



# Insect-mediated apparent competition between mammals in a boreal food web

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**While the important role of animal-mediated interactions in the top-down restructuring of plant communities is well documented, less is known of their ensuing repercussions at higher trophic levels. We demonstrate how typically decoupled ecological interactions may become intertwined such that the impact of an insect pest on forest structure and composition alters predator–prey interactions among large mammals. Specifically, we show how irruptions in a common, cyclic insect pest of the boreal forest, the spruce budworm (*Choristoneura fumiferana*), modulated an indirect trophic interaction by initiating a flush in deciduous vegetation that benefited moose (*Alces alces*), in turn strengthening apparent competition between moose and threatened boreal caribou (*Rangifer tarandus caribou*) via wolf (*Canis lupus*) predation. Critically, predation on caribou postoutbreak was exacerbated by human activity (salvage logging). We believe our observations of significant, large-scale reverberating consumer–producer–consumer interactions are likely to be common in nature.**

insect outbreaks | habitat selection | species interactions | species conservation | apparent competition

Community and population ecology have been first and foremost studied through direct resource–consumer interactions. There is growing recognition, however, that indirect effects of species interactions can shape ecosystems as much as direct effects (1), and sometimes in surprising ways. The loss of top predators, for example, cannot only cascade down to impact bird, mammal, invertebrate, and plant abundance or richness, but predator removal can trigger a wave of resource–consumer changes that can even ultimately alter stream morphology (2). The risk that human-induced or natural changes in community composition have rippling effects on seemingly independent components of the environment has strong relevance to management and conservation planning.

Apparent competition is one common indirect interaction increasingly reported in field studies; it occurs between two prey species through a common, shared enemy (e.g., predator or pathogen) (3). Apparent competition pervades many natural ecosystems (4, 5), and it can impact ecological communities to the extent that local prey populations may disappear (5). Various factors can trigger apparent competition, notably species introductions or loss (4, 6, 7) and pulses in resource availability (8, 9). For example, masting seed crops can exert apparent competition among songbird populations, mediated through generalist predator populations (10). Resource pulses can also be linked to the life cycle of animal species. Spawning Pacific salmon (*Oncorhynchus* spp.) provides wolves (*Canis lupus*) with a seasonal increase in food abundance that can support the predator at densities sufficient to maintain local ungulate populations at relatively low numbers (9). Wolves feed only a portion of the year on salmon, and the fish completes its life cycle with very limited interaction with wolves; yet, this interaction has a strong impact on the terrestrial food web involving several primary consumers.

Insect outbreaks are also recurrent events but with multiyear cycles (11). Despite their relatively long cycles, these events can be the dominant disturbance agent of ecosystems, especially in

temperate forests (12). Insects have been recognized as ecosystem engineers (13) because their impact on trees generates resources for various organisms [e.g., other insects, small mammals, and birds (14)]. However, the influence of insect infestations goes much beyond the addition of new resources, as they can modulate energy flow across food webs (15). Changes in canopy cover due to insect defoliation alter abiotic conditions (e.g., solar radiation at ground level) in a way that promotes the growth of understory shrubs and herbaceous vegetation (16). This tends to benefit biodiversity associated with early-seral vegetation at the expense of species dwelling in mature forests (15). For example, positive responses of elk (*Cervus canadensis*) and mule deer (*Odocoileus hemionus*) have been reported a few years following mountain pine beetle (*Dendroctonus ponderosae*) outbreaks, while red squirrel (*Tamiasciurus hudsonicus*) and coyotes (*Canis latrans*) declined (14, 15). Although the reaction of species to insect outbreaks can be diverse, the potential impact on ecosystem structure and function is undeniable. What remains unclear is how the impact of these cyclic events might reverberate into higher trophic levels to modulate both direct and indirect food web interactions. Clarifying these effects on population and community dynamics is likely to be critical, however, to conservation and management, especially when species of concern are involved. Here, we provide rare empirical evidence that a forest insect pest can trigger apparent competition in a boreal food web between large mammals—one of which is a threatened species—via a shared predator.

## Significance

**Despite the growing recognition that indirect interactions within species networks can determine food web dynamics, empirical evidence remains rare. We demonstrate how the impact of insects on forest structure and composition can reverberate across trophic levels by altering apparent competition in a large-mammal food web subjected to timber extraction. Spruce budworm outbreaks initiated a flush in deciduous vegetation that benefited moose, which translated into apparent competition between moose and boreal caribou through wolf predation. Mortality risk of caribou became indirectly related to patterns of insect and human activities, with the ungulate experiencing higher risk when selecting stands severely infested by budworms and subsequently logged. We expose cascading effects of insect–forest interactions on large-mammal relations in human-altered ecosystems.**

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The authors declare no competing interest.

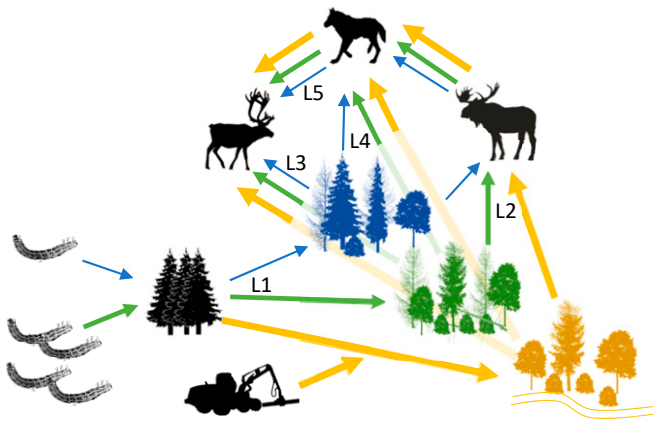
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**Fig. 1.** Simplified schematic of a boreal caribou–wolf–moose system illustrating the indirect effects of a SBW outbreak on trophic interactions. Links L1 to L5 are described by arrows. The blue arrows indicate effects for an early or less-impacted stage of SBW outbreak (e.g., 3 y of defoliation), and green arrows indicate effects at a later or more severe outbreak stage (e.g., 10 y of defoliation). The yellow arrows represent effects of salvage logging inclusive of the associated road network introduced by logging.

