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Habitat, Climate, and Fisher and Marten Distributions

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ABSTRACT Since the mid-twentieth century, fisher populations (*Pekania pennanti*) increased in several eastern jurisdictions of North America, particularly in the northern part of the species' range. Changes in fisher distribution have led to increased overlap with the southern portion of the range of American marten (*Martes americana*), whose populations may be locally declining. This overlap occurs particularly in habitats undergoing natural and anthropogenic modification. The objective of our study was to determine the respective effects of habitat changes and climatic conditions on fisher and marten populations in Quebec, Canada, based on trapper knowledge. We analyzed annual fisher and marten harvest (number of pelts sold/100 km^2) between the 1984–1985 and 2014–2015 trapping seasons using linear mixed models. Fisher harvest increased with the increased abundance of mixed forests >12 m tall, resulting from decades of forest harvesting. Fisher harvest decreased with increasing spring rains, which can affect survival when rearing young. Marten harvest decreased with increasing winter rains, which lower thermoregulation capacity and hamper movements by creating an ice crust on the snowpack, reducing access to subnivean areas. Decline in marten harvest during the 30-year study period coincided with an increase in fisher harvest, suggesting possible interspecific competition. Results highlight that managers should strive to maintain mixedwood stands taller than 12 m to maintain high quality habitat for fishers. Our study confirms the importance of working with trappers to assess furbearing population trends in response to habitat changes and climatic conditions.

KEY WORDS American marten, fisher, forest harvesting, furbearer management, mixedwood forest, mustelids, pelt sales, rain.

Unregulated harvest and habitat loss led to declines in populations of several forest carnivores in North America (Tapper and Reynolds 1996, Krohn 2012). Fisher (*Pekania pennanti*) and American marten (*Martes americana*) are 2 North American mustelids whose populations decreased because of overexploitation for fur and loss of habitat due to timber harvesting (Powell et al. 2003, Williams et al. 2007). After a decline during the mid-nineteenth century, fisher populations have rebounded since the mid-twentieth century in the eastern portion of the species' range, particularly in the northeastern United States, and in the Canadian provinces of Ontario and Quebec (Bowman et al. 2006, Lancaster et al. 2008, Krohn 2012, Lewis et al. 2012, LaPoint et al. 2015). Fisher recovery is due to translocation efforts, natural recolonization (Carr et al. 2007*a*, Stewart et al. 2017), habitat modification, and beneficial effects from climate change (Lancaster et al. 2008). In some cases, fisher re-establishment could result in declines in marten populations due to interspecific competition (Krohn et al. 1997, Fisher et al. 2013, Manlick et al. 2017). Because of its larger size, fisher is a dominant competitor of marten (Krohn et al. 1997). Interference competition from fishers could have forced martens to leave shared territories (Tannerfeldt et al. 2002). Marten populations, however, appear to be recovering in several parts of eastern North America shared with fisher (Aylward et al. 2018) but not in Quebec. Fisher harvest in Quebec is generally increasing, whereas that of martens is decreasing (Poulin et al. 2006, Suffice et al. 2017, Lavoie et al. 2019). According to Poulin et al. (2006), increased fisher harvesting in Quebec is more strongly associated with population increases than with increased trapping pressure.

Anthropogenic disturbance and climatic conditions can upset established equilibria and induce changes in habitat use by species (Graham and Grimm 1990, Lodge 1993). North American forests have been affected by human activities over recent decades (e.g., agricultural intensification, urbanization, forest logging; Reif 2013, Bridger et al. 2017). Forest logging differs from natural disturbances in terms of frequency, intensity, and spatial extent. It has resulted in younger, more fragmented forests with different tree species composition (Schulte et al. 2007, Boucher et al. 2014, Grondin et al. 2018). This in turn increased the number of wildlife species requiring early successional habitat but reduced the number of species requiring mature contiguous forest (Drapeau et al. 2000, Plante et al. 2018). Such modifications in the structure and composition of forest landscapes have a direct effect on habitat availability for mustelids (Buskirk 1992, Payer and Harrison 2005, Spencer et al. 2015).

At the population level, fishers are associated with dense forests and high, closed canopies used as resting sites (Buskirk 1992, Powell and Zielinski 1994, Potvin et al. 2000, Powell et al. 2003). Large-diameter trees often provide cavities used as refuges by fishers, whereas conifers intercept snow, reducing accumulation on the ground and facilitating fisher movement (Powell et al. 2003). The absence of important predators in northern portions of the fisher’s range could explain the use of more open land cover types than elsewhere in its distribution (Wengert et al. 2014), particularly along forest edges adjacent to agricultural fields and in younger forests (Suffice et al. 2017). Fishers also find important food sources in such cover types: snowshoe hare (*Lepus americanus*) and cervid carcasses (Potvin et al. 2005). In contrast, martens are more dependent upon protective cover from predation and inclement weather (Powell et al. 2003).

Consequently, martens occupy mature forests with dense cover and complex structure close to ground level, where they hunt for small mammals (Buskirk and Ruggiero 1994, Bissonette et al. 1997, Chapin et al. 1998, Potvin et al. 2000, Fuller et al. 2005). Recovery of marten populations in the northeastern United States coincides with the re-establishment of older, larger forest patches (Aylward et al. 2018). The association between marten and old, dense coniferous stands, however, is not exclusive (Cheveau et al. 2013). For example, snowshoe hares, which are more important prey for marten in the eastern than in the western portion of its range, are associated with early successional hardwood stands (Potvin et al. 2000).

Altered snow conditions in recent years have also directly affected the northern distribution of mesocarnivores (including fisher and marten) with differing effects depending upon species (Pozzanghera et al. 2016). The energy expenditure associated with animal movement through snow varies according to snow depth and the lift it provides, together with the speed of the individual's movements (Crête and Larivière 2003). Snow conditions particularly affect fisher dispersal (Raine 1983, Krohn et al. 2005, Carr et al. 2007*b*, Garroway et al. 2011, Bertrand et al. 2017) because they are larger and heavier than martens and exert greater foot loading (18.2–32.0 g/cm^2 vs. 9.1–12.2 g/cm^2). Compared to martens, movements of fishers tend to be more strongly constrained by deep, uncompacted snow (Kilpatrick and Rego 1994, Krohn et al. 2005). Presence of an ice crust resulting from freeze-thaw events increases snow lift, which can facilitate fisher movements (Suffice et al. 2017). Conversely, the ice crust limits subnivean access (Berteaux et al. 2017), which is the principal medium through which martens move (Raine 1987, Sherburne and Bissonette 1994, Krohn et al. 2005). Climate change could simultaneously be a challenge to marten populations at the southern edge of the species' distribution (Lavoie et al. 2019), and benefit fisher at the northern edge of its distribution (Manlick et al. 2017). Understanding the influences on wildlife distribution is important to decipher the role of human activities and establish best practices for timber and wildlife management considering climate change.

In a previous study documenting the knowledge of Quebec trappers about fisher and marten habitat use (Suffice et al. 2017), lack of exclusivity of both species to coniferous forests was highlighted, although marten was more closely associated with coniferous forests than fisher. Fisher apparently also uses open environments, including agricultural fields and younger forests. Moreover, climate change increases the frequency of freeze-thaw events that cause the formation of an ice crust on snow surface, favoring fisher movements and accessibility to new territories. According to trappers, fisher is less affected by forest management than marten, and the species also seems to benefit to a greater extent from the effects of climate change. The increase in winter rainfall frequency and forest cover changes have been identified by trappers as the major factors that may explain changes in fisher and marten abundance (Suffice et al. 2017). Our objective was to quantify the respective effects of habitat change and climatic conditions on the numbers of fishers and martens trapped in Quebec between the 1984–1985 and 2014–2015 trapping seasons. We tested hypotheses developed using a combination of local knowledge from trappers and a literature review (Table 1). We predicted that fisher and marten would be more abundant in forests with complex internal structure, regardless of the canopy dominance. We predicted that fisher would use more open stands and agricultural fields than marten. We predicted that rainfall on snow would promote fisher movement and survival but reduce marten survival.

