

Snag dynamics in partially harvested and unmanaged northern hardwood forests¹

Mark C. Vanderwel, John P. Caspersen, and Murray E. Woods

Abstract: We used data from hardwood-dominated permanent sample plots in Ontario to estimate the probability of a tree falling during the 5 year period in which it dies ("tree fall"), and likewise the 5 year probability of snag fall. Tree fall probabilities ranged from 5% to 31% across species, with smaller dead trees more likely to be downed than larger ones. Expected half-lives (median time from death to fall) for 25 cm diameter snags varied from 5 to 13 years among species. Fall rates were higher for 10 cm diameter snags but relatively constant for 20–60 cm diameter snags. Recent harvesting substantially increased the probabilities of both tree fall and snag fall, with the former effect most pronounced for small individuals. We used these estimated fall rates to simulate snag dynamics in uneven-aged sugar maple (*Acer saccharum* Marsh.) stands. Mean snag densities were 32 and 50 snags/ha in selection-management and old-growth scenarios, respectively. Fifty-four percent of this difference was attributable to the lower density of live trees in the selection-management scenario, while 31% was attributable to losses of snags during harvesting. Silvicultural practices that strategically increase tree mortality rates, together with snag retention, as far as safety permits, during harvesting, could represent an effective approach to snag management under the selection system.

Résumé : Nous avons utilisé les données de placettes échantillons permanentes de l'Ontario dominées par des feuillus pour estimer la probabilité de chablis des arbres au cours des cinq années suivant leur mort et la probabilité de chablis des chicots. La probabilité de chablis des arbres morts récemment a varié de 5 % à 31 % selon l'espèce avec des risques de chablis plus élevés pour les petits arbres que les plus gros. La demi-vie escomptée (la médiane du temps s'écoulant entre la mort et la chute de l'arbre) des chicots de 25 cm de diamètre a varié de 5 à 13 ans selon l'espèce. Le taux de chablis était plus élevé pour les chicots de 10 cm de diamètre, mais il était relativement constant pour les chicots de 20 à 60 cm de diamètre. Les coupes récentes ont substantiellement augmenté la probabilité de chablis des arbres morts récemment et des chicots avec un effet plus prononcé dans le cas des individus de petite taille morts récemment. Nous avons utilisé ces taux estimés de chablis pour simuler la dynamique des chicots dans des peuplements inéquiennes d'érable à sucre (*Acer saccharum* Marsh.). La densité moyenne des chicots s'élevait à 32 et 50 chicots à l'hectare respectivement pour des scénarios de coupe de jardinage et de maintien de la forêt ancienne. Cinquante-quatre pourcent de cette différence était attribuable à la plus faible densité d'arbres vivants dans le scénario de coupe de jardinage alors que 31 % de cette différence était attribuable à des pertes de chicots pendant la récolte. Les pratiques sylvicoles qui augmentent stratégiquement le taux de mortalité des arbres, de concert avec la rétention de chicots dans la mesure où le permet la sécurité pendant la récolte, pourraient constituer une approche efficace d'aménagement des chicots dans un système de coupe de jardinage.

[Traduit par la Rédaction]

Introduction

Management of snag resources is an important component of ecologically based forestry practices that aim to provide structural features important to wildlife (McComb and Lindenmayer 1999). While snags are used by many species of birds and mammals in northern hardwood forests (Evans and Conner 1979; Tubbs et al. 1987; Freedman et al. 1996), snag resources tend to be adversely affected by the uneven-aged silvicultural systems that are used to manage these for-

ests. Numerous comparisons have shown partially cut northern hardwood stands to have a decreased abundance of snags relative to old-growth stands (Goodburn and Lorimer 1998; McGee et al. 1999; Crow et al. 2002; Doyon et al. 2005). Experimental work has further demonstrated that girdling trees at harvest can offset declines in snag abundance in the short term, but the persistence of snag resources through this approach is still uncertain (Keeton 2005). Though such comparative and experimental studies are certainly valuable, they provide limited insight into the processes underlying re-

Received 25 November 2005. Accepted 27 June 2006. Published on the NRC Research Press Web site at <http://cjfr.nrc.ca> on 12 December 2006.

M.C. Vanderwel² and J.P. Caspersen. Faculty of Forestry, University of Toronto, 33 Willcocks Street, Toronto, ON M5S 3B3, Canada.

M.E. Woods. Southern Science and Information Section, Ontario Ministry of Natural Resources, 3301 Trout Lake Road, North Bay, ON P1A 4L7, Canada.

¹This article is one of a selection of papers published in the Special Issue on the North American Forest Ecology Workshop.

²Corresponding author (e-mail: mark.vanderwel@utoronto.ca).

Table 1. Descriptions of snag decay classes from Anderson and Rice (1993).

Decay class	Description
1	Tree is recently dead; top is intact; most fine branching is still present; bark is intact
2	Top is intact; most of the fine branches have dropped; more than 50% of the coarse branches are left; bark may begin to loosen
3	Top is intact; fewer than 50% of the coarse branches are left; bark may or may not have sloughed off
4	Top is broken; no coarse branches remain; bark may or may not have sloughed off; height is at least 6 m
5	Top repeatedly broken; no coarse branches remain; bark may or may not have sloughed off; height is less than 6 m

duced snag abundances in managed hardwood stands over the harvest rotation. Such knowledge requires a more detailed understanding of the dynamics of snags in managed and unmanaged hardwood stands.

Simulation models that project snag abundance over time are potentially valuable tools for comparing different options for management of snags (Morrison and Raphael 1993; Mellen and Ager 2002; Wilhere 2003; Vanderwel 2005). Fundamentally, models of this type are based on a balance of snag inputs and outputs, where inputs are jointly determined by the rate of tree mortality and the probability of trees remaining standing at the time of death, and outputs are determined by the rate of snag fall. Management activities can affect the processes of both snag creation and loss. Through simulation models, researchers can explore the consequences of these effects to better understand the relative importance of the various factors involved in determining snag abundance in managed hardwood stands. In turn, this information can suggest approaches that are likely to be most effective for ameliorating losses of snags under selection management.