Boreal populations of woodland caribou (*Rangifer tarandus caribou*) are classed as threatened across most of their range in Canada (17), with well-known population declines resulting from apparent competition with other herbivores (18–20). Wildfire and logging are the dominant factors threatening boreal caribou by driving the observed apparent competition, which is principally mediated by wolves. Disturbed areas provide high-quality food for deciduous-browsing moose (*Alces alces*) and deer (*Odocoileus* spp.), and subsequent increases in these prey populations triggers a numerical response in wolves. This increase in wolf numbers intensifies predation risk to boreal caribou, which select for old-growth forests and displace to the latter to avoid predation (18). The construction of linear corridors such as roads and trails can also impact caribou, as these features can steepen the functional response of wolves to prey density (i.e., increase prey detection/hunting efficiency) (21, 22). Collectively, such habitat changes alter the spatial dynamics and hence interaction rates of predators and apparent competitors (23, 24). Because the main agents of caribou declines are habitat driven, much attention is currently devoted to the role of fire and anthropogenic disturbance in the process. However, a cyclic insect outbreak can also generate secondary succession in forests. Although insect outbreaks often disturb larger areas than wildfires and logging in boreal forests (25), little information exists on how outbreaks might impact on survival of boreal caribou through direct and indirect food web interactions.

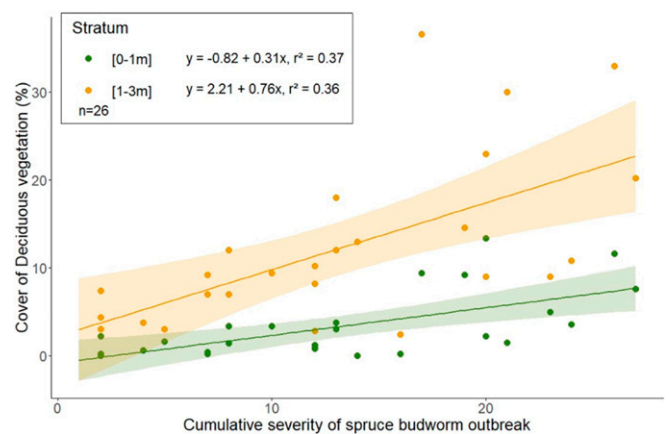
We assessed the impact of the common spruce budworm (SBW, *Choristoneura fumiferana*) on the distribution, survival, and trophic interactions of boreal caribou in an area subject to current outbreak of budworm. The SBW is one of the most damaging outbreaking insects in the boreal and subboreal forests of North America, with irruptions recurring every 30 to 35 y resulting in tree mortality after 5 to 6 y of defoliation (16, 26). SBW-damaged stands are often salvage logged following disturbance (27), which serves to expand resource extraction road networks (28). With climate change and a northerly expansion of SBW distribution, boreal caribou ranges are also at risk for experiencing increasing SBW outbreaks. Building on the hypothesis of disturbance-mediated apparent competition (29, 30) and taking advantage of detailed data on SBW outbreaks, forest succession, and multiple mammal populations in Québec, Canada, we predicted that outbreaks of SBW would induce apparent competition between caribou and moose through their common predator, the wolf (links L1 to L5, Fig. 1). We predicted that reductions in canopy cover in conifer stands caused by relatively

severe outbreaks would stimulate growth in deciduous vegetation (L1, blue versus green links, Fig. 1). Deciduous vegetation is prime food to moose, whereas boreal caribou focus much more on lichens and graminoids (31). We further expected the latter to result in a detectable numerical response in moose (L2), thereby increasing local prey available to wolves. Mortality risk for caribou was therefore expected to be higher in forest stands most severely impacted by SBW (L5), especially if the infected stands enhanced predator–prey encounter rates (i.e., both wolves and caribou selectively using those stands, L3 and L4). Finally, we assessed the effect that salvage logging of SBW-infested stands (SBW<sub>cut</sub> hereafter) could exacerbate apparent competition (yellow links) by providing additional deciduous vegetation that attracts more moose (thereby wolves) and increases predation risk for boreal caribou (Fig. 1, larger arrows).

## Results

**Link 1: Post-SBW Outbreak Vegetation Growth.** Our field sampling confirmed that stands within the 0.063-km<sup>2</sup> plots impacted by higher cumulative severity of SBW outbreak were covered by a greater proportion of deciduous vegetation at two different heights (strata: 0 to 1 and 1 to 3 m) of vegetation of differing availability to large herbivores in this system (Fig. 2). Both height strata were positively correlated (Pearson’s correlation = 0.72,  $P < 0.01$ ).