STUDY AREA

The province of Quebec is divided into 96 fur-bearing animal management units (FAMUs; Fig. 1). Our analysis included 71 FAMUs, ranging in size from 169 km^2 to 23,820 km^2, representing 346,750 km^2 from 1984 to 2015. We excluded territories above 51° N, which have not been extensively exploited for fur, and Anticosti Island, where fishers and martens are absent. We also had to remove FAMUs corresponding to beaver (*Castor canadensis*) reserves where furbearer exploitation is exclusive to Indigenous people and where data on the number of annual trappers are not recorded.

Tree species included maple (*Acer* spp.), birch (*Betula* spp.), poplar (*Populus* spp.), balsam fir (*Abies balsamea*), pine (*Pinus* spp.), and spruce (*Picea* spp.). We divided FAMUs into 3 zones that differed in logging intensity. First, the southernmost zone included areas in the sugar maple (*Acer saccharum*)–bitternut hickory (*Carya cordiformis*) and sugar maple–basswood (*Tilia americana*) bioclimatic domains (hardwood forests, 11 FAMUs). These forests were mostly on private land and had been relatively untouched by timber exploitation compared to those in the other zones. Second, the intermediate zone included areas in the sugar maple–yellow birch (*Betula alleghaniensis*) and balsam fir–yellow birch domains (mostly mixed forests, 35 FAMUs), which have been mainly managed through partial cuts. Third, the northernmost zone included areas in the balsam fir–paper birch (*Betula papyrifera*) and black spruce (*Picea mariana*)–feather moss domains (mostly coniferous forests, 25 FAMUs), mainly managed with clearcuts.

Land use in the study area consisted mainly of forest harvesting and agriculture, and to a lesser degree, urban development. The study area was flat (mostly within 500 m above sea level) except for a few mountainous areas with the highest peak reaching 1,181 m above sea level. The study area had a cold and wet continental climate. On average, temperature remained near or below the freezing point from November to March, but typically exceeded 10° C from June to September (climate normals 1981–2010, Gouvernement du Québec 2019). Annual precipitation averaged 1,000 mm, of which about 75% fell as rain. Average monthly precipitation was >55 mm. The annual snowfall averaged 275 cm. Snowfall started as early as October, but snow did not significantly accumulate on the ground until November. Snowfall usually ended in April, occasionally in May.

In Québec, fisher and marten can hunt American red squirrel (*Tamiasciurus hudsonicus*), northern flying squirrel (*Glaucomys sabrinus*), striped chipmunk (*Tamias striatus*), snowshoe hare, and gallinaceous birds, including ruffed grouse (*Bonasa umbellus*) and spruce grouse (*Falcipennis canadensis*), especially in winter. Other dietary components include carcasses of white-tailed deer (*Odocoileus virginianus*), North American moose (*Alces americanus*), and North American beaver. Fisher can hunt larger-sized preys such as muskrat (*Ondatra zibethicus*), woodchuck (*Marmota monax*), striped skunk (*Mephitis mephitis*), and North American porcupine (*Erethizon dorsatum*). Fisher and marten can also eat wild fruit such as red raspberries (*Rubus idaeus*) and nuts such as beaked hazelnut (*Corylus cornuta*). The main predators of marten and fisher are raptors, mostly owls (e.g., great horned owl [*Bubo virginianus*]), eagles (bald eagle [*Haliaeetus leucocephalus*], golden eagle [*Aquila chrysaetos*]), falcons, hawks, and terrestrial large predators, mostly grey wolf (*Canis lupus*), coyote (*Canis latrans*), red fox (*Vulpes vulpes*), and Canada lynx (*Lynx canadensis*). Bobcat (*Lynx rufus*) and cougar (*Puma concolor*) are rare or absent in Québec.

METHODS

Pelt Sales Data

The Quebec Ministry of Forests, Wildlife and Parks (MFFP; Ministère des Forêts, de la Faune et des Parcs) recorded the number of pelts sold in each of the FAMUs since the 1984–1985 trapping season (Oct–Mar). Trappers capture martens and fishers using the same devices (i.e., body gripping traps set on a live tree or on a pole; Gouvernement du Québec, and Fédération des trappeurs gestionnaires du Québec 2019). The length of the trapping season remained constant over the study (i.e., Oct–Mar). To account for variation in area among FAMUs, we calculated pelt yield (number of pelts sold/100 km^2)/FAMU/year. Part of the harvest is not traded as raw pelts and can be tanned and processed for crafts. Despite some limitations, we consider that pelt sales data are a reasonable index of harvest that can be used to assess temporal changes in populations of low-density species such as mustelids (Gese 2001, Kawaguchi et al. 2015).

All pelt sales in Quebec are supposed to be recorded in a provincial register, including trapping season, FAMU, and trapper certificate number. Interviews with trappers, however, revealed that only part of the harvest is recorded (Suffice et al. 2017). As a result, we treated the number of pelts sold adjusted for trapping effort as an index of population size. We used 2 variables to account for potential variations in trapping effort: the number of trappers that sold ≥1 marten or 1 fisher pelt in a given FAMU in a given year, and the average auction price of a marten pelt in the previous year.

Habitat and Climate Data

Between 1984 and 2015, the forests of Quebec were subjected to 3 governmental decadal inventories during 1979–1990 (Ministère de l'Énergie et des Ressources du Québec 1984), 1990–2002 (Létourneau et al. 2009), and 2002–2018 (Lemieux et al. 2015). The governmental forest mapping is produced at the stand scale by interpretation of aerial photographs. These inventories make it possible to follow major trends in forest structure and composition. We used maps from the SIFORT (Système d'Information Forestière par Tesselle) database (Pelletier et al. 2007), composed of 14-ha polygons that are each assigned the stand characteristics of the eco-forest map polygon found at its center. It takes approximately 10 years to inventory the entire forest territory of Quebec. Thus, all FAMUs are not inventoried the same year. We matched pelt sales data from each trapping season (1984–2015) in each FAMU with the trends in forest structure and composition that were nearest in time and that covered the largest area of each FAMU.

For each FAMU, we calculated the area that was covered by forest and by agriculture as a percentage of area. We grouped forest stands into 6 major forest cover types by combining 2 criteria considered important for mustelids: structure as described from height classes (4–12 m, >12 m) and tree species composition (deciduous, mixed, coniferous; Potvin et al. 2000, Purcell et al. 2012, Cheveau et al. 2013). We considered stands that were 4–12 m in height to be young forests. Stands taller than 12 m generally consist of mature and old-growth forests with large-diameter trees, together with moribund and dead trees (snags; downed dead wood), which provide diversity in structures used by fisher and marten. Yet presence of trees taller than 12 m does not necessarily mean that a stand should be considered mature. Relative contributions of young, mature and old forests in the >12 m height class depend on bioclimatic domain and on the dynamics of natural and anthropogenic disturbances. In the hardwood forest zone, very few intact old-growth forests remain (Angers et al. 2005), given that these areas have experienced anthropogenic disturbances such as conversion of forests to agricultural use (Jobin et al. 2003, Domon and Bouchard 2007) or urban development (Domon et al. 2000). Stands taller than 12 m are more likely to consist of relatively young forests that have only recently reached 12 m, or mature forests that have been disturbed by low-intensity logging or sugar maple syrup production in the past. The mixed forest zone marks the transition between temperate and boreal forests, where stands are mainly harvested by partial cuts. In the coniferous forest zone, prior to the recent deployment of commercial forestry, landscapes were dominated by forests >100 years old (Bergeron et al. 2006). Consequently, stands that are taller than 12 m in this zone are mainly mature and old growth.

We mapped changes in forest composition and the area of land under agriculture in each FAMU by computing the difference in area of a given cover type between the forest inventories of the 1980s and 2010s. We designated forest stands 4–12 m tall as being either dominated by deciduous (deciduous 4–12 m), mixedwood (mixedwood 4–12 m), or coniferous (coniferous 4–12 m) species. We gave similar designations to stands >12 m tall (deciduous >12 m, mixedwood >12 m, coniferous >12 m).