In this study we use permanent sample plot data from central and southern Ontario to estimate the probability of a tree falling during the 5 year interval in which it dies, and likewise the 5 year probability of snag fall. These probabilities are estimated as functions of size, species, and (in the case of snags) decay class, as well as local basal area (BA) and the occurrence or intensity of partial harvesting within the past 5 years. We also quantify transition rates among snag decay classes and combine these with estimated fall rates to project snag survivorship over time. We then incorporate our tree- and snag-fall estimates into a simple simulation model of snag dynamics in old-growth and selection-managed stands of sugar maple (*Acer saccharum* Marsh.) to evaluate the relative contributions of various factors that potentially reduce snag abundance under the selection silvicultural system.

Methods

Field data

Data on dead tree dynamics were obtained from the Ontario Ministry of Natural Resources' network of growth and yield permanent sample plots in central and southern Ontario (42–48°N, 74–85°W). In our analysis we included all plots located in site regions 4E, 5E, 6E, and 7E (Hills 1959) that had been measured twice and were dominated by hardwood species (>50% of plot BA). This selection procedure yielded a total of 198 plots within an area of approximately 170 000 km² in the Great Lakes – St. Lawrence and Deciduous forest regions (Rowe 1972). The great majority of plots

were dominated by sugar maple, sometimes in association with yellow birch (*Betula alleghaniensis* Britt.), white ash (*Fraxinus americana* L.), American beech (*Fagus grandifolia* Ehrh.), or basswood (*Tilia americana* L.). Other plots were dominated by red oak (*Quercus rubra* L.), lowland hardwoods (red or silver maple (*Acer rubrum* L. or *Acer saccharinum* L.)), or intolerant hardwoods (trembling aspen (*Populus tremuloides* Michx.) or white birch (*Betula papyrifera* Marsh.)). Twenty-eight of the plots had been subjected to partial harvesting between measurements.

Each plot consisted of three 0.04 ha circular subplots within a 0.64 ha area. In the first inventory, all live and standing dead trees ≥ 2.5 cm in diameter at breast height (DBH) within these subplots were tagged and their species and DBH were recorded. Very small diameter trees are generally not considered to have value for vertebrate wildlife as snags, so we retained only those trees and snags ≥ 7.5 cm DBH for our analyses. Each snag was assigned to one of five decay classes based on its external characteristics (Anderson and Rice 1993; Table 1). Plots were remeasured 3–9 years after they were first established (mean \pm SD interval = 5.2 ± 1.1 years), at which time the status of all trees and snags from the first measurement was reassessed (alive, standing dead, fallen dead, or cut). Fallen dead trees were assigned to a downed woody debris decay class following Maser et al. (1979).

Estimating the probability of falling

We used a regression approach to estimate the probability of falling during a 5 year period (P) for (i) trees that died between measurements (hereinafter “tree fall”) and (ii) trees that were dead and standing at the first measurement (hereinafter “snag fall”). Our remeasurement data did not enable us to distinguish trees that died and fell at the same time from trees that died, became a short-lived snag, then fell before the next measurement. We use the term tree fall to include both these modes of death and to represent the probability of a newly dead tree being downed, given that it was alive and standing 5 years earlier.

Potential predictor variables included a tree's or snag's species, diameter, and (in the case of a snag) decay class, as well as local BA and the occurrence or intensity of partial harvesting during the period between measurements. As is common for models based on binomial data, we estimated the probability of falling as a logistic function of a linear combination of these predictors and selected interaction terms, $f(X)$,

$$[1] \quad P = \frac{e^{f(X)}}{1 + e^{f(X)}}$$

Different sets of variables were used to develop nested statistical models that in turn included or excluded terms for selected predictors. These models were compared via a series of likelihood-ratio tests to determine which ones best fit the data. In the following we describe the predictor variables, then explain how the models were fit to the data.

Dummy variables were created to represent the 10 and 11 commonest tree species in the tree fall and snag fall data sets, respectively. Less common species were grouped into dummy variables representing either other hardwoods or assorted conifers. Both linear and nonlinear effects of size were represented by specifying first- and second-order polynomials of either DBH or its natural logarithm. Local BA was calculated from the first measurement of the subplot in which each tree or snag was located. Harvesting was also represented at the subplot level in one of three ways: by the BA of trees removed, either untransformed or following a $\ln(x + 1)$ transformation, or as a binary variable indicating the occurrence of cutting. Decay class was represented in the snag-fall model by a series of dummy variables. In addition, we considered two-way interaction terms to test whether the effect of harvesting varied by diameter, BA, or (in the snag-fall model) decay class, and whether the effect of BA varied with diameter. We did not include an interaction between harvesting and species because sample sizes for most species were low in harvested plots. Interaction terms used the same forms for diameter and harvesting as their main effects.

To fit the models to the data we needed to account for both correlations among observations from the same plot and variable remeasurement intervals among plots. Within-plot correlations were taken into consideration by adding a normally distributed random plot-effect term (mean = 0, standard deviation = σ_{plot}) to the linear component of the model (Penner et al. 1995). We dealt with variable interval lengths by using a compound-interest formula (Flewelling and Monserud 2002) to rescale the 5 year probability of falling in eq. 1 (P) and obtain the predicted probability of an individual tree or snag i falling (P_i) in the t years between measurements

$$[2] \quad P_i = 1 - (1 - P)^{t/5}$$

We then compared these P_i values with the observed data to calculate maximum-likelihood parameter estimates and the log-likelihood of each model, using a nonlinear mixed-model routine in SAS[®] version 8.2 (PROC NLMIXED; SAS Institute Inc. 1999). Differences in $-2 \times \log$ -likelihood (deviance, D) between nested sets of models were compared with the critical value from a χ^2 distribution ($\alpha = 0.05$, $df = q$, where q is the difference in the number of parameters) to select the models that best fit the data.

Projecting snag decomposition and longevity

Under the framework of a stage-based matrix model, snag survivorship can be projected over time by coupling decay-class-specific fall rates with a transition matrix describing the 5 year probability of advancing from one decay class to another (Raphael and Morrison 1987). We therefore used the individuals that did not fall (both newly dead trees and snags) to estimate 5 year probabilities of undergoing each possible decay-class transition. Because remeasurement intervals varied among plots, we could not simply take the ob-

served frequency of each transition. We therefore corrected for variable interval lengths but did not otherwise analyze factors that could affect snag decay class transitions.