**Link 2: Moose Density.** Moose occurred at a density of 0.60 individual/10 km<sup>2</sup> (95% CIs: 0.36 to –0.83) when the SBW infestation started in 2006 and then rose to 1.01 individual/10 km<sup>2</sup> (95% CI: 0.59 to 1.43) in 2018 during the infestation (i.e., a 70% increase in moose density over 13 y) ( $P = 0.07$ ). In 2006, when the outbreak began, moose density was positively related to the proportion of deciduous vegetation ( $R^2 = 0.24$ ,  $P < 0.001$ ,  $n = 48$ ). In 2018, areas (60-km<sup>2</sup> plots) with high availability of deciduous-dominated stands tended to have low mean cumulative severity of SBW (Pearson’s correlation = –0.54,  $P < 0.01$ ,  $n = 44$ ). In this spatial context, multiple regression showed that moose density simply remained positively associated with the proportion of deciduous vegetation in the area ( $R^2 = 0.17$ ,  $P = 0.02$ ) without an independent link to the mean cumulative severity of the ongoing SBW outbreak ( $P = 0.51$ ). A connection between moose density and SBW became apparent, however, when considering stands that were impacted by SBW and then logged (SBW<sub>cut</sub>). Indeed, moose density in 2018 was higher in areas with proportion of SBW<sub>cut</sub> > 20% than areas with SBW<sub>cut</sub> ≤ 20% ( $U = 76.5$ ,  $P = 0.04$ ; Fig. 3). The difference reflected local increases in moose density

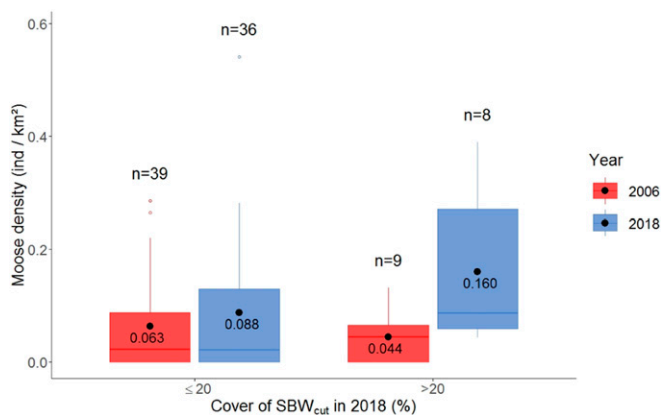


**Fig. 2.** Observed percentage cover of available deciduous vegetation in SBW-infested forest stands in relation to an index of budworm cumulative severity in 2018 (Côte-Nord region, Québec, Canada). The points represent raw values, and colored ribbons indicate 95% CIs.

because moose density increased (though marginally) between 2006 and 2018 ( $U = 18.0, P = 0.09$ ) in areas that became characterized by a high proportion of SBW<sub>cut</sub> (>20%) in 2018 (Fig. 3). Thus, it was the proportion of deciduous vegetation itself that influenced moose, which did increase moose density especially in areas characterized by a high proportion of SBW<sub>cut</sub>.

**Links 3 and 4: Caribou and Wolf Habitat Selection Models.** Resource selection functions (RSFs) during the winter monitoring period showed that relative to open conifer forests (the reference category), caribou selected mixed forests and open areas whereas they avoided burned stands and cuts (Table 1). Wolves selected mixed forests, dense conifer forests, and burned stands <20 y old, whereas they avoided older burned stands. While accounting for these basic habitat selection patterns, the analysis revealed that caribou (L3, Fig. 1) and wolves (L4, Fig. 1) both responded to the impact of SBW on habitat features. Specifically, caribou avoided areas with high SBW cumulative severity (Table 1), while most (but see *Consequences of Habitat Selection and Use to Caribou Survival*) also avoided SBW<sub>cut</sub> more than cuts of all age classes and burned stands >5 y (Table 1). Wolves selected SBW<sub>cut</sub>, whereas they avoided young cuts (<20 y old) that had not been impacted by SBW.

**Link 5: Consequences of Habitat Selection and Use to Caribou Survival.** Concurrent resource selection of wolves and caribou revealed consequences for the survival of caribou, consistent with predictions. Of the 118 female boreal caribou monitored from 2005 to 2018, 23 (19%) died from predation in winter during the monitoring period. Individuals that died displayed a similar level of avoidance of SBW<sub>cut</sub> ( $P = 0.58$ , Table 1) but marginally stronger selection ( $P = 0.09$ , Table 1) of areas with higher SBW cumulative severity. The difference in habitat selection strategies [*sensu* (32)] became particularly evident when contrasting individual RSFs developed depending on caribou's fate (*SI Appendix, Table S1*). Individuals that remained alive avoided areas with high SBW cumulative severity ( $\beta = -1.682$ ; SE = 0.621, *SI Appendix, Table S1.a*), whereas caribou that died did not and even tended to select severely impacted stands ( $\beta = +0.585$ , SE = 0.366, *SI Appendix, Table S1.b*).



**Fig. 3.** Relationship between moose density and percentage cover of salvage-logged forest stands (Côte-Nord region, Québec, Canada). We compared moose density before and after SBW outbreak (2006 versus 2018) within areas that were subject to salvage logging, with a spatial reference where salvage logging was low (<20%), conforming to a before-after-control-impact design. The boxplots describe moose density in 2006 and in 2018 in relation to the percent cover of areas infested by SBW for at least 1 y and then cut (SBW<sub>cut</sub>) within plots (each 60 km<sup>2</sup>) characterized by a low (<20%) or a high (>20%) percent cover of SBW<sub>cut</sub> in 2018. The black points correspond to the mean density of moose, the center value is the median, edges of the box are 25th and 75th percentiles, and whiskers represent  $\pm 1.5$  the interquartile range.

Furthermore, the survival analysis indicates that mortality risk increased with the use of areas strongly impacted by the insect and then harvested (SBW<sub>cut</sub>, Table 2).

