$  or “Birch” (square-root-transformed percent cover of white birch),  $X_4$  or “Dominant browsing-tolerant (DBT) taxa” (square-root-transformed percent cover of grasses and Canada thistle), and  $X_5$  or “Herb richness” (number of herbaceous taxa per quadrat),  $\theta$  (site random variable),  $\tau$  (random variable associated with tree groups that are within each site). We present the generalized additive mixed model (GAMM) in R for each d-sep claim in each *basis set*, where  $f_i$  represents the regression spline function for the continuous variable  $X_i$ . In (generalized) linear mixed models (G)LMM,  $f_i$  is replaced by the regression parameter  $\beta_i$  (not shown here). The chi-square statistic is the critical value (at  $\alpha = 0.05$ ) to compare with the value of the  $C$  statistic associated with each hypothesis (see *Confirmatory multilevel path analysis*).

Using multilevel path analyses, we found disagreement with Hypothesis 1, which states that the abundance of white birch is independent of the abundance of DBT taxa after accounting for the effects of soil disturbance and the presence or absence of a fence. Instead, our data supported Hypothesis 2 which states that both disturbance types indirectly affected the abundance of DBT taxa, through a competition process involving white birch. We found a higher abundance of white birch in fenced quadrats and with increasing intensity of soil disturbance, results that concur with other empirical studies that have demonstrated how white birch abundance declines due to deer browsing (Casabon and Pothier 2008) and increases with soil disturbance (Prévost 1997). In addition, the abundance of DBT taxa was independent of fencing and soil disturbance intensity when conditioned on the abundance of white birch. This result does not support the causal explanation that disruption of belowground interactions and soil conditions created by soil disturbance played a significant role in controlling DBT taxa abundance. Instead, the negative relationship between

white birch and DBT taxa strongly suggests that competition by white birch is an important mechanism to control the abundance of DBT taxa, and might be partly responsible for the difference in vegetation physiognomy observed between fenced and unfenced quadrats. The direct effect of white birch on DBT taxa, however, must be interpreted with caution because many variables in our system were probably not measured. Interspecific competition processes are more likely to be indirect throughout an asymmetric use of available resource(s) by one species located at the top of the competitive hierarchy, compared to another species located at a lower rank of competitive hierarchy. Hence, identifying the limiting resource(s) allowing white birch to dominate over DBT taxa remains to be explored in future studies.

Our third hypothesis proposed that deer browsing and soil disturbance directly influenced herb richness, irrespective of the presence and abundance of DBT taxa or white birch. This hypothesis reflects an individualistic perception of plant communities, where direct effects of disturbance on a dependent variable

TABLE 2. Extended.

<i>P</i> value (G)LMM	<i>P</i> value GAMM	<i>C</i> statistic (G)LMM   GAMM	$\chi^2$ (df)
0.0005	0.0004	15.202   15.648	5.991 (2)
0.1763	0.1797	3.471   3.433	5.991 (2)
0.1763 0.0587 $2.4 \times 10^{-5}$	0.1797 0.0065 $2.6 \times 10^{-7}$	30.417   43.764	12.592 (6)
0.1763 $5.3 \times 10^{-6}$ 0.2783	0.1797 $4.6 \times 10^{-8}$ 0.3280	30.325   39.452	12.592 (6)
0.1763 $2.4 \times 10^{-5}$	0.1797 $2.6 \times 10^{-7}$	24.746   33.758	9.488 (4)
0.1763 0.8598 0.7589	0.1797 0.1618 0.3580	4.325   9.130	12.592 (6)

(e.g., species richness) are evaluated without accounting for interspecific relationships. Our initial analyses using univariate tests suggested that fencing interacted with soil disturbance to influence herb richness. However, when the statistical partial independence of DBT taxa and white birch was explicitly included in the causal graph, this hypothesis was no longer supported (Fig. 4C, Table 2). This situation occurs because the fence treatment not only prevented deer access to vegetation, but also modified the abundance of dominant plants. The change in abundance of dominant plants caused by disturbances, in turn, probably altered interspecific relationships, and hence the relative importance of competitive and facilitative interactions in the organization of plant communities. Therefore, rejecting Hypothesis 3 suggests that important processes, involving interspecific interactions, can be missed when the response of species richness is solely evaluated as a function of disturbance intensity.