The decay classes constitute a series of ordered categories. With ordinal data such as these, it is necessary to first estimate the cumulative probabilities, $P(y \geq Y_k)$, of being in or above each category, Y_k . The probability of being in a given category, $P(y = Y_k)$, can then be calculated as

$$[3] \quad P(y = Y_k) = P(y \geq Y_k) - P(y \geq Y_{k+1})$$

We used this equation to determine the probabilities that individuals would be in each possible higher decay class after a 5 year period. To correct for variable interval lengths, we used eq. 2 to estimate cumulative probabilities that a given tree or snag advanced to each set of higher decay classes. Five year maximum-likelihood cumulative probabilities were estimated from the data (PROC NLIN in SAS[®]) and used to calculate decay class transition probabilities. This procedure was carried out separately for trees that were initially alive (but died between measurements) and snags in each of the five decay classes at the first measurement.

With the resulting decay class transition matrix and decay-class-specific snag fall rates, we projected snag survivorship over time. Given an initial cohort of snags in decay class 1, subsequent inputs (I_m) and outputs (O_m) for each of the m decay classes were calculated at 5 year timesteps as

$$[4] \quad I_m = \sum_{i=1}^{m-1} N_i(1 - F_i)T_{im}$$

$$[5] \quad O_m = N_m \left[F_m + (1 - F_m) \sum_{j=m+1}^5 T_{mj} \right]$$

where N is the decay-class-specific density of snags at the end of the previous timestep, F is their 5 year fall rate in the absence of harvesting, and T is the probability of a snag that did not fall moving from one decay class to another. N and F are each subscripted according to the decay class, and T is double-subscripted according to, first, the decay class from which a snag comes and, second, the decay class into which it moves. For each timestep, the change in snag density within each decay class (ΔN_m) is equal to $I_m - O_m$. Snag survivorship to time t equals the density of all snags standing at time t divided by the initial density of snags in class 1.

Simulating snag dynamics

We used our estimates of rates of tree fall, snag fall, and decay-class transition, together with parameters for live stand structure and mortality drawn from other sources, to develop simple simulations of snag dynamics in managed and unmanaged uneven-aged stands of sugar maple. These simulations combined the decay-class and fall dynamics described by eqs. 4 and 5 with continuous snag inputs from the standing death of live trees and direct losses of snags from harvesting. At 5 year intervals, snag densities were projected by decay class and 5 cm DBH class under two model scenarios: (1) nonaggrading old-growth stands and (2) stands managed under the selection silvicultural system. As described in detail in the following, we also ran simulations in

Table 2. Parameter values used in simulations of snag dynamics in old-growth and selection-managed stands of sugar maple.

	Old-growth stands	Selection-managed stands
Live stand structure and natural mortality		
Initial basal area (m ² /ha)	30	18
Annual basal area increment (m ² ·ha ⁻¹ ·year ⁻¹)	0	From eq. 7
Min. DBH (cm)	10	10
Max. DBH (cm)	75	60
<i>q</i> value	1.39	1.39
Natural mortality rate, M_d (%/5 years)		
10–60 cm DBH	4.7	4.7
≥65 cm DBH	11.8	—
Position after death, D_d	From eq. 9 ($H = 0$)	From eq. 9 ($H = 0$)
Snag-decay class after death, T_m	From Table 5	From Table 5
Postharvest effects		
Increased mortality, ΔM_d (%/5 years)		
10–15 cm DBH	—	5.2
15–20 cm DBH	—	2.4
20–25 cm DBH	—	1.1
25–30 cm DBH	—	0.5
≥30 cm DBH	—	0
Position after death, D_d	—	From eq. 9 ($H = 1$)
Snag decomposition and fall		
Falls at harvest	—	From eq. 8
Falls at other times, F	From eq. 10 ($BA_H = 0$)	From eq. 10 ($BA_H = 0$)
Decay-class transitions, T	From Table 5	From Table 5

which the selection-management scenario was modified to evaluate the contribution of various subsets of the parameters to the difference in snag abundance between old-growth and selection-managed stands. We ran all simulations for 60 years to remove any influence of starting conditions (no snags were present initially), but we only report snag densities for the final 20 year period.

Old-growth scenario

In designing the simulation model, we sought to obtain reasonable estimates for snag inputs without representing the growth and death of trees in a detailed or mechanistic fashion. Accordingly, new snag inputs in DBH class d and decay class m from the death of live trees (I'_{dm}) were calculated as

$$[6] \quad I'_{dm} = L_d M_d (1 - D_d) T_m$$

where L_d is the density of live trees in that DBH class, M_d is their 5 year mortality rate, D_d is the proportion of newly dead trees that are downed at the end of the timestep, and T_m is the proportion of newly dead standing trees that are in snag-decay class m at the end of the timestep.

The parameter values that specify the density and mortality of trees (Table 2) were derived from published literature and were considered representative of old-growth sugar maple stands in the Great Lakes region. Live tree density within each DBH class (L_d) was calculated from stand BA, given a negative exponential diameter distribution characteristic of uneven-aged stands. In our old-growth scenario, BA was held constant at 30 m²/ha under the assumption that these stands had reached equilibrium and were no longer increasing in BA. This equilibrium BA was based on the level at which the BA increment typically approaches zero in Ontario (Penner 2003), though individual old-growth hardwood

stands may sometimes support a higher BA than this. The shape of the diameter distribution was specified by a q value, defined as the ratio of tree densities in adjacent 5 cm diameter classes, together with minimum and maximum bounds for DBH. These stand structure parameters were based on values published by the Ontario Ministry of Natural Resources (OMNR 1998, 2000). Five year mortality rates (M_d) were derived from data on sugar maple mortality in mature and old-growth forests in Michigan and Wisconsin (Lorimer et al. 2001). Though these data are not from the same area as our plots, we considered them to be the most suitable estimates of mortality, given the scarcity of unmanaged old-growth sugar maple stands in Ontario and elsewhere. Trees ≥65 cm DBH were assigned a higher mortality rate than smaller trees in our old-growth scenario, as was found by Lorimer et al. (2001).

Our estimates of tree fall in the absence of harvesting were used to specify the proportion of dead trees that did not enter the snag pool (D_d). Snag inputs were distributed among decay classes (T_m) using our decay class transition matrix for newly dead trees.

Selection-management scenario

The selection-management scenario was designed with the same basic structure as the old-growth scenario, but differed in three key respects. These changes consisted of (i) reduced live-tree density and maximum tree DBH; (ii) short-term increases in mortality and treefall after harvesting; and (iii) losses of snags as a result of harvesting operations. Each of these changes potentially affects snag abundance within selection-managed stands.