**Discussion**

We show that the impact of SBW on boreal forests can resonate broadly across the community by triggering an important indirect effect, apparent competition between two large herbivores. Increases in availability of deciduous vegetation as a result of SBW infestation of conifer stands generated a suite of spatial and demographic responses in moose, wolves, and caribou indicative of disturbance-mediated apparent competition (29, 30). Critically, however, salvage logging of conifer stands post-SBW outbreak in our study area facilitated an increase in predation mortality risk for boreal caribou, an ungulate threatened with extinction (33). More generally, our study demonstrates that typically independent food webs (conifer–insect versus vegetation–moose–caribou–wolf) may interact such that the impact of an insect pest on forest structure and composition alters predator–prey interactions among large mammals. We draw this conclusion by providing quantitative support to predictions of three key processes involved in insect-driven apparent competition for our study area (Fig. 1).

First, the outbreak of SBW increased the abundance of deciduous vegetation in coniferous stands (L1, Fig. 1). For this to happen, outbreaks need to be sufficiently severe and last long enough for the old-growth canopy to open up and for pioneer, shade-intolerant plant species (i.e., deciduous, hardwood vegetation) to proliferate (16). The impact of an insect outbreak thus depends on the duration and severity of its infestation (15), as we observed from our SBW cumulative severity index.

Second, the increase in deciduous vegetation we documented reflected a numerical response of moose (L2, Fig. 1), with the population density of moose using the same survey methods increasing by 70% over a 13-y period post-SBW outbreak. Covariation between moose density and availability of deciduous (hardwood) vegetation is well established (34). Moose, which are hardwood browsers (24), are most abundant in early to midseral stages of boreal forest succession (35, 36) where hardwood trees and deciduous shrubs are generally high in palatable biomass (37). Moose did not alter their overall distribution following the outbreak, as they generally remained most closely associated with forest stands rich in deciduous vegetation. Such close affinity with food-rich areas is a basic expectation from ideal-free distribution principles (38). That said, we observed moose density to become especially high in areas largely comprised of deciduous stands and of stands first infested by SBW but then also logged. Outbreak-modified habitat selection patterns for moose are not unique to SBW, as Ivan et al. (15) recently outlined a positive association between bark beetle (*Dendroctonus* spp.) outbreaks and the distribution of various ungulates, including moose.

Third, mortality rate of caribou was higher in areas impacted by SBW (L5, Fig. 1). While the insect could have altered the hunting efficiency of wolves, it is unclear whether the overall outcome would be positive for the predator. On one hand, severe SBW infestations generally occur in forest stands with complex vegetation structure and high lateral cover (39) and result in forest stands with more abundant dead wood (40), which might reduce hunting efficiency especially of cursorial predators. On the other hand, salvage logging of SBW-impacted stands removes standing trees and requires deployment of a road network that is known to increase the search efficiency of wolves (21, 22, 41). Without excluding this possibility, our study was designed to evaluate the notion that the increase in caribou mortality could be indirectly linked to the response of moose to landscape changes. The tight link between wolf abundance and ungulate density, especially moose density (18), is well documented. Although no longitudinal data exists on the demographic response of wolves to prey availability in our study area, the expected numerical

**Table 1. Summary of the habitat selection models**

Variables	Caribou			Wolf		
	$\beta$	SE	<i>P</i> value	$\beta$	SE	<i>P</i> value
Conifer dense	-0.212	0.009	<0.001	0.225	0.033	<0.001
Mixed	0.070	0.009	<0.001	0.494	0.023	<0.001
Open area	0.143	0.011	<0.001	-0.066	0.038	0.084
Other	-1.268	0.010	<0.001	-0.385	0.031	<0.001
Burned ( $\leq 5$ y old)	-2.868	0.091	<0.001	0.747	0.041	<0.001
Burned (6 to 20 y old)	-1.453	0.054	<0.001	0.520	0.034	<0.001
Burned ( $\geq 21$ y old)	-0.407	0.016	<0.001	-0.513	0.057	<0.001
Cut ( $\leq 5$ y old)	-0.719	0.026	<0.001	-0.531	0.048	<0.001
Cut (6 to 20 y old)	-1.152	0.031	<0.001	-0.377	0.034	<0.001
Cut ( $\geq 21$ y old)	-0.339	0.047	<0.001			
Distance to road	0.587	0.004	<0.001	-0.146	0.013	<0.001
SBW cumulative severity	-1.505	0.534	0.005	-0.019	0.016	0.252
SBW <sub>cut</sub>	-2.429	0.462	<0.001	0.359	0.076	<0.001
Mortality status $\times$ SBW cumulative severity	2.119	1.250	0.090			
Mortality status $\times$ SBW <sub>cut</sub>	0.505	0.904	0.576			
Random effects for caribou	Variance	95% CI				
SBW cumulative severity	16.580	(10.758, 25.563)				
SBW <sub>cut</sub>	6.103	(3.648, 10.208)				
k-fold: $r_s$	0.697			0.852		

Mixed-effects logistic regression models of habitat selection of 16 wolves and 118 caribou during the winter period in the Côte-Nord region, Québec (Canada), with their selection coefficients ( $\beta$ ); SE, and *P* value. Reference category is open conifer forest. SBW<sub>cut</sub> represents areas infested by SBW for at least 1 y and then cut. Mortality status indicates if individuals remained alive throughout the study (0) or died (1).

Models were robust to cross-validation as indicated by high mean Spearman rank correlations ( $\bar{r}_s$ ).

response of wolves to increased moose density during the SBW outbreak explains the increased risk of caribou mortality.