We summarized rainfall abundance to evaluate the potential for ice crust formation on the snow surface. We obtained daily meteorological data with BioSIM 11.4.6.0 (Régnière and St-Amant 2007, Régnière et al. 2017). The software interpolates regional temperature and precipitation data for a given location from nearby weather stations, adjusted for differences in elevation, latitude, and longitude using regional gradients. We extracted the data from BioSIM corresponding to the distance-weighted average of the 3 weather stations that were closest to the centroid of each FAMU. We then compiled the data to obtain the sum of rainfall (mm) and the number of days with rainfall for the trapping season (15 Nov–1 Mar); the winter preceding the trapping season (15 Nov–30 Apr), to test for the delayed effect (1-yr lag) of rain on adult survival and reproduction; and the period of cold spring rainfall during the first few weeks of life of young mustelids (15 Mar–30 May, before the trapping season; Macdonald and Newman 2002). We calculated cold spring rain based on the number of days when rainfall was greater than the third quartile of the distribution for daily rainfall data (>1.7 mm), and when the minimum temperature was less than the third quartile of the distribution for daily minimum temperature data (<2.2 °C). We used the same spring period for both species, considering that female fishers and martens give birth in late March or April (Powell et al. 2003). For descriptive purposes, we modeled temporal variation in climatic variables by linear regressions with year as an explanatory variable at the level of each FAMU. We then mapped the estimate of the regression slope of each FAMU to illustrate variations of the climatic variables across years.

Statistical Analyses

We applied a logarithmic transformation to homogenize the variance of fisher and marten yield data (number of pelts sold/100 km^2). We analyzed changes in yield/FAMU/year using linear mixed models in the nlme package of R 3.4.2 (Pinheiro et al. 2018). We included a random intercept and random year slope for each FAMU in the models. We included the 2 variables in each model to reflect variations in trapping effort: the number of trappers that traded ≥1 marten or fisher pelt in a given year and the average auction price of a marten pelt in the previous year. All models included a continuous first-order autocorrelation structure (CAR1; Pinheiro and Bates 2000) between consecutive observations from a given FAMU to account for the time series structure of the data. We formulated 7 candidate models based on hypotheses derived from interviews with local trappers and from a literature review (Table 1). These hypotheses involved the effects of rain on mustelid mobility and young survival, the importance of forest age and dominant cover type, and the effect of open areas. We added 9 models combining different uncorrelated variables ($|r| < 0.7$) in the analyses: stands 4–12 m and rain conditions (3 models), stands taller than 12 m and rain conditions (3 models), and agricultural fields and rain conditions (3 models), resulting in 16 candidate models. We standardized all numeric variables prior to analysis.

We conducted independent analyses for the 3 geographical zones under study. We estimated parameters by maximum likelihood. We used model selection based on the Akaike's Information Criterion for small samples (AIC_c) to identify the top models ($\Delta\text{AIC}_c < 4$) associated with our biological hypotheses (Table 1). We quantified the effect of variables appearing in the top models with multi-model inference using the shrinkage estimator (AICcmodavg package; Burnham and Anderson 2002, Mazerolle 2017). We model-averaged coefficients and predictions across all models.

RESULTS

During 1984–2015, annual fisher yield averaged 2.31 ± 2.38 (SD) individuals/100 km^2 in the hardwood forest zone, 1.64 ± 1.78 individuals/100 km^2 in the mixed forest zone, and 0.21 ± 0.35 individuals/100 km^2 in the coniferous forest zone (Fig. 2). During the same period, mean annual marten yield was 2.86 ± 5.24 individuals/100 km^2 in the hardwood forest zone, 7.97 ± 5.50 individuals/100 km^2 in the mixed forest zone, and 7.57 ± 5.37 individuals/100 km^2 in the coniferous forest zone.

Habitat and Rain Changes

Habitat proportions by FAMU were characteristic of each of the 3 zones (Fig. S1, available online in Supporting Information). The cover of agricultural fields changed very little within FAMUs ($\bar{x}$ average percent change between the first and the third forest governmental decadal inventories for FAMU area [range of percentage change] = -0.72 % [-5.41% – 1.27%]; Fig. S2, available online in Supporting Information). Similarly, there were few variations within FAMUs in terms of deciduous stand cover for each height class: 4–12 m =-0.98% (-9.42% – 5.34%) and >12 m =-0.95% (-10.13% – 5.57%; Fig. S3, available online in Supporting Information). In contrast, the area of mixedwood stands generally increased for both height classes: 3.08% for 4–12 m (-10.41% – 36.19%) and 3.18% for >12 m (-10.58% – 11.84%). The area of coniferous stands >12 m mainly decreased (-1.44% [-14.19% – 13.92%]), whereas those in the 4–12-m height class remained relatively stable (0.66% [-9.57% – 10.75%]), although there were increases in the northernmost FAMUs. Changes in forest composition and area under agriculture varied across FAMUs, especially in the coniferous forest zone where mean forest age decreased. The proportion of mature forest was higher in the hardwood forest zone. Stand area in the 4–12-m height class declined (Fig. S3), whereas the area of stands >12 m increased (Fig. S4, available online in Supporting Information).

Number of days with rain and amount of rain that fell during the 3 periods showed inter-annual variations of different amplitudes among zones (Figs. S5, S6, available online in Supporting Information). Variation of rain conditions between 1984 and 2015 also varied among FAMUs (Figs. S7, S8, available online in Supporting Information). Over the study period, the number of days with rain during winter increased in the northern and western parts of the study area, whereas it decreased in the southeast. Rainfall increased in most areas, suggesting an increase in days with heavy rains. The number of days with cold rain (>1.7 mm; min. temp <2.2° C) increased only in a few areas.

Fisher Yield

Models that included rainfall during the previous winter or cold rain during the previous spring had the most support ($0.46 <$ Akaike weight [ω_i] < 0.62) for all 3 zones (Appendix A). Models that combined the availability of stands >12 m, with rain during the previous winter ($\omega_i = 0.62$), cold rain during the previous spring ($\omega_i = 0.24$), or rain during the trapping season ($\omega_i = 0.09$) were the most parsimonious for the hardwood forest zone. For the mixed forest zone, the model with only cold rain during the previous spring had twice the weight of the model including cold rain during the previous spring and the cover of agricultural fields ($\omega_i = 0.46$ vs. $\omega_i = 0.24$), and 4 times the weight of models including the availability of stands 4–12 m ($\omega_i = 0.11$) or >12 m ($\omega_i = 0.09$). The model that combined the availability of stands >12 m, with cold rain during the previous spring had 84% of the weight for the coniferous forest zone ($\omega_i = 0.84$). All other models had much less support ($\Delta AIC_c > 4$).

Annual fisher yield increased over time in all 3 zones but more so in the mixed forest zone (Table 2; Fig. 3). Annual fisher yield in all 3 zones increased with the number of trappers having sold ≥1 marten or fisher pelt, but the effect was stronger in the hardwood forest zone. Annual fisher yield in all 3 zones decreased with the average selling price of a marten pelt at the auction from the previous year, but the effect was weak. Annual fisher yield in the hardwood and coniferous forest zones increased with the area covered by mixedwood stands >12 m (Fig. 4), but there was no similar relationship in the mixed forest zone. Fisher yield in the hardwood and coniferous forest zones decreased despite increases in the area covered by deciduous stands >12 m. Within mixed and coniferous zones, fisher yield decreased with increases in the number of cold days with rain during the spring preceding the trapping season, but these relationships were weak (Table 2).

Marten Yield

In the hardwood forest zone, the null model had the greatest weight to explain variation in marten yield (Appendix B; $\omega_i = 0.25$). Models that included cold rain during the spring preceding the trapping season ($\omega_i = 0.19$), the availability of stands 4–12 m ($\omega_i = 0.16$), or both ($\omega_i = 0.10$) shared the majority of the rest of the weight. Models that included the availability of stands >12 m ($\omega_i = 0.05$), the amount of agricultural fields ($\omega_i = 0.04$), or rain during the previous winter ($\omega_i = 0.04$) had weak support. In the mixed forest zone, the model consisting of the amount of agricultural fields and rain during the previous winter had the entire support ($\omega_i = 1$). In the coniferous forest zone, the top-ranked model included the availability of stands 4–12 m and rain during the trapping season (Appendix B). This model had 3 times the weight of the second-ranked model (0.57 vs. 0.13), which consisted of the rain during the trapping season. A third model consisting of the amount of agricultural fields and rain during the trapping season had 12% of the support. Marten yield decreased over time in the hardwood forest and mixed forest zones (Table 3), yet no such relationship was in the coniferous forest zone. Annual marten yield in all 3 zones increased with the number of trappers having sold ≥1 marten or fisher pelt, but the effect was stronger in the mixed and coniferous forest zones (Table 3).