Following OMNR (1998), we specified a postharvest residual BA of 18 m²/ha and maximum DBH of 60 cm for the

selection-management scenario (Table 2). In addition, live-stem density (L_d) increased with time since harvest because managed stands are not in equilibrium. Rather than explicitly tracking the growth of individual trees or cohorts, we simply incremented stand BA between timesteps and recalculated live-stem densities within each DBH class, given the same negative exponential diameter distribution. We used Penner's (2003) yield curve for the tolerant hardwood forest unit in Ontario to calculate annual basal area increment (BAI)

$$[7] \quad \text{BAI} = (1.9385 + 10.0020\text{AGS})\text{BA}^{1.6559} - 1.9173\text{BA}^{1.6593}$$

where BA is stand basal area and AGS is the fraction of acceptable growing stock (taken to be 0.41, the average value in Penner (2003)). The result was then multiplied by 5 to obtain an increment for each 5 year timestep. A harvest was simulated after each fourth timestep (to represent a 20 year cutting cycle), at which point BA was reset to the postharvest level of 18 m²/ha.

In the timestep immediately following harvesting, mortality rates were increased to account for the effects of felling damage and stress on trees. Five year mortality rates (M_d) were increased from 0% to 5%, depending on tree size (Table 2), using the postharvest increases in mortality rates reported by Caspersen (2006). In the same interval, probabilities of tree fall (D_d) were obtained from our estimates for subplots in which harvesting had recently occurred. These modifications were designed to account for short-term effects of management on snag inputs for up to 5 years after harvesting.

Lastly, at the time of each harvest we removed a portion of the snags present. Each snag's probability of falling as a direct result of harvesting (P) was calculated as the expected increase in the 5 year probability of falling in harvested (P_H) versus nonharvested (P_{NH}) subplots, divided by the expected probability of the snag remaining standing midway through the interval

$$[8] \quad P = \frac{P_H - P_{NH}}{\sqrt{1 - P_{NH}}}$$

We calculated this value for snags in each DBH class, then multiplied respective snag densities at the time of harvest by $1 - P$ to represent the loss of snags during harvesting operations.

Modified selection-management scenarios

We first ran simulations using parameter values for the old-growth and selection-management scenarios to determine the expected differences in snag densities between the two. Next we modified the selection-management scenario by swapping in various subsets of the old-growth parameter values that govern (i) stand structure (M1), (ii) postharvest mortality and tree fall (M2), and (iii) snag fall during harvest (M3). Snag densities in the selection-management scenario were then subtracted from each of these modified selection-management scenarios. Because simulated differences in snag density between managed and unmanaged stands could only arise from a combination of these three factors, varying each one in turn allowed us to evaluate its independent con-

tribution to the overall difference in snag density between the old-growth and selection-management scenarios. For example, the effect of snag falls during harvest was assessed by running a selection-management simulation where no snags were directly removed by harvesting (M3) and comparing the result (M3 minus selection-management scenario) with the total difference between the old-growth and selection-management scenarios (i.e., old-growth scenario minus selection-management scenario). Using this approach, we were able to partition differences in snag density between the old-growth and selection-management scenarios among various factors that might affect snag abundance in managed stands.

Results

Tree fall

Of the 15 575 trees (≥ 7.5 cm DBH) that were initially alive in the permanent sample plot data set, 1110 trees (≥ 7.5 cm DBH) died in the interval between measurements, excluding those that were cut during harvesting (Table 3). Overall, fewer than 25% of these newly dead trees had fallen to the ground, though the percentage was much higher within subplots that had been harvested. Of the fallen trees, 8% were in downed woody debris decay class 1, 11% were in class 2, 71% were in class 3, 6% were in class 4, and 4% were in class 5.

Comparisons of different model forms showed that a linear term for DBH and a binary term for the occurrence of harvesting produced the best fit to the data for tree falls. With terms for species, DBH, BA, and harvesting included, dropping any of these predictors would result in a significantly poorer fit (species: $D = 33.2$, $df = 11$, $p < 0.001$; DBH: $D = 6.6$, $df = 1$, $p = 0.010$; BA: $D = 4.2$, $df = 1$, $p = 0.040$; harvesting: $D = 45.3$, $df = 1$, $p < 0.001$). The addition of a significant two-way interaction between diameter and harvesting ($D = 7.3$, $df = 1$, $p = 0.007$) showed that the effects of harvesting varied with tree size. Interactions between local BA and harvesting ($D = 1.5$, $df = 1$, $p = 0.221$) and local BA and DBH ($D = 0.2$, $df = 1$, $p = 0.655$) were not significant. Our final model thus estimated the logit of the probability of tree fall as a linear combination of species, DBH, BA, the occurrence of harvesting (H), and the product of DBH and the occurrence of harvesting

$$[9] \quad f(X) = \alpha + \beta_{\text{species}} + \delta\text{DBH} + \theta\text{BA} + \iota H + \lambda(\text{DBH} \times H) + \epsilon_{\text{plot}}$$

$$\epsilon_{\text{plot}} \sim N(0, \sigma_{\text{plot}})$$

where $f(X)$ is related to the probability of falling by eq. 1, α is the reference level for sugar maple in our dummy variable coding scheme, β_{species} is a species-specific parameter that accounts for interspecific variation around the reference level, and ϵ_{plot} represents a normally distributed plot-level error term with standard deviation σ_{plot} . The maximum-likelihood estimates of the parameters in eq. 9 are listed in Table 4.

Holding DBH constant in eq. 9 for purposes of comparison, there was relatively large variation in the probability of tree fall across species. Basswood was the species most likely to fall within 5 years of death (31% for a 25 cm DBH

Table 3. Numbers of trees and snags (≥ 7.5 cm DBH), by species, that were either alive, standing dead, fallen, or cut at remeasurement in 198 permanent sample plots in central and southern Ontario.