Apparent competition can also be driven by behavioral traits (5). This would be the case, for example, when adjustments in the predator's search for a given prey results in more frequent encounters with another. Prey species with large home ranges and site fidelity, such as boreal caribou (42, 43), should be particularly prone to trait-mediated apparent competition. Wolves hunt by targeting areas rich in moose's food, including deciduous or mixed stands and disturbed areas where early-seral vegetation has emerged (23, 24, 44). Accordingly, we found not only moose that were particularly abundant in areas characterized by a high proportion of SBW<sub>cut</sub> but also that wolves made selective use of these stands. This attraction of wolves for SBW<sub>cut</sub> impacted a segment of the caribou population, with individuals avoiding less strongly (Table 1) or using more intensively SBW<sub>cut</sub> (Table 2) more likely to die from predation. Our study provides a demonstration that the strength of apparent competition between caribou and moose in a caribou-moose-wolf system can also depend on the indirect effects of an insect, SBW, on the availability of deciduous vegetation.

Given that caribou-moose-wolf interactions have evolved in environments shaped by a recurrence of insect outbreaks, including SBW irruption, we might expect that caribou populations would cope with enhanced predation risk resulting from asymmetrical apparent competition. What is most concerning, however, is that mortality rates following SBW infestation in our study area were clearly exacerbated by postoutbreak logging. Salvage logging during insect outbreaks has become a common practice across the boreal forest in North America (27). With climate change, SBW infestations are expected to spread northward (45), which should increase the spatial overlap between SBW outbreaks and caribou distribution in areas where most of the unlogged, primitive forests (46–48) that can be subjected to salvage logging occur. In fact, the current outbreak is expanding northward and is impacting areas that had not been previously affected by outbreaks

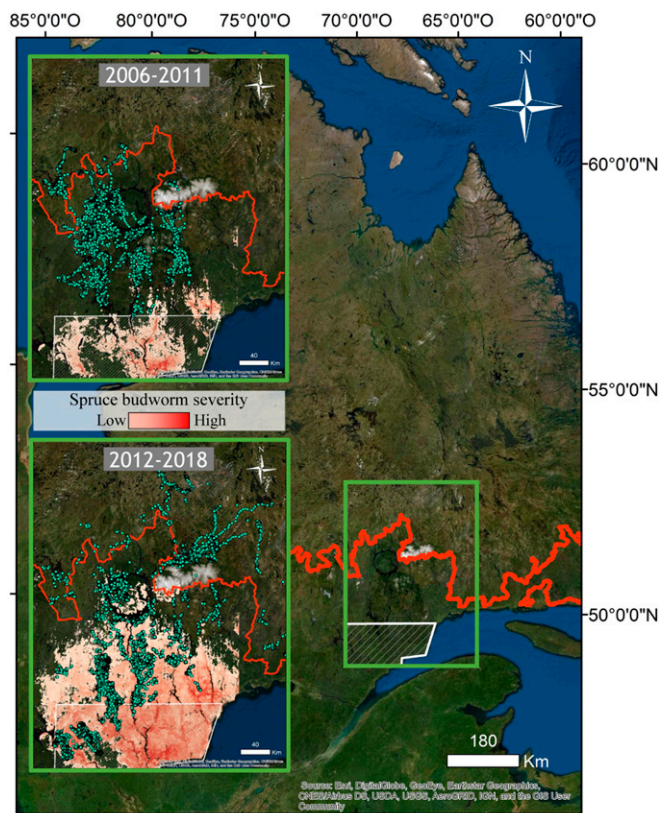
(49). By the end of our study, the SBW infestation overlapped with one-half the radio-collared caribou (Fig. 4). Our study provides a textbook example of cumulative effects (50) between natural and anthropogenic disturbance on food web properties, albeit in the context of an interaction that has thus far been missed by researchers and is to the literature on boreal caribou conservation.

Our findings also expose potential risks involved with the current paradigm for boreal caribou management for habitat, notwithstanding the risk of ignoring the additive or interactive impacts of climate change on forest insect outbreaks in caribou range. Current recommendations are largely based on the limitation of total disturbance (fire and anthropogenic) of caribou habitat to 35% (20). At first glance, salvage logging could be seen as a favorable option in this context, as it mostly involves the disturbance of areas already mapped under a disturbance footprint (51), thereby keeping the disturbed area largely constant (excepting the addition of haul

**Table 2. Summary of caribou hazard analysis**

Variables	$\beta$	SE	<i>P</i> value
% Burned	-10.646	9.235	0.250
% Cut ( $\leq 5$ y old)	-3.016	14.506	0.840
% Cut (6 to 20 y old)	26.538	5.677	<0.001
% SBW <sub>cut</sub>	20.619	8.500	0.015
SBW <sub>ms</sub>	-0.048	0.092	0.600
Random effects	Variance		
% SBW <sub>cut</sub>	$0.633 \times 10^{-1}$		
SBW <sub>ms</sub>	$0.764 \times 10^{-5}$		

Coefficient ( $\beta$ ), SE, and *P* value of the Cox-proportional hazards model evaluating female boreal caribou survival between 2005 and 2018. % Cut and % Burned represent the percent cover of the variable; % SBW<sub>cut</sub> represents the percent cover of areas infested by SBW for at least 1 y and then cut, and SBW<sub>ms</sub> represents the mean cumulative severity of the SBW outbreak within individual winter home range.



**Fig. 4.** Study area in the province of Québec, Canada. The green boxes represent maps of the distribution and defoliation severity based on aerial survey data of the SBW outbreak (68) in 2011 (*Top*) and 2018 (*Bottom*) within the study area. The blue dots represent the distribution of GPS radiocollared caribou in 2006 to 2011 and 2012 to 2018 used in the analyses. The red line represents the northern limit for forest management activities. The hatched area defines Hunting Area 18 in Côte-Nord region within the study area.

roads). Our study underscores that salvage logging of SBW-impacted forests is not compensatory to natural disturbance but highly likely to exacerbate the mortality risk of caribou. Moreover, salvage logging can disrupt postdisturbance succession (52), removes biological legacies (e.g., snags), and reduces the value of wildlife habitat (40, 53, 54). There is a real danger that SBW outbreaks cumulative with postoutbreak salvage logging will present additive and not compensatory risk to the persistence probability of boreal caribou populations. Whether this finding also applies to other scenarios of salvage logging, from fire, or other insect outbreaks (e.g., from bark beetle), is plausible but unknown. Still, with the ongoing global changes in boreal ecosystems, there is a risk that pest insects become an indirect driving force behind the northward range recession of boreal caribou.