Annual marten yield in the mixed and coniferous zones decreased with the average selling price of a marten pelt at the auction from the preceding year (Table 3). The price of a marten pelt had a greater effect on annual marten yield than on annual fisher yield, but the effect was weak in both cases. No habitat variable (forest cover or agricultural cover) explained changes in marten yield in the hardwood forest and coniferous forest zones. In the mixed forest zone, marten yields decreased with increasing cover of agricultural fields (Fig. 5). Marten yield decreased with the number of days with rain and the amount of rainfall in the winter preceding the trapping season in the mixed forest zone (Fig. 6). In the coniferous forest zone, marten yield increased with the amount of rainfall during the trapping season (Fig. 7).

DISCUSSION

Habitat Changes

Fisher.—Fisher yield increased in all 3 zones, but more strongly in the hardwood forest and mixed forest zones. Although still low, fisher yield increased in the coniferous forest zone, where the species is at the northern edge of its range and densities are inherently low. The abundance of mixedwood stands >12 m increased fisher yields in both hardwood and coniferous forest zones. Deciduous stands >12 m were not a good indicator of fisher populations at the landscape scale. According to other studies, the coniferous component of stands appears to be particularly important for fishers in Quebec (Proulx 2006, Sauder and Rachlow 2014, Fuller et al. 2016). Kelly (1977) determined that fishers avoid forest stands that are composed of ≥74% deciduous trees. Deciduous-dominated stands probably do not provide fishers with optimal conditions for winter movement. Because of their crown form, boreal softwood species provide cover that protects fishers by intercepting precipitation, including snow. In winter, fishers preferentially use dense stands with a large conifer component (mixed or dominant), given lower accumulations of snow on the ground, thereby facilitating movements (Raine 1983, Hopkinson et al. 2004). Within a forest matrix dominated by deciduous tree species, the coniferous component becomes particularly attractive for fisher movement. In the mixed forest zone, no habitat variable could explain increases in fisher yields, yet the habitat appears to remain adequate for the needs of fisher populations.

In the coniferous forest zone, the increase in fisher yield was associated with mixedwood stands >12 m, which have increased in proportion over the past 30 years. On the one hand, a mixed species composition provides the best compromise for fisher in terms of structures that can intercept snow while providing a variety of prey (Powell et al. 2003). On the other hand, in the coniferous forest zone, the amount of deciduous stands >12 m reduces fisher yields. These forest stands have little or no structure to intercept snow. Logging intensity in the coniferous forest zone favored early successional species, such as trembling aspen (*Populus tremuloides*), at the expense of conifers that dominated the canopy in pre-industrial times (Boucher et al. 2014, Grondin et al. 2018).

Modifications of the cover type and their associations with fisher captures support the hypotheses based on trapper knowledge (Table 1). Indeed, trappers have reported that fishers in Quebec use forests where the deciduous component has increased (Suffice et al. 2017). Fishers especially use forests with complex structures, both vertically (several layers of vegetation) and horizontally (downed woody debris; Powell and Zielinski 1994). The deciduous component provides fishers with a diversity of structure and an abundance of prey species (Poulin et al. 2006). Studies in eastern Maine and Connecticut, USA, reported that fishers live in mixedwood and deciduous stands (Arthur et al. 1989, Kilpatrick and Rego 1994). Trappers in our study area shared their concerns about the availability of large hollow trees in which the fisher could find refuge and raise their young (Suffice et al. 2017). Indeed, fishers typically use resting sites in large living trees with cavities or broken tops, or in large dead trees (Gess et al. 2013, Green 2017). The size of the trees that can be used as resting sites varies according to bioclimatic zone and tree species available (Weir and Almuedo 2010, Aubry et al. 2013). In the eastern portion of its range, fishers mainly use deciduous trees with an average diameter at breast height >50 cm (Erb et al. 2013, Gess et al. 2013). In northern Quebec, trees >30 cm in diameter are rare (Vaillancourt et al. 2008), yet fisher populations have increased in the coniferous forest zone (spruce-moss bioclimatic domain). As in other regions, fishers in Quebec may use ground-level dens more than large-diameter trees (Kilpatrick and Rego 1994, Gess et al. 2013, Green 2017).

In interviews conducted by Suffice et al. (2017), trappers noted that they were capturing greater numbers of fishers at farmland edges and that the animals could use relatively open landscapes. Our analyses could not confirm these observations by trappers made at a finer spatial scale. The quantity of agricultural fields in Quebec varied little between 1984 and 2015. Furthermore, the amount of land under agriculture likely does not reflect the quantity of edge between agricultural fields and forest stands used by fishers (Bridger et al. 2017).

Marten.—No habitat variable explained the decrease in marten yields in the hardwood forest and mixed forest zones, where stands have increased both in area and height. We found no change in marten yield over time in the coniferous forest zone. In addition, changes in forest cover across Quebec did not influence marten populations, yet martens have been reported to occupy mature forest stands with dense cover and complex structure (Buskirk and Ruggiero 1994, Bissonette et al. 1997, Chapin et al. 1998, Potvin et al. 2000, Fuller et al. 2005). Indeed, Cheveau et al. (2013) reported that in a predominantly coniferous (spruce) landscape, mixedwood stands were selected at home range and landscape scales. Trappers mentioned that they often capture marten in deciduous stands (Suffice et al. 2017). In conifer-dominated landscapes, martens seek out a diversity of habitat attributes to find food and protection. The quantity of coniferous stands, however, does not explain marten yields in Quebec, maybe because simply defining stands according to their height class does not reflect their structural complexity (McCann et al. 2014). Further, by analyzing interactions at such a broad spatial scale, habitat loss observed by trappers at the trapline scale and its effect on local marten populations were likely underestimated.

Changes in Rain Conditions

The variables describing rain conditions contributed to the most supported models in all 3 zones, but only the amount of cold rain during the previous spring influenced fisher yield in the mixed and coniferous forest zones. Although fisher yield decreased with increasing amount of cold rain during the previous spring, fisher yield increased in both zones. As expected, in the mixed forest zone, marten yields decreased with increasing amounts of rainfall and number of days with rainfall in the winter preceding the trapping season. The amount of rainfall during the trapping season increased marten yields only in the coniferous forest zone. Rain increases snow density and promotes ice crust formation on the snow surface that could limit access to subnivean areas used for cover and to access food (Callaghan and Johansson 2015, Williams et al. 2015, Domine et al. 2018). Cold rain could also exert direct effects on marten thermoregulation (Taylor and Buskirk 1994). Martens have few fat reserves, which makes them potentially vulnerable to the cold when their fur is wet (Buskirk and Harlow 1989). Increased rainfall could incur greater natural winter mortality in adult martens. By limiting marten access to subnivean space, rain-induced snow-crusting can cause marten to move more in search of food resources. Increasing rainfall during the trapping season facilitates traveling by snowshoe or snowmobile, and potentially increases the efficiency of trappers. Moreover, rain can increase marten vulnerability to trapping. High marten yields during a rainy trapping season can lead to a lower harvest in the following year. Phenomena that are observed at the local scale by Quebec trappers are difficult to capture at the provincial scale. In addition, our study used data over 30 years, which represents a relatively short time scale compared to longer-term climate change. The use of average weather conditions over large areas (FAMUs) and annual time steps was also unlikely to portray spatial and temporal variation that would better represent freeze-thaw events affecting animal survival.

Weather conditions favoring increased snow load-bearing capacity could also have indirect effects on marten and fisher populations by influencing interspecific competition. Karniski (2014) observed responses along these lines in the Adirondack Mountains, northeastern United States. More compact snow favors movement of coyote and red fox, which are 2 potential competitors or predators of martens and fishers (Pozzanghera et al. 2016, Suffice et al. 2017). Thus, snow compaction could have an indirect negative effect on marten and fisher by increasing competition with other mesocarnivores, which would also mitigate the positive effect of snow compaction on fisher movement.