Species	Trees							Snags			
	Unharvested subplots			Harvested subplots				Unharvested subplots		Harvested subplots	
	Alive	Standing dead	Fallen	Alive	Standing dead	Fallen	Cut	Standing	Fallen	Standing	Fallen
Sugar maple	7 218	346	74	568	34	50	155	292	324	15	41
White birch	318	29	2	1	1	1	1	74	51	0	0
White ash	651	50	15	12	2	1	5	47	56	0	3
Ironwood ^a	758	32	16	30	0	8	1	30	59	0	5
Yellow birch	535	35	4	23	0	2	6	45	30	4	4
Red oak	727	51	5	10	1	0	3	46	33	0	1
Black cherry ^b	—	—	—	—	—	—	—	48	27	0	1
Basswood	470	36	17	14	0	0	5	16	43	0	1
Red maple	614	27	7	13	0	2	4	21	32	2	0
Trembling aspen	311	36	5	5	0	0	10	30	26	0	0
American beech	474	33	5	13	0	1	4	23	25	0	1
Other hardwoods	1 715	121	38	32	1	3	1	107	140	1	1
Assorted conifers	295	11	5	18	1	2	2	41	23	1	9
Total	14 086	807	193	739	40	70	197	820	869	23	67

^a*Ostrya virginiana* (Mill.) K. Koch.^bBlack cherry (*Prunus serotina* Ehrh.) is grouped with other hardwoods in the data set for trees because only one such individual that died had fallen between measurements.**Table 4.** Parameter estimates and standard errors for models describing the probability of having fallen for a tree that died within the previous 5 years and the 5 year probability of snag fall.

	Tree-fall model (eq. 9)		Snag-fall model (eq. 10)	
	Estimate	SE	Estimate	SE
α	-0.805	0.392	5.691	1.378
β_{species}				
White birch	-0.907	0.707	-0.481	0.289
Ironwood	1.056	0.349	0.837	0.269
White ash	0.057	0.356	0.092	0.235
Red oak	-0.881	0.547	-0.264	0.272
Yellow birch	-0.454	0.518	-0.380	0.268
Black cherry			-0.542	0.288
Basswood	1.149	0.375	1.163	0.366
American beech	-0.546	0.518	0.069	0.328
Red maple	0.336	0.465	0.348	0.337
Trembling aspen	-0.404	0.657	0.189	0.393
Other hardwoods	0.444	0.267	0.466	0.180
Assorted conifers	1.151	0.585	-0.293	0.291
γ_{dc}				
Decay class 2			0.177	0.188
Decay class 3			0.542	0.191
Decay class 4			0.702	0.185
Decay class 5			0.528	0.172
δ	-0.016	0.010		
ζ			-3.777	0.976
η			0.531	0.167
θ	-0.026	0.013		
ι	3.389	0.599		
κ			0.157	0.034
λ	-0.084	0.035		
σ_{plot}	0.465	0.205	0.234	0.083

tree in a 30 m²/ha BA subplot), whereas white birch was the least likely (5%). For sugar maple, the commonest species, a 25 cm DBH tree was estimated to have a 12% chance of falling by the end of the 5 year interval in which it died, given a subplot BA of 30 m²/ha and no harvesting. The effect of diameter was relatively small in unharvested subplots, with the probability of tree fall ranging from 7% to 15% for 10–60 cm DBH sugar maples (Fig. 1). Harvesting activity greatly increased this probability among smaller trees: a newly dead 10 cm DBH sugar maple had an estimated 69% chance of being downed after a harvest, whereas for a 40 cm DBH tree the probability was equivalent to that expected in the absence of harvesting (Fig. 1). Lower local BA was associated with modest increases in the probability of falling across all plots, with a newly dead 25 cm DBH sugar maple having a 15% and 10% probability of falling in 20 and 40 m²/ha subplots, respectively.

Snag fall

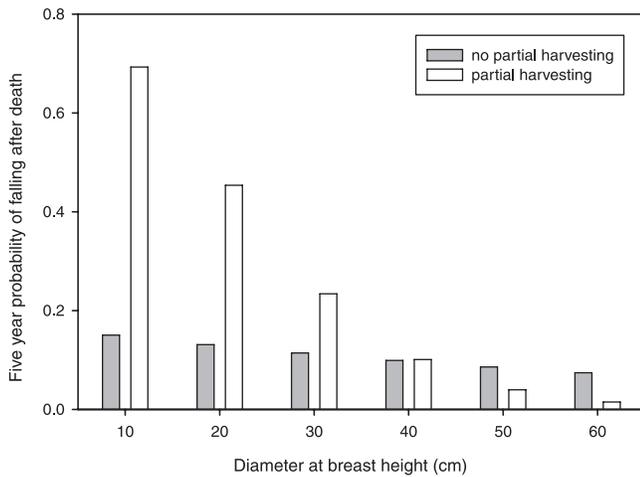
The permanent sample plot data set used to develop the snag-fall model included 1779 snags (≥ 7.5 cm DBH), more than half of which had fallen by the time they were remeasured (Table 3). At remeasurement, fewer than 1% of the fallen snags were in downed woody debris decay class 1, 4% were in class 2, 78% were in class 3, 12% were in class 4, and 5% were in class 5.

For estimating probabilities of snag fall, a second-order polynomial of $\ln(\text{DBH})$ produced a better fit to the data than any of the other model forms considered. A linear function of BA removed represented the effect of harvesting better than a $\ln(x + 1)$ transformation or a binary indicator of the occurrence of harvesting. With terms for species, decay class, diameter, and harvesting included, removing any of these predictors resulted in a significantly poorer fit (species: $D = 42.5$, $df = 12$, $p < 0.001$; decay class: $D = 18.5$, $df = 4$, $p < 0.001$; diameter: $D = 49.2$, $df = 2$, $p < 0.001$; har-

Table 5. Matrix of the 5 year conditional probabilities of a snag or recently dead tree of any species moving from one decay class to another, given that it did not fall.

Subsequent decay class	Initial decay class					
	Alive (<i>n</i> =857)	1 (<i>n</i> =139)	2 (<i>n</i> =135)	3 (<i>n</i> =121)	4 (<i>n</i> =186)	5 (<i>n</i> =258)
1	0.290	0.045				
2	0.229	0.186	0.165			
3	0.196	0.329	0.379	0.351		
4	0.124	0.166	0.204	0.346	0.527	
5	0.161	0.274	0.252	0.303	0.473	1.000

Fig. 1. Estimated probability of falling for sugar maple trees that died within the previous 5 years, by diameter at breast height (DBH), in subplots with an initial basal area of 30 m²/ha where partial harvesting had and had not occurred.



vesting: $D = 28.1$, $df = 1$, $p < 0.001$). Local BA did not significantly affect the probability of snag fall ($D = 0.2$, $df = 1$, $p = 0.665$). Neither a two-way interaction between harvesting and decay class ($D = 7.6$, $df = 4$, $p = 0.107$) nor one between harvesting and diameter ($D = 4.1$, $df = 2$, $p = 0.129$) was significant. The final snag-fall model therefore estimated the logit of the probability of falling over 5 years as a linear combination of species, decay class, $\ln(\text{DBH})$, $\ln(\text{DBH})^2$, and BA removed during harvesting (BA_H)

$$[10] \quad f(X) = \alpha + \beta_{\text{species}} + \gamma_{\text{dc}} + \zeta \ln(\text{DBH}) + \eta \ln(\text{DBH})^2 + \kappa \text{BA}_H + \epsilon_{\text{plot}}$$

$$\epsilon_{\text{plot}} \sim N(0, \sigma_{\text{plot}})$$

where $f(X)$ is related to the probability of falling by eq. 1, α is the reference case for decay class 1 sugar maple in our dummy variable coding scheme, and γ_{dc} is a decay-class-specific parameter that accounts for variation in fall rates among the decay classes. The maximum-likelihood estimates of the parameters in eq. 10 are listed in Table 4.