The impact we observed of SBW on large-mammal interactions occurred via forest-structure transformation and a subsequent pulse in resources for large herbivores. Previous studies have underscored the far-reaching consequences of resource pulses, including cascading effects across food webs (55–57). For example, suitable weather conditions can result in a vegetation pulse of acorns (most event) triggering a numerical response of rodents and then of predatory birds, with subsequent negative demographic effects on other bird species (10, 58, 59). Trophic cascades have also been initiated with the input of food and nutrients from the ocean by seabirds, providing nutrients for terrestrial plants as well as food for terrestrial consumers (60–62) in correlation with pulses in fish stocks (61, 63). Predation has been shown to modulate such effects,

for example with introduced predators like foxes preying on birds reducing nutrient transport from ocean to land, and negatively affecting soil fertility (64, 65). While predator-mediated apparent competition is also known from island systems (66) and, more recently, in the context of abiotic (rainfall) limitation (58), the relationships we show here is in that we link the former to a resource pulse initiated by a consumer (SBW), itself likely limited by abiotic conditions.

Our findings are relevant at large ecological scales in both space and time. The SBW is a common forest pest of the boreal forest, and SBW outbreaks occur in the periodically every 30 to 40 y (67) or longer (26). However, with generation times  $\leq 10$  y (33, 68, 69) and a typical longevity  $< 20$  y (33, 70, 71) for the three mammal species we considered in this study, multiple cohorts of individuals are expected to experience little to no SBW infestations during their lifetimes. This means that SBW–forest interactions and that of moose–wolf–caribou may generally operate independently at low levels of SBW. However, when an outbreak occurs, its impact on forests are likely to couple these otherwise independent interactions, ricocheting across the large-mammal food web. SBW therefore acts as an ecological engineer with its actions on forest structure and composition ultimately leading to enhanced apparent competition [*sensu* (10)] between boreal caribou and moose. Furthermore, human activities, such as salvage logging, strengthened the strength of interactions between SBW–forest and plant–caribou–moose–wolf systems. Including humans as an additional species which might manipulate trophic interactions may be particularly important in human-impacted ecosystems.

### Conclusion

Here, we provide empirical evidence that ecosystem engineering by a common insect (SBW) can ricochet along a chain of ecological interactions to be felt by an apex mammalian predator before bouncing back down to impact an ungulate via apparent competition. Our study demonstrates that the cascading effects of SBW in boreal ecosystems can ultimately increase the mortality rate of a threatened ungulate, especially when human activities further disturb the system. Such insights are particularly critical in the context of global change, given evidence suggesting that both anthropogenic disturbances and climate change have the potential to disturb top-down and bottom-up control mechanisms that regulate ecological communities (72, 73). By integrating the spatiotemporal dimension and severity of forest insect outbreaks simultaneously with other natural and anthropogenic disturbances, our study highlights how multiple disturbances can act on a boreal system by altering species densities and higher-trophic-level interactions. Our finding of an insect-mediated interaction strong enough to bounce back into higher-trophic-level apparent competition highlights the far-reaching role of multilevel indirect interactions on food web dynamics.

### Materials and Methods

**Study Area.** The 92,000-km<sup>2</sup> study area (48°N to 54°N, 63°W to 73°W) covering was located in the Côte-Nord region of Québec, Canada (Fig. 4). The northern part of the study area is part of the spruce-moss domain and is dominated by black spruce with balsam fir. Insect outbreaks and wildfires are the major natural disturbances (74). The southern part of the study area belongs to the eastern spruce-moss subdomain of the eastern boreal forest, mostly dominated by balsam fir and white spruce (*Picea glauca*, [Moench] Voss) mixed with white birch (*Betula papyrifera*, Marsh). Forest harvesting has been the main source of forest disturbance since the late 1990s (75). This southern part is subject to SBW outbreaks, a forest insect (Lepidoptera: Tortricidae) that undergoes periodic population-level increases and causes widespread defoliation of host trees over large areas. Salvage logging during these insect outbreaks has become a usual practice to recover some of the economic value that would otherwise be lost (27). Measures have been established, including preventive harvesting, adapted silvicultural interventions, as well as aerial organic insecticide sprays. The latest SBW outbreak in the study area started in 2006 and remains ongoing. The insect

first impacted the southern part of the study area before the outbreak gradually progressed northward (Fig. 4).

**Habitat Characteristics.** We characterized the study area using the Canadian National Forest Inventory (CNFI) forest cover maps (76), corresponding to L1 in Fig. 1. These maps are a  $k$ -nearest neighbor interpolation at a 250-m resolution of the CNFI photograph plot data acquired in 2001 (see ref. 61). To estimate forest composition, we used the relative proportions of species groups (needle-leaved and broad-leaved species), treed land, and tree crown closure maps from these CNFI data. We created five land cover classes based on the Earth Observation for Sustainable Development of Forests Land Cover Classification Legend (77): closed-canopy conifer forest (needleleaf > 75% and crown closure > 60%), open-canopy mature conifer forest (needleleaf > 75% and crown closure ≤ 60%), mixed forest (needleleaf > 25% and deciduous > 25%), open area (vegetation > 50% and vegetation nontreed ≥ vegetation treed), and other (nonvegetation ≥ 50%). Land cover maps were updated every year by adding roads, recent (<5 y), regenerating (6 to 20 y), and old (21 to 50 y) cutblocks/fires based on information provided annually by local forestry companies (78) and from the Canadian National Fire Database (79).