Curiously, although Hypotheses 4 and 5 accounted for a negative effect of white birch on herb richness (based on observations of high competitive abilities by white birch compared to neighboring species) these were also rejected. We reject these hypotheses because the prediction of independence between abundance of DBT taxa and herb richness was not supported by our data. Rather, the relationship between abundance of DBT taxa and herb richness was significantly positive within and outside exclosures, indicating that grasses and Canada thistle, usually considered as undesirable weeds, may in fact play an important role in maintaining herbaceous species and functional diversity in boreal plant communities. Among those taxa present in both fenced and unfenced quadrats, 11 were positively

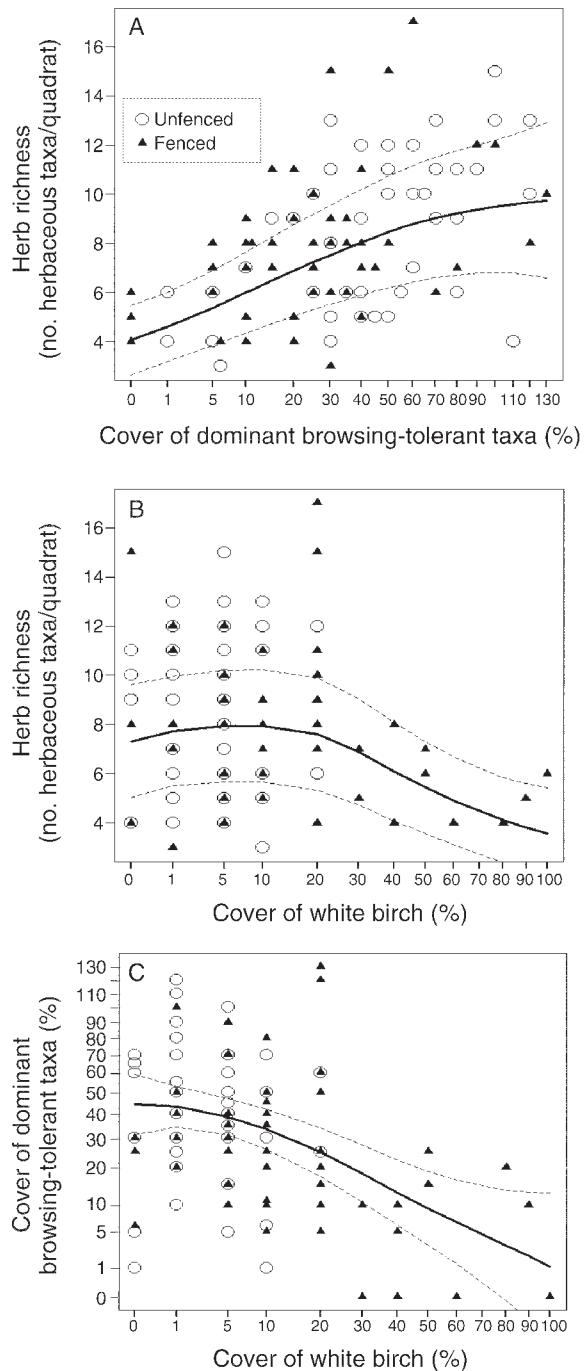


FIG. 3. Relationships between (A) herb richness and percent cover of dominant browsing-tolerant (DBT) taxa composed of grasses and Canada thistle; (B) herb richness and percent cover of white birch; and (C) percent cover of DBT taxa vs. percent cover of white birch. Solid lines show the predicted mean values, and dotted lines are 95% confidence intervals. Both were estimated with cubic regression splines. For clarity, values for the percent cover of white birch and DBT taxa are presented on a square-root scale.