Holding DBH constant at 25 cm in eq. 10 for purposes of comparison, the estimated 5 year probability of falling for sugar maple ranged from 28% in decay class 1 up to 43% in decay class 4. Smaller snags had notably higher fall rates, with a 10 cm DBH sugar maple having probabilities of falling of 45% and 62% in the same respective decay classes. There was also substantial variation among species, with a 25 cm DBH basswood having a 55%–71% chance of falling

over 5 years and a black cherry of the same size having a 18%–31% probability of falling.

Harvesting between measurements increased the probability of snag fall appreciably. We estimate that a snag that had a 50% chance of falling over 5 years in the absence of harvesting would have a 69%, 83%, and 91% chance of falling following BA reductions of 5, 10, and 15 m²/ha, respectively. Given a large number of such snags, and assuming that harvesting occurred midway through a 5 year interval, these respective levels of harvesting would be expected (using eq. 8) to remove 26%, 46%, and 58% of the snags that were standing at the time of harvest.

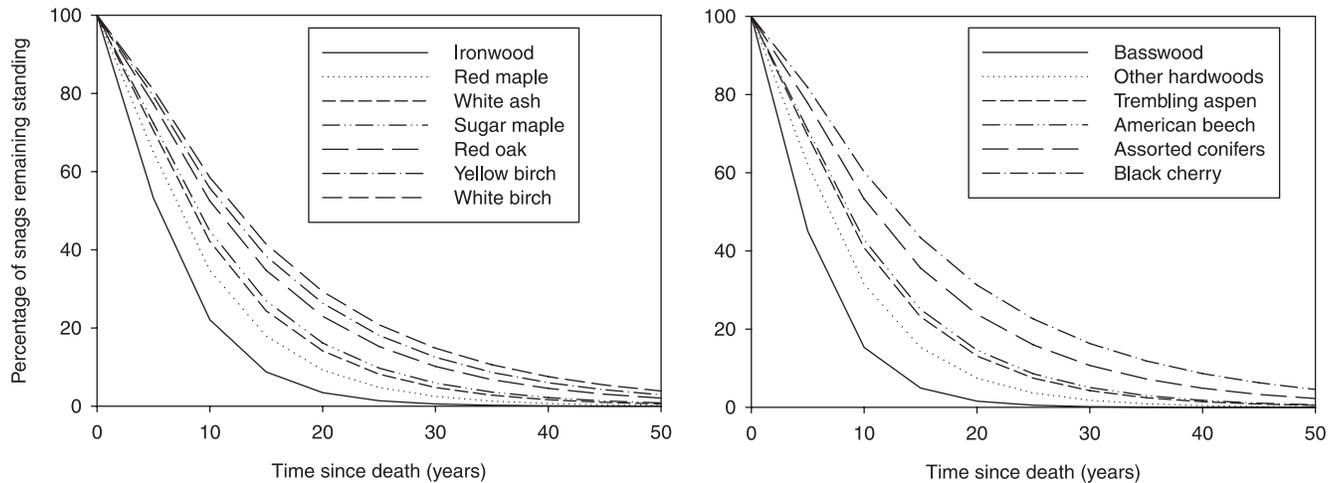
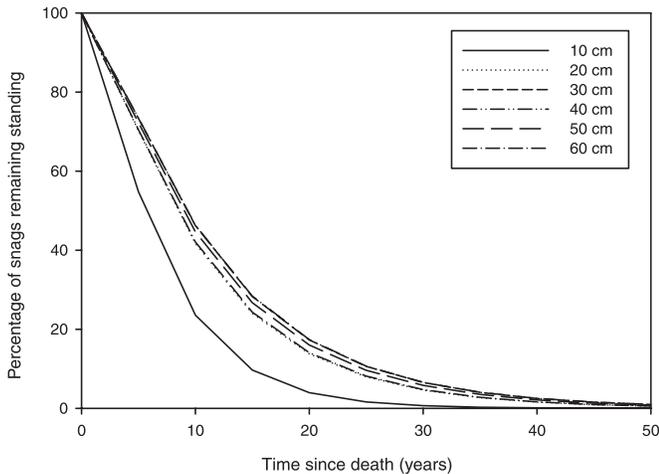
With these snag-fall estimates and our decay class transition matrix (Table 5), we projected snag survivorship over time by species (Fig. 2) and DBH (Fig. 3). Fall rates increased after the first 5 years as snags advanced past decay class 1 and experienced higher fall rates in later decay classes. For snags of 25 cm DBH, projected half-lives (median times to fall) ranged from 5 years for basswood up to 13 years for black cherry. The effects of diameter were most pronounced among small snags: 10 cm DBH sugar maple snags had a projected half-life of only 6 years, whereas those between 20 and 60 cm DBH had a projected half-life of 9 years.

Simulations of snag dynamics

In our simulations of snag dynamics, old-growth and selection-managed stands of sugar maple supported an average density of 50 and 32 snags/ha, respectively (Table 6). Lower densities of live trees in the selection-management scenario independently accounted for most of this difference (10 snags/ha, or 54%). The effect of an increased probability of falling shortly after harvesting on snag recruitment was largely offset by a higher mortality rate during this period. The net effect of these processes was a slight decrease in snag density in the selection-management scenario (1 snag/ha, or 7% of the total difference), particularly among smaller individuals. The loss of snags as a direct result of harvesting independently accounted for 6 snags/ha (31% of the difference in snag density), the effect being four times as great in the first decade after harvesting as in the second decade. The remainder of the difference (1 snag/ha, or 8%) was attributable to the joint effects of two or more of the three factors.