Cumulative Effects and Relative Importance of Habitat and Climate Change

In this study, changes in forest cover exerted stronger effects on fisher than did rainfall conditions. Too much emphasis is sometimes placed on climate change in biodiversity scenarios, when other variables that arise from human activities may have similar or even greater effects at shorter time scales (Titeux et al. 2016). Modifications of wildlife habitats through land use conversion and exploitation of natural resources are considered to be among the most important and immediate threats to biodiversity (Newbold et al. 2015). Climate change and human activities exert cumulative effects on plant and animal species compositions, the changes of which can affect the distribution of fisher and marten (Carroll 2007, Lawler et al. 2012, Lavoie et al. 2019). The greatest change in the forest landscapes of North America is the migration or even reduction of conifer-dominated stands, which are replaced by mixedwood or deciduous stands (Lawler et al. 2012, Purcell et al. 2012, Zielinski et al. 2012). An increased risk of windthrow is also expected to occur in eastern Canada, mainly through an increased period during which the ground is unfrozen (Saad et al. 2017). These changes could favor the creation of micro-habitats for small mammals and create new structures that could be exploited in the subnivean environment.

In addition to logging, climate change that affects forest fire regimes is expected to result in the loss of late-successional vegetation, which may increase the probability of extirpation of associated species, such as fisher and marten (Bergeron et al. 2010, Lawler et al. 2012, Purcell et al. 2012). Changes in winter conditions should facilitate the movement of fishers and other mesocarnivores, and may change the partitioning of niches based upon snow characteristics (Whiteman and Buskirk 2013, Manlick et al. 2017). Indeed, many medium-sized predators have already expanded their ranges, which can affect food webs and trophic controls (Prugh et al. 2009, Pokallus and Pauli 2015). Species conservation and habitat management in response to climate change pose the challenge of balancing the need to maintain current habitat and anticipate future changes in habitat and species distributions. Climate change scenarios predict conditions that favor fishers, but data that have been obtained by Zielinski et al. (2017) suggest that martens may be able to shift their niche to include warmer, less snowy areas. Conservation of interacting species at the boundaries of their ranges requires managers to be aware of interspecies tolerance, how each would uniquely respond to future climates, and how potential climate refuges could be integrated into existing habitat (Morelli et al. 2016, Zielinski et al. 2017).

Inter-Specific Relations: The Missing Link?

Abundance of prey, competitors, and predators have been identified by trappers as major factors that may explain changes in fisher and marten abundance (Suffice et al. 2017). Behavioral changes caused by interspecific competition and by intraguild predation or interspecific killing can have repercussions on the distribution of individuals, even species (King and Moors 1979, Tannerfeldt et al. 2002, Eriksson et al. 2019).

Unfortunately, prey, competitor, and predator abundance variables were unavailable at the scale of our study. Variation in marten catches could be more closely related to fluctuations in food supply (Cheveau et al. 2004, Jensen et al. 2012, Fauteux et al. 2015) than to habitat quality or climatic variation, although this remains to be demonstrated. Environmental changes in recent decades have contributed to changes in the distribution of fishers but also of other marten competitors. An assessment of the co-occurrence of mesocarnivores, as was conducted by Gompper et al. (2016), would make it possible to better consider the role of biotic factors in population dynamics.

Manlick et al. (2017) suggested that landscape homogenization leads to niche compression and that marten populations would be limited through increased competition with fishers. Dietary overlap between marten and fisher likely intensifies interspecific competition through interference, as previously demonstrated in Wisconsin, USA (Manlick et al. 2017). Dietary overlap is also a major predictor of intraguild predation (Donadio and Buskirk 2006), as observed by McCann et al. (2010) in Wisconsin, where fishers were the most common cause of winter mortality in marten. An inverse relationship between marten and fisher occurrence has already been observed in several sympatric populations, where coexistence has been attributed to mechanisms that reduce competition for shared resources, such as spatiotemporal segregation, differential habitat selection, and contrasting use of snow cover (Krohn et al. 1997, Fisher et al. 2013). In our analyses, marten yields declined in the hardwood and mixed forest zones, where fisher yields had increased the most. In the coniferous forest zone, where increases in fisher yield were low, marten yield has yet to decrease. These results suggest that habitat use by fisher and marten in Quebec may be influenced especially by interspecific relationships, but this remains speculative. Thus, the co-occurrence characteristics of the 2 species need to be studied at a finer spatial scale.

MANAGEMENT IMPLICATIONS

Pelt sales data can contribute to documentation of trends in furbearing populations over the long-term and over large spatial scales (e.g., provincial or state forest zones). Closer partnerships between government and wildlife users could also improve the efficiency of population monitoring for species that are difficult to sample. In our case, involving trappers in such a process contributed to the construction of testable hypotheses on species ecology that can inform species management. To improve the quality of the information provided by trappers in future research, we suggest they should be invited by wildlife state and provincial agencies to share information on trapping effort and capture location. In addition, trappers could supply carcasses to researchers to help monitor long-term fisher and marten physical condition and reproductive success according to changing winter climate conditions.

The negative effect of winter rain on fisher and marten populations highlights the need for protective cover to cope with climate change, particularly in an industrial forest landscape. Although coniferous trees intercept rainfall and snowfall, old hardwood trees can provide natural cavities for thermoregulation. Thus, managers should strive to promote and maintain mixedwood stands taller than 12 m to maintain protective cover and high-quality habitat for fishers.

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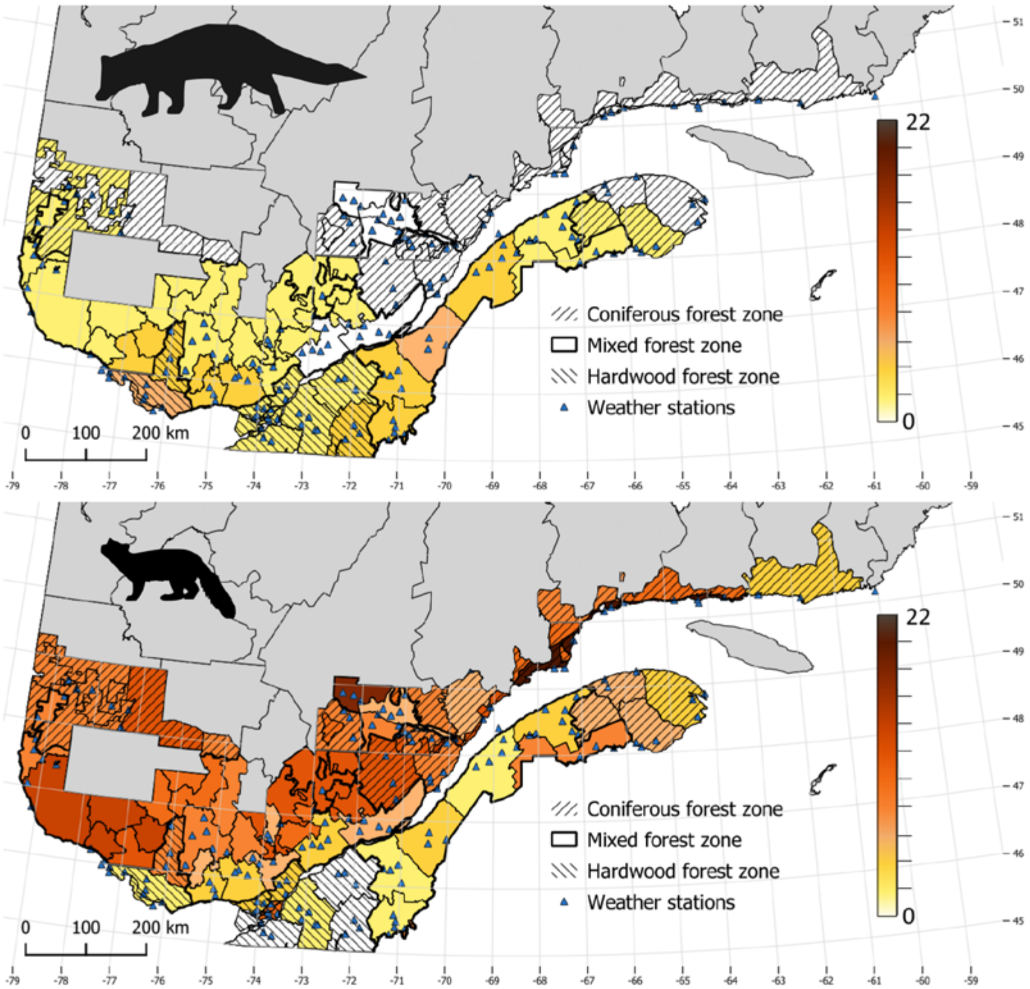
Figure Captions