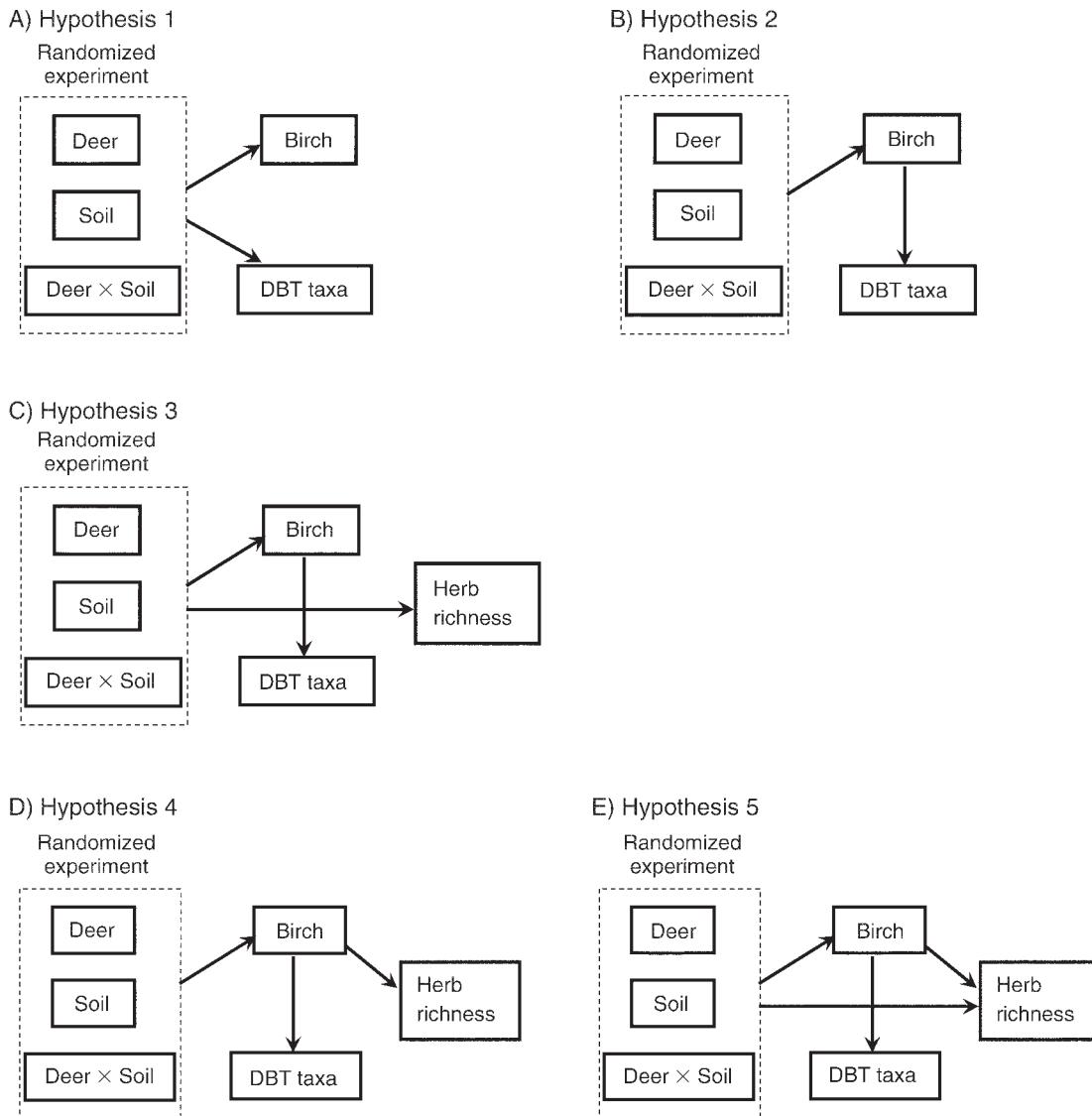


FIG. 4. Directed acyclic graphs (DAGs) representing the five hypotheses of causal structure between the presence or absence of a fence preventing deer browsing (Deer), the intensity of soil disturbance intensity (Soil), the interaction between these two types of disturbance (Deer  $\times$  Soil), the cover of white birch (Birch), the cover of dominant browsing-tolerant taxa composed of grasses and Canada thistle (DBT taxa), and the number of herbaceous taxa per quadrat (Herb richness). For each hypothesis, disturbance treatments are organized in a randomized experiment (dotted rectangle) and test the effects of  $X_1 \times X_2$  (interaction between Deer and Soil).

correlated with the abundance of DBT taxa (Appendix C), indicating that the hypothesis of associational defenses (Hay 1986) or associational avoidances (Milchunas and Noy-Meir 2002), where susceptible plants may gain protection from herbivores by growing close to unpalatable or repellent plants, is insufficient, on its own, to explain the increased herb richness in fenced quadrats. Our results also diverged from those of Callaway et al. (2005), who found a facilitative effect of unpalatable invader species on richness, but only in unfenced quadrats. A possible explanation for our divergent results might be that DBT taxa directly facilitated the presence of other plants by decreasing

environmental harshness, improving substrate quality for seed germination, or increasing the availability of a resource, which allows some herbaceous plants to coexist with DBT taxa when the abundance of white birch is low. The detailed mechanisms for this are unknown, however, and additional controlled experiments are necessary to disentangle the positive effect of habitat improvement vs. protection from herbivores of DBT taxa, especially in a multispecies context.