Discussion

Forest-management practices have traditionally attempted to manipulate stand structure such that mortality, and its perceived wastage of timber, is minimized. More recently, recognition of the ecological functions of dead trees has

Fig. 2. Projected survivorship of 25 cm DBH snags over time, by species.**Fig. 3.** Projected survivorship of sugar maple snags over time, by DBH.

brought to light the need for management practices that ensure the continuous provision of standing and downed deadwood (Hagan and Grove 1999; Harmon 2001). To help ensure that deadwood resources are maintained over time, it is important to have good information on the dynamics of snag creation and snag fall. Incorporating such knowledge into simulation models can aid in assessing the effects of forest management on snag abundance, and in developing effective approaches for managing snags over the harvest rotation.

Tree fall

Standing death was the commonest form of tree mortality in the absence of harvesting, as has been reported elsewhere for hardwood forests in eastern North America (Tyrrell and Crow 1994; Runkle 2000; Busing 2005). Agents that induce standing death, such as disease and suppression, thus appeared to be the most prevalent causes of mortality in our plots. In areas with lower BA, newly dead trees had a modestly greater probability of falling, presumably as a result of increased susceptibility to wind. However, even though wind is regarded as an important cause of disturbance in this re-

gion (Frelich 2002), it does not appear to be the primary agent of chronic mortality (Lin et al. 2004).

Harvesting greatly increased the likelihood of tree fall among smaller individuals that died. This was to be expected, as harvesting operations typically produce large quantities of debris by knocking over small, unmerchantable stems. Although this practice removes potential future snags, these dead trees may still serve important ecological functions if they are left in place as downed woody debris.

Snag fall

Expected snag fall times were intermediate to others reported from eastern North America. In central Ontario, half of eastern white pine (*Pinus strobus* L.) and red pine (*Pinus resinosa* Ait.) snags were projected to fall about 17 and 30 years after death, respectively (Vanderwel 2005). In northern Quebec, it has been estimated that half of the snags created by stand-replacing fires in stands dominated by black spruce (*Picea mariana* (Mill.) BSP) fall after 16 years (Boulanger and Sirois 2006). Among predominantly coniferous species in Maine, median snag-fall times were reported to vary between 6 and 10 years (Garber et al. 2005). Tyrrell and Crow (1994) found that eastern hemlock (*Tsuga canadensis* L. Carrière) snags in Wisconsin and northern Michigan seldom lasted 5 years without breaking or falling, and Moorman et al. (1999) observed that over 50% of snags in pine and hardwood stands in South Carolina fell within 3 years of death. To our knowledge, snag falls have not been examined for most of the species in our data set, making our results a valuable contribution to understanding the dynamics of standing dead trees in eastern North America.

In past studies of snag dynamics, it has often been reported that fall rates decrease with increasing snag diameter (Keen 1955; Landram et al. 2002; Garber et al. 2005). While we likewise found a substantial size effect, it appeared to be restricted to the smallest snags (Fig. 3). Larger diameter snags may stand for longer because of the greater stability imparted by their higher proportion of decay-resistant heartwood (Sellin 1994). Smaller snags are likely colonized by decay fungi more quickly, resulting in a shorter time to fall.

Decay class had a significant effect on the probability of snag fall, with early decay class snags less likely to fall than those in later classes. Coupling decay-class-specific fall rates

Table 6. Average snag densities (per hectare) during specified time periods for the old-growth and selection-management scenarios and for modified selection-management runs (M1, M2, M3) in which subsets of old-growth parameter values were swapped in for the selection-management values.

Parameter set	0–10 years after harvesting		10–20 years after harvesting		0–20 years after harvesting	
	All snags (≥10 cm DBH)	Large snags (≥25 cm DBH)	All snags (≥10 cm DBH)	Large snags (≥25 cm DBH)	All snags (≥10 cm DBH)	Large snags (≥25 cm DBH)
Old-growth	50 (+22)	21 (+9)	50 (+15)	21 (+7)	50 (+19)	21 (+8)
Selection management	28 (0)	12 (0)	35 (0)	14 (0)	32 (0)	13 (0)
Stand structure (M1)	38 (+10)	16 (+4)	46 (+10)	19 (+5)	42 (+10)	17 (+4)
Post-harvest effects (M2)	30 (+2)	12 (+0)	36 (+1)	14 (+0)	33 (+1)	13 (0)
Snag falls at harvest (M3)	40 (+11)	15 (+4)	38 (+3)	16 (+1)	38 (+6)	15 (+3)

Note: Values in parentheses were calculated by subtracting the snag densities in the selection-management scenario, and represent the loss of snags independently attributable to one (M1, M2, M3) or all (old-growth) of the three factors discussed in the text.

with a decay class transition matrix allowed us to represent the change in probability of falling over time in our projections of snag survival. Accordingly, some of our projections showed evidence of a slight “lag” period, where probability of snag fall was initially low after a tree died (Harmon et al. 1986; Garber et al. 2005). This period was short, however, as snags were quick to advance to decay classes 3 and higher (Table 5).

Harvesting had a pronounced effect on snag survival in subplots that had been cut between measurements, with the magnitude of the impact increasing with harvest intensity. Normally, many snags are felled during harvesting to remove potential safety hazards in accordance with Ontario’s health and safety regulations. In addition, a number of snags are likely to be knocked down incidentally in the course of normal felling and skidding operations. The net result of these processes is a substantial loss of snags in managed stands as a direct consequence of harvesting activities.

Simulations of snag dynamics

Simulated snag densities in the selection-management and old-growth scenarios (Table 6) were consistent with empirical estimates from northern hardwood stands (Goodburn and Lorimer 1998; McGee et al. 1999). Our simulation model supported the finding in these field studies that uneven-aged managed stands had lower densities of large snags than old unmanaged stands. Our model further showed a strong effect of management on small- as well as large-snag density. Neither Goodburn and Lorimer (1998) nor McGee et al. (1999) observed such an overall effect across all snag size classes, but Doyon et al. (2005) did find a reduction in total snag density within managed hardwood forests in Quebec. Our simulation results are further supported by the results of ongoing work on snags in Ontario. In southwestern Ontario, snag densities in selection-managed and unmanaged stands have been estimated at 30 and 49 snags/ha, respectively (K.A. Elliott, Ontario Ministry of Natural Resources, London, Ontario, personal communication, 2005). In Algonquin Provincial Park (central Ontario), hardwood stands that had received a selection harvest within the previous 1–10 years reportedly had about 20 snags/ha, those harvested 11–20 years earlier had about 40 snags/ha, and those that had not been harvested had about 50 snags/ha (B.J. Naylor, Ontario Ministry of Natural Resources, North Bay, Ontario, personal communication, 2005). Based on these comparisons, we believe that our simulations generated very reason-

able snag densities for selection-managed and old-growth hardwood stands.