Figure 1. Average yields (number of pelts sold/100 km^2) per year for fisher (top) and marten (bottom) according to fur-bearing animal management unit (FAMU) in Quebec, Canada, between the 1984–1985 and 2014–2015 trapping seasons. Hatched areas represent the 3 zones separated according to forest logging intensity, from the least intensive in the south to the most intensive in the north. The map was constructed with the program Nødebo in QGIS 2.160 (https://www.qgis.org/en/site/, accessed 21 Jul 2019), using North American Datum of 1983 (NAD 83)-Quebec Lambert projection (European Petroleum Survey Group: 32198).


22
0
Coniferous forest zone
Mixed forest zone
Hardwood forest zone
Weather stations
0
100
200 km
-79
-78
-77
-76
-75
-74
-73
-72
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-70
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Figure 2. Annual variation in fisher (left) and marten (right) yields according to fur-bearing animal management unit (FAMU) in Quebec, Canada, 1984–2015, for the coniferous (top), mixed (center), and hardwood (bottom) forest zones. Boxes represent the first and third quartiles (interquartile distance), and the horizontal line within the box is the median. Lower and upper whiskers represent scores outside the middle 50%. Open circles are outliers beyond 1.5 times the interquartile distance.

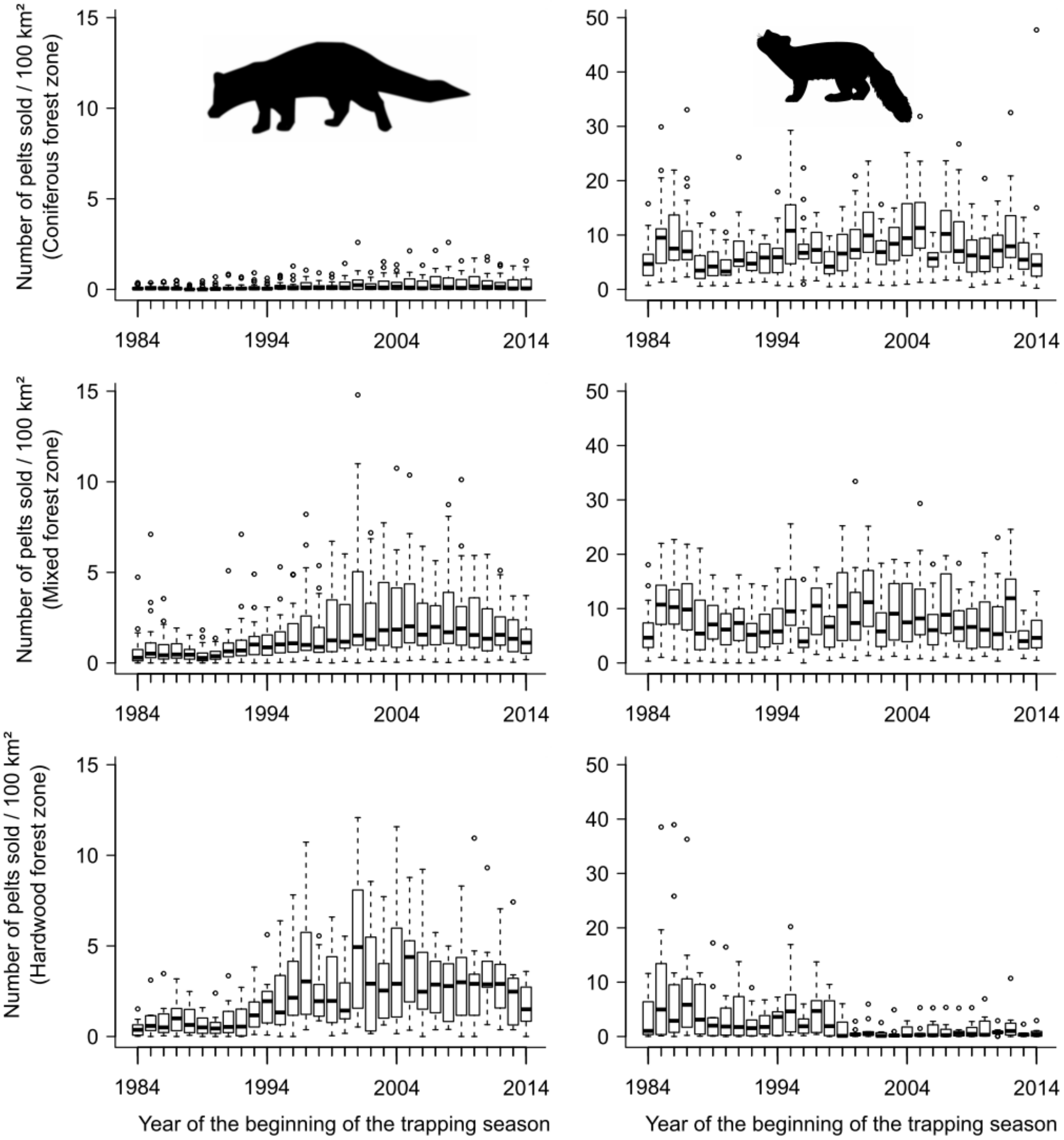

Figure 3. Effect of year on fisher (left) and marten yields (right) predicted from multi-model inference for each forest zone (hardwood, mixed, coniferous) of Quebec, Canada, 1984–2015. Black lines denote estimates; dotted lines represent unconditional 95% confidence intervals. Note that axes are not at the same scale but reflect differences in yield between forest zones for the 2 species.