SBW outbreaks were mapped annually based on aerial surveys characterizing damages caused by SBW since 2006 (80). In-flight surveyors delineated polygons of insect damage using topographic maps and assign a severity class to an estimate of current-year defoliation to each polygon. Defoliation severity classes were recorded as low (1 to 35%), medium (36 to 70%), and high (71 to 100%). We quantified the cumulative severity of the outbreak by summing the estimated severity for each year (2006 to 2018) and created maps with 250-m resolution (corresponding to blue and green links of L1 in Fig. 1). We also determined a covariate “SBW<sub>cut</sub>” that corresponded to pixels infested by SBW for at least 1 y and then cut (yellow link, L1, Fig. 1).

**Post-SBW Outbreak Vegetation Growth.** To evaluate the availability of deciduous vegetation in stands impacted by the SBW outbreak and test our prediction that the reduction in canopy cover caused by SBW in coniferous stands would result in greater deciduous vegetation (blue and green links L1, Fig. 1), we used the map of cumulative outbreak severity calculated in 2018. We visited 26 of those 250-m pixels in Fall 2019 (18 September to 23 September) to validate the relationship between SBW cumulative severity and the percentage cover of deciduous vegetation of two height strata (0 to 1 m and 1 to 3 m classes). September was the best period to record the maximum defoliation severity of the year, once larvae have finished feeding (from May to July). Within each pixel, we visually estimated the percentage (based on 10% cover classes) of deciduous vegetation in five circular (10 m radius) plots. The plot centers were located at 250 m of the road, and the other plots were located in each of the four cardinal directions, 50 m from the central plot. Average values were used in subsequent analysis.

**Moose Density.** We assessed the influence of SBW outbreak on moose abundance (L2 in Fig. 1) by comparing moose densities before and during SBW outbreak. We used data from aerial surveys of moose conducted in 2006 and in 2018, hunting zone 18, in the Côte-Nord region of Québec (81). The double sampling method (82) has been applied for the aerial survey of 72 plots of 60 km<sup>2</sup> in 2006 and 62 plots in 2018. For analyses, we considered all survey plots that overlapped the study area, delimited with radio-collared caribou and wolves (Fig. 4). A total of 48 plots of the 72 surveyed in 2006 and 44 of the 62 plots surveyed in 2018 were in the study area. Based on those 92 (48 + 44) plots, we estimated moose density while considering a visibility rate of 0.68 in 2006 and 0.70 in 2018 (81). We compared moose density using Poisson Generalized Linear Models (GLM), but we detected model overdispersion and thereby corrected the SEs using a quasi-Poisson GLM model (83). For each survey plot, we extracted the mean cumulative severity of SBW and the percent cover of SBW<sub>cut</sub> from the map of the cumulative severity of SBW outbreak in 2018 and deciduous vegetation from CNFI forest cover maps (76). To test our predictions that SBW outbreak triggers apparent competition, corresponding to L2 in Fig. 1, we evaluate the importance of vegetation characteristics on moose densities in 2018 by building a multiple regression to better understand if the cumulative severity of SBW and the proportion of deciduous vegetation could explain change in moose densities. Finally, we used the Mann-Whitney  $U$  test to compare moose density in plots with low (<20%) and high (>20%) percent covers of SBW<sub>cut</sub> in 2018 to test our hypothesis that moose densities would be higher in plots with high cover of cuts, which would increase the availability of deciduous vegetation.

**Telemetry.** A total of 133 global positioning system (GPS)-collared adult female caribou were monitored from March 2005 to December 2018, with each individual being followed for an average of 23.1 mo (range: <1 to 56 mo). Animal capture and handling protocols adhered to guidelines under the Canadian Council on Animal Care and were approved by Université Laval animal protection committee. The GPS collars were programmed to collect a location every 1, 2, 3, 4, 8, or 16 h depending upon collar type and year. For wolves, 16 adults (eight females and eight males) were followed from March 2005 to December 2018, with each individual being tracked for an average of 19.6 mo (range: <1 to 49 mo). The collars were programmed to acquire a location every 1, 4, 6, or 10 h. Statistical analysis accounted for the differences in sampling intensity (see *Caribou and Wolf Habitat Selection*). We focused our investigation on winter (January to mid-May). Although caribou mortalities can occur year-round, our study focuses on winter because 1) most mortalities occurred during winter in our study area (38 mortalities, including 23 from predation, 2 from natural death, and 13 from unidentified causes); 2) winter is the only season when we observed enough mortality events to investigate the impacts of disturbances on survival (38 mortalities in winter versus 19 mortalities in the three other seasons); and 3) winter is recognized as a critical mortality season for ungulates (84). Mortality sites were visited to identify the cause of death using standard diagnostic methods [i.e., predation, natural, or unidentified (85)]. We kept for our study only caribou which survived during the monitoring period in addition to caribou which died from predation. Consequently, we kept 118 caribou for analyses.