Our simulation model was relatively simple and did not attempt to capture all processes potentially affecting snag dynamics. Over large spatial and temporal scales, for example, snag dynamics are partly driven by episodic natural disturbances that occasionally produce large pulses of tree mortality and snag recruitment. Such processes were not incorporated into our model scenarios because we designed the simulations to capture the principal differences in snag dynamics between managed and unmanaged stands under equilibrium conditions. The simulation results are therefore best interpreted in this context.

Partitioning of the difference in snag densities between managed and unmanaged stands showed that lower BA and tree densities under the selection system accounted for most of the difference in snag density between the old-growth and selection-management scenarios (Table 6). Harvesting removes trees from the stand before they are able to develop into snags. Snag density is known to be tightly linked with that of live trees (Ferguson and Archibald 2002), so it is perhaps not surprising that the difference in tree density explained the largest share of the difference in simulated snag abundance. This effect may be especially pronounced for the largest size classes of trees and snags, the supply of which is most strongly diminished by uneven-aged management (McGee et al. 1999).

The loss of snags as a direct result of harvesting had a large impact in the first decade after harvest, but much less of one in the second decade (Table 6). Although harvesting initially removed 31% of the existing snags in the simulation, these would have fallen over time anyway had they not been lost through harvesting. As a result, the effect of harvest-related losses of snags tapered off such that, over the course of the 20 year cutting cycle, its relative impact was only moderate.

We assumed that mortality rates were higher in managed stands during the first 5 years after harvesting. This increase in mortality had an almost negligible effect on snag density in our simulations. In addition to being restricted to the short term and acting on small trees, postharvest mortality usually resulted in tree fall. Thus, potential harvest-related increases in mortality are not expected to make a substantial contribution to snag abundances in managed hardwood stands.

If long-term mortality rates are substantially decreased by reduced competition in managed stands (Bédard and Majcen

2003), then relative snag abundances would be further reduced under the selection system. Mortality rates could also differ between managed and unmanaged stands if declining trees are selected for, or against, during harvesting. For example, stand-improvement cutting, in which dying and poorly formed trees are targeted for removal, may be expected to decrease subsequent mortality. The practice of high-grading, which removes the largest and most valuable trees, could have the opposite effect. In Ontario, tree-marking guidelines specify that declining and poor-quality trees be removed to improve subsequent stand growth and yield, but also retained in some cases to provide wildlife habitat (OMNR 2004). The net effect on mortality and snag inputs within selection-managed stands is unclear. Direct quantitative comparisons of mortality rates in managed and old-growth stands, and between good- and poor-quality trees, would be of value for assessing this potential effect in future modeling work.

Snag management under the selection system

The loss of snags that we project to occur under the selection system has the potential to negatively affect wildlife species that depend on these resources. Unfortunately, data on the density of snags required by various snag users are limited, so consequences for wildlife are difficult to ascertain. Our simulated snag abundances exceed those needed to support maximum woodpecker populations, as estimated by a nesting habitat model (Evans and Conner 1979). Recent work by Holloway and Malcolm (2006), however, suggests that red squirrels (*Tamiasciurus hudsonicus* (Erxleben, 1777)) are likely to be negatively affected by such a reduction in snag density. Further research into the functional relationships between snag density and the abundance of snag users would certainly aid in setting objective management targets (Franklin and Maser 1988). In the interim, it is prudent to adopt a precautionary approach and try to mitigate management-induced losses of snags to the extent that is feasible.

To be most effective, snag management practices should offset the principal factors that negatively affect snag abundances in managed stands. In the present study we found that harvesting causes an increase in snag falls, but that the effect of this direct loss of snags dissipates over time. Current forest-management guidelines in Ontario encourage the retention of snags during selection harvesting when they are not considered to represent a safety hazard (OMNR 1998). In the northeastern United States, experimental trials have further shown that postharvest snag densities can be elevated by girdling low-vigour trees (Keeton 2005). Practices such as these may lessen the immediate negative effect of harvesting on snags, but are not expected to have a great impact in the longer term, based on the expected times to snag fall reported here. Retaining or creating snags at harvest could yield short-term benefits for snag-dependent wildlife (Stribling et al. 1990), but this by itself seems to be insufficient for maintaining snag habitat up to the time of the subsequent harvest.

Maintaining snags over time requires adequate snag inputs from the standing death of live trees. In our simulations we found that selection management reduced snag densities considerably through a lower density of live stems. Unfortu-

nately, live stand structure is not easily amenable to modification under the constraints of the selection system: retaining a higher residual BA would result in lower stand growth and tree regeneration and a potentially substantial reduction in timber yield (OMNR 1998).

An alternative approach would be to attempt to increase snag inputs by promoting greater mortality among live trees. Current guidelines in Ontario mandate the retention of six live cavity trees per hectare during selection harvesting (OMNR 1998). In addition to providing immediate habitat for cavity users, cavity trees are often in decline and predisposed to die (Fan et al. 2003). Many of these trees would gradually become snags over time, and could contribute to snag inputs in selection-managed stands. Large cavity trees in particular would be of high value for potentially offsetting the decreased availability of snags in the largest size classes. An analysis of snag management through cavity tree retention, however, would require a quantitative understanding of the dynamics of cavity tree formation and mortality. Mortality rates also could be increased by adapting tree marking prescriptions to retain some suppressed trees or localized clusters of trees. Under these conditions trees face increased competition for light and nutrients. They would be more likely to succumb to limited resource availability, resulting in greater mortality, and snag inputs, within selection-managed stands. Silvicultural practices that strategically increase tree mortality rates, in concert with the retention of snags, as far as safety permits, during harvesting, could represent an effective approach to snag management in northern hardwood stands under the selection system.

Acknowledgements

We are grateful to John Parton, Brian Naylor, Ken Arie, and two anonymous reviewers for their constructive suggestions on earlier drafts of the manuscript. This research was funded by a Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant to JPC.

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