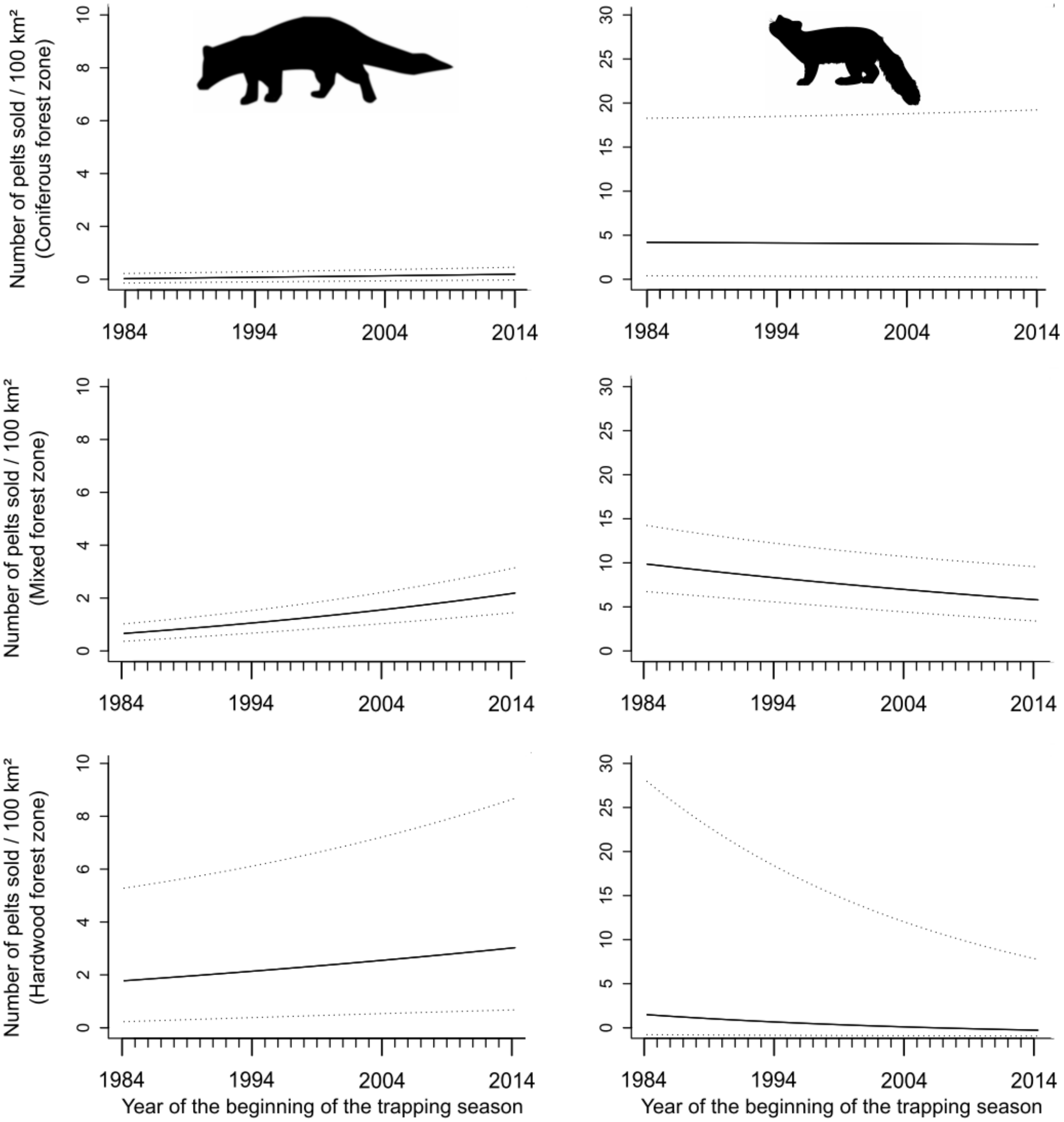

Figure 4. Predicted fisher yield as a function of the fur-bearing animal management unit percentage of deciduous (top) and mixedwood (bottom) stands >12 m in the hardwood forest zone (HFZ, left) and the coniferous forest zone (CFZ, right) of Quebec, Canada, 1984–2015. Black lines are estimates; dotted lines represent unconditional 95% confidence intervals.

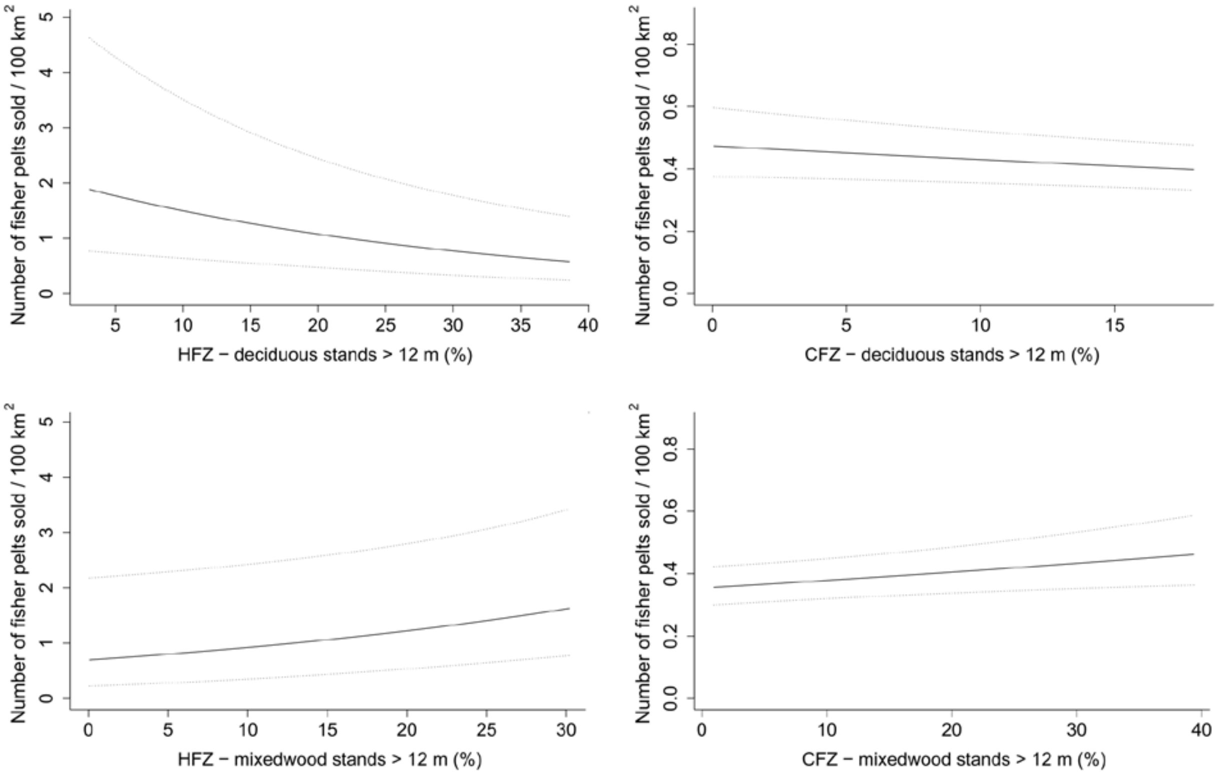

Figure 5. Predicted marten yield as a function of the percentage of agricultural fields in fur-bearing animal management units of the mixed forest zone (MFZ) of Quebec, Canada, 1984–2015. The black line is the estimate; dotted lines represent unconditional 95% confidence intervals.

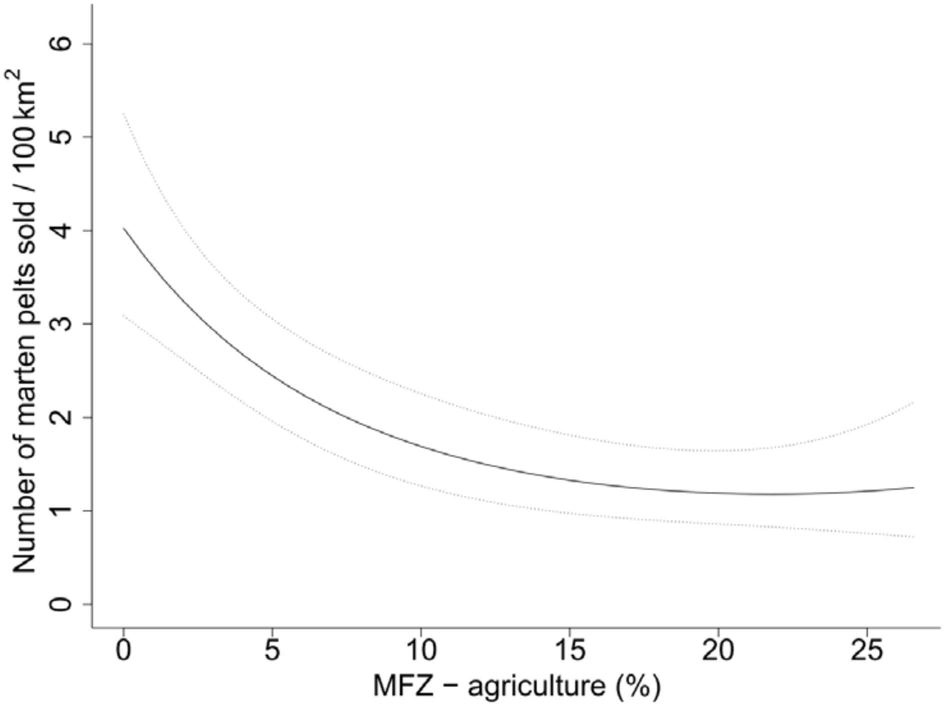

Figure 6. Predicted marten yield as a function of the number of days with rain (top) and amount of rain (bottom) that fell in the winter preceding the trapping season in the mixed forest zone (MFZ) of Quebec, Canada, 1984–2015. The black line is the estimate; dotted lines represent unconditional 95% confidence intervals.