**Caribou and Wolf Habitat Selection.** We developed RSFs (86) for caribou and wolves to assess habitat selection and test our predictions related to L3 to 5 (Fig. 1). RSFs compare resource characteristics of observed (scored 1) and random (scored 0) locations (87). To delineate the annual winter home range of each animal, we used the 100% minimum convex polygon (MCP) for each radio-collared caribou, whereas for wolves, we drew 95% MCP of all radio-collared members of its pack. This latter approach excluded extraterritorial excursions (88, 89). GPS locations (i.e., observed locations) were then paired with random locations (5× the number of observed locations) to define resource availability within the MCP for each individual (caribou) and pack (wolf). Although the MCP should exceed the home range of an individual (90), our intent was not to determine the actual home range but rather to delineate an area that could be considered broadly available to the individual in winter. Such broad-scale assessment was deemed necessary here because disturbances can influence animal movements over several kilometers (20), and the MCP provided a satisfactory overview of resource selection by including landscape at the edge of their seasonal home ranges. RSFs were implemented using a mixed-effects logistic regression expressed as

$$w(x) = \exp\left(\beta_0 + \left(\beta_1 + \gamma_{1jk}\right)x_{1ij} + \dots + \left(\beta_n + \gamma_{nj k}\right)x_{njij} + \gamma_{0jk}\right),$$

where  $w(x)$  represents the RSF scores (relative probability of selection or odds ratio),  $\beta_0$  is the fixed intercept,  $\beta_n$  is the selection coefficient for the  $n^{\text{th}}$  variable,  $x_{njij}$  is the value of the  $n^{\text{th}}$  variable for the  $i^{\text{th}}$  location for the  $j^{\text{th}}$  individual,  $\gamma_{0jk}$  is the random intercept specific to the  $j^{\text{th}}$  individual at year  $k$ , and  $\gamma_{nj k}$  is the random slope for the  $n^{\text{th}}$  variable specific to the  $j^{\text{th}}$  individual at year  $k$  (only for caribou model). For caribou RSFs, we included a random intercept for individuals and for the year and a random slope associated with SBW covariates to take into account the nonindependence among an individual's locations within a given year and the different collar schedules (91). For wolves, we used a random intercept for individuals within pack and year because a given pack could include more than one collared wolf (91, 92). We fitted the weighted logistic regression model (using  $W = 5,000$ ) with fixed intercept variance at  $10^6$  to ensure the convergence of the models, following procedures outlined in ref. 93.

To assess the overall effect of SBW outbreak on the use of boreal caribou and wolves in managed forests, we created a model that accounted for both natural and anthropogenic disturbances, together with land cover types. Closed-canopy conifer forest, open-canopy mature conifer forest, mixed forest, open area, SBW<sub>cut</sub>, recent (<5 y), regenerating (6 to 20 y), and old (21 to 50 y) cutblocks/fires and other land covers were represented by categorical covariates. SBW outbreak severity was centered and scaled. Wolves displayed such broad-scale avoidance of old cuts that this land cover type was almost never available among observed or random locations and, therefore, could not be included in the analysis. We could not directly consider the behavioral response of radio-collared wolves and caribou to spatial patterns in moose density because moose surveys were only conducted in the southern portion of the study area, whereas radio-collared individuals were tracked throughout the area. This is why we did not directly

test the link between wolf and moose in Fig. 1. Instead, we indirectly tested this link by assessing the response of caribou and wolves to SBW-impacted forests (links L3 and L4). We did not detect multicollinearity issues, given that variance inflation factors of all covariates were <4 (94) for both species.

We evaluated model robustness using *k*-fold cross-validation by developing RSFs with 80% of the locations (training set) and then by testing the predictive power of these RSFs with the 20% withheld locations (testing set). To evaluate the predictive success of the RSF model we used the R package *IndRSA* (95) using 10 repetitions of fivefold cross-validation with 10 bins of equal size and calculated the averaged Spearman's rank correlation coefficient ( $\bar{r}_s$ ) (96).

**Consequences of Habitat Selection and Use to Caribou Survival.** First, to link SBW covariates with caribou mortality in the RSF model, we identified factors linked to caribou mortality (link L5, Fig. 1) by adding interaction terms between mortality status (remained alive throughout the study = 0, died = 1) and SBW-related covariates. Then, we used a Cox-proportional hazards regression model (97) to evaluate whether the proportion of natural and anthropogenic disturbances within winter home range had an effect on the mortality risk of caribou. We calculated the 95% Brownian bridge movement kernel (98) of each individual from its winter locations, which provides an estimate of use intensity across its home range (98, 99). We used these kernels to estimate more specifically the percent cover of landscape variables used by individuals. It reflected habitat features in the immediate vicinity of caribou at the time of surveys by removing outliers and ensuring that only core areas of use were compared.

We considered the percent cover of forest that had been cut 0 to 5 y or 6 to 20 y ago, the percent cover of burned area, and the percent cover of SBW<sub>cut</sub>. To test the effect of the cumulative severity of the SBW outbreak on mortality risk, we calculated the mean cumulative severity of defoliation

(SBW<sub>ms</sub>) within individual caribou winter home ranges. Survival analysis considered "year" as a random effect by using random intercept to account for potential temporal variability because the cumulative defoliation in areas affected by the SBW outbreak increased over years. We included random coefficients for SBW covariates to consider variation in individual-level responses. The Cox model is especially suited to situations like ours, whereby individuals are followed and die or survive over different time intervals. For the survival analysis, we only used characteristics of the home range from the previous winter when an individual was followed over more than one winter, and time was defined as the total period of monitoring for that individual. We did not detect any multicollinearity issues, given that variance inflation factors were <4 (94) for all covariates. The proportional hazard assumption of our model (excluding the random factors) was not violated according to the Schoenfeld test ( $P > 0.30$ ) (100). All analyses were conducted in program R using the packages *survival* (101), *coxme* (102), *MuMIn* (103), *IndRSA* (95), *glmmTMB* (104), and *lme4* (105).

**Data Availability.** Information on animal distribution data have been deposited in Dryad (<https://doi.org/10.5061/dryad.j3tx95xds>) (106). All other study data are included in the article and/or *SI Appendix*.

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