Although we did not measure the effect of positive interactions on population dynamics of specific plants, the observed changes in herb richness as the abundance of DBT taxa increased might have important conse-

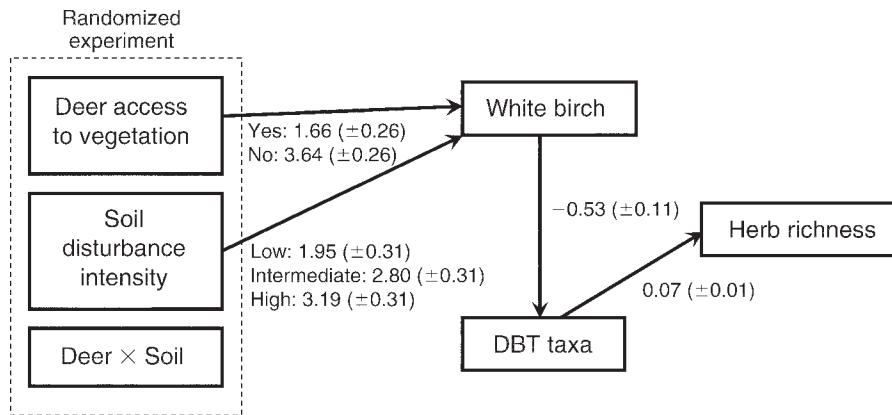


FIG. 5. Exploratory directed acyclic graph (DAG) representing the causal structure among presence or absence of a fence preventing deer browsing (Deer), intensity of soil disturbance (Soil), the interaction between these two types of disturbance (Deer  $\times$  Soil), cover of white birch (square-root-transformed), cover of dominant browsing-tolerant (DBT) taxa composed of grasses and Canada thistle (square-root-transformed), and herb richness. The exploratory DAG illustrates the complex chain of effects from the application of disturbance treatments to herb richness. Unstandardized coefficient estimates ( $\pm$ SE) are shown for each pair of connected variables based on GLMM analyses.

quences for the ecosystem on Anticosti Island. DBT taxa might act as refuges from deer browsing for beneficiary herbaceous species, and these refuges may serve as sources of propagules that could be important in the recovery of the plant community following heavy overbrowsing. Based on partial independence relationships among five variables (the fencing and soil disturbance treatments, abundance of white birch, abundance of DBT taxa, and herb richness), we propose a new model that fits our data well and accounts for interactions between competition and facilitation processes that influence herb richness (Fig. 5). In this model, protection from deer browsing and soil disturbance has direct positive effects on the abundance of white birch, but it indirectly influences the abundance of DBT taxa and herb richness. This model considers facilitation by DBT taxa as a driving factor controlling herb layer richness, whereas white birch plays a regulatory role by decreasing or increasing facilitative processes through its competitive effect with DBT taxa. The model also implies that when white birch abundance increases, facilitator taxa decrease, which ultimately has a negative effect on herb richness. Determining whether our model is generally successful at predicting and explaining complex interactions in early-successional plant communities on Anticosti Island and in similar ecosystems will require further testing with independent data sets. This model could also be improved by adding other browsing-intolerant species potentially involved in competition processes with grasses and Canada thistle, and by including abiotic variables to consider micro-habitat conditions.

Our study supports the rich literature that demonstrates the importance of interdependent relationships among plants, and particularly the prevalence of facilitative effects (Callaway 1995, Brooker et al. 2008). Our results also concur with previous studies

showing that these interdependent relationships can have strong cascading effects on the organization of entire plant communities. Hacker and Gaines (1997:1997) showed that “when facilitator species are not identified, the influence of direct positive interactions can be overlooked or masked by the assumed mechanism of competitive release.” Most importantly, we have illustrated the importance of accounting for dominant taxa in comparative studies of plant diversity, even when in situ randomized experiments are used. This approach can be easily achieved using traditional vegetation surveys together with path analyses, extended to a multilevel context when required. Use of this approach can reveal unexpected, partial correlations and indirect effects that are much more informative than the simple direct effect of disturbance treatments on plant communities.

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#### APPENDIX A

Mean horizontal cover and the percentage of quadrats in which a taxon is present for each taxon inventoried on Anticosti Island seven years after seed-tree group cutting, as a function of the intensity of site preparation and the presence or absence of a fence preventing deer browsing (*Ecological Archives* A021-025-A1).

#### APPENDIX B

Mean values of cumulative richness, quadrat richness, Sørensen Floristic Similarity Index, and horizontal cover for each treatment combination of fencing and soil disturbance intensity by plant groups (*Ecological Archives* A021-025-A2).

#### APPENDIX C

Spearman rank correlations between the abundance of each herbaceous taxon and the abundance of dominant browsing-tolerant taxa as a function of the presence or absence of a fence preventing deer browsing (*Ecological Archives* A021-025-A3).