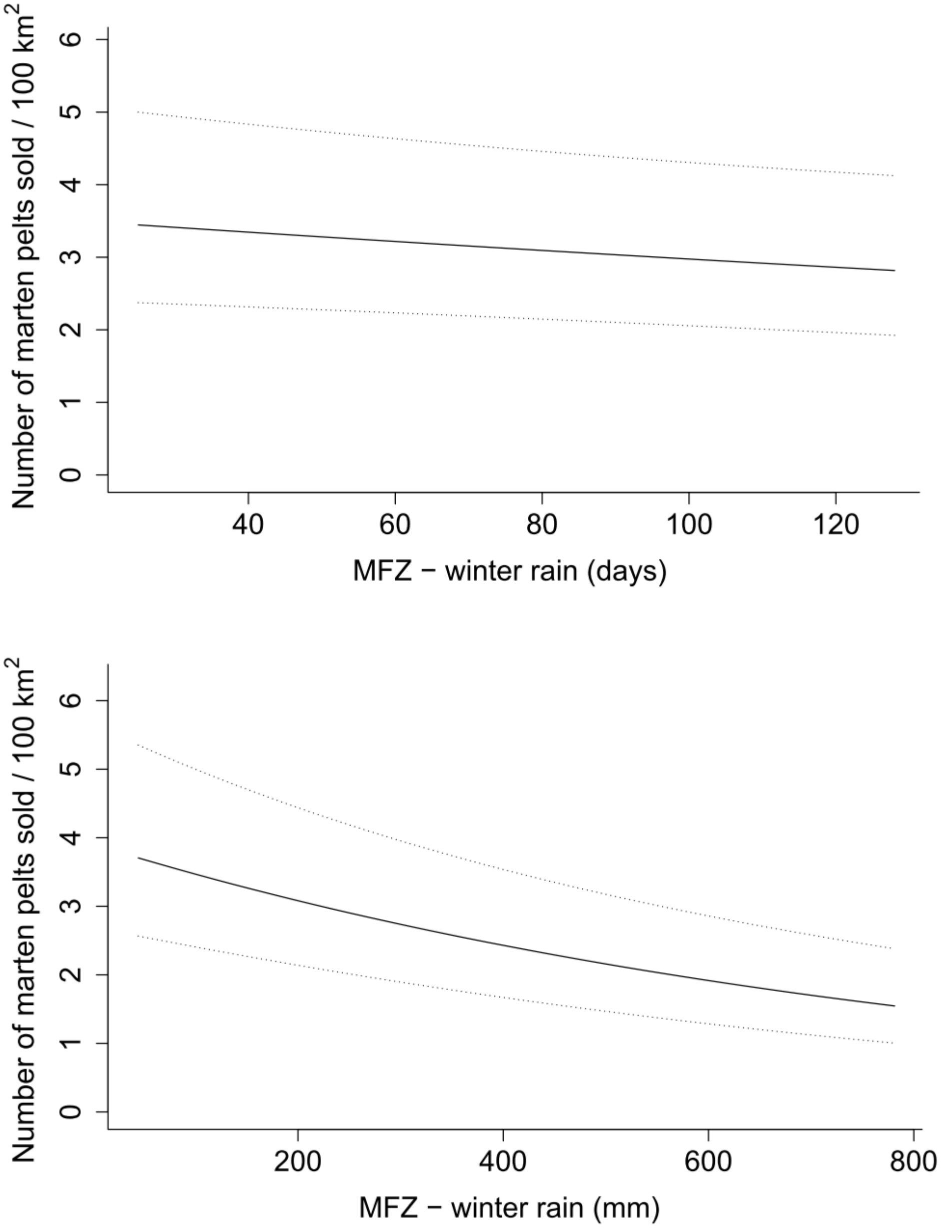

Figure 7. Predicted marten yield as a function of the amount of rain that fell during the trapping season in the coniferous forest zone (CFZ) of Quebec, Canada, 1984–2015. The black line is the estimate; dotted lines represent unconditional 95% confidence intervals.

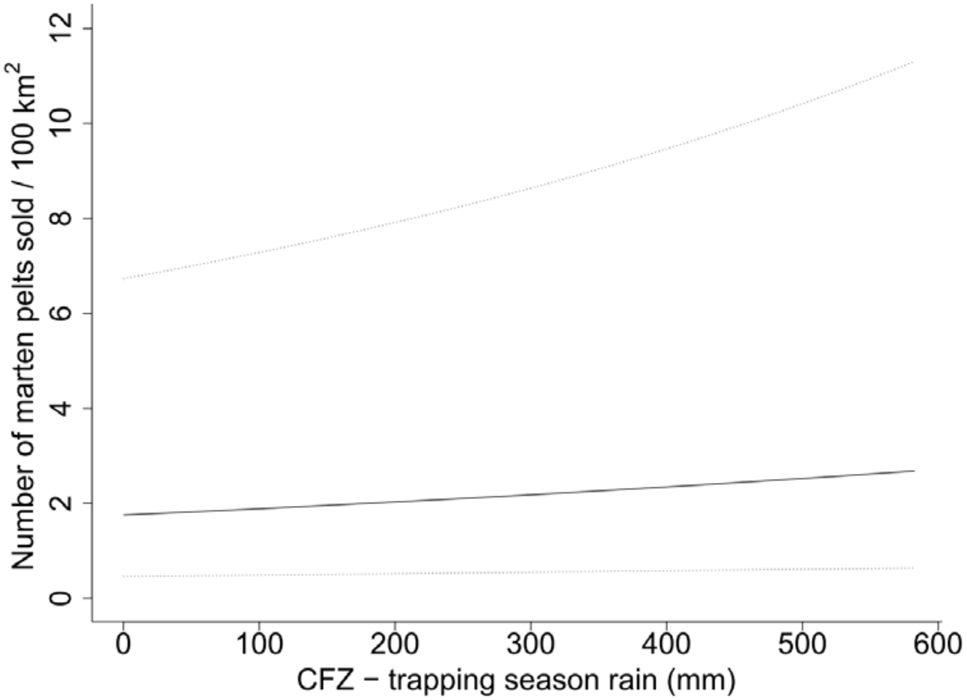

Table 1. Hypotheses tested using linear mixed models to analyze variation in fisher and marten yields per fur-bearing animal management unit (FAMU) per year in Quebec, Canada, 1984–2015. We derived hypotheses from interviews with local trappers (Suffice et al. 2017).

Hypothesis	Model	Explanatory variables	Predicted fisher response	Predicted marten response
Trappers capture more fishers but fewer martens over time (Poulin et al. 2006, Suffice et al. 2017). Number of captures increases with trapping effort and pelt price from previous year.	Null	Year + (year | FAMU)	+	−
		+ number of trappers	+	+
		+ marten pelt price from previous year	+	+
Fishers can use younger and more open forests than the old stands described in the literature (Suffice et al. 2017). Lack of important predators (such as cougar or bobcat) in the northern part of its range in Quebec could explain the use of open areas by fisher (Wengert et al. 2014). Martens depend on a dense canopy offering protection against predation and inclement weather. Forests with trees <12 m in height do not have these characteristics.	Stands 4–12 m cover	Deciduous 4–12 m cover	+	−
		+ mixedwood 4–12 m cover	+	−
		+ coniferous 4–12 m cover	+	−
		+ null model		
Fishers need large trees used as refuge and to raise young; such trees are found in older forests, which can also provide protective cover by intercepting snow (Aubry et al. 2013). The structural complexity of older forests increases the availability of prey dependent on dead wood (small mammals; Fauteux et al. 2012) and a dense cover	Stands >12 m cover	Deciduous >12 m cover	+	+
		+ mixedwood >12 m cover	+	+
		+ coniferous >12 m cover	+	+
		+ null model		

(snowshoe hare; Fuller and Harrison 2013). Old coniferous stands are more amenable to a complex internal structure and a dense canopy on which marten depends (Cheveau et al. 2013). However, martens also use hardwood stands, as long as they are old and dense (Suffice et al. 2017).				
In the absence of important predators, fishers can use more open areas such as agricultural fields (Suffice et al. 2017). The ecotone between forest and agricultural fields may offer a greater diversity of prey for fisher. However, more agricultural fields also means less forest on which fishers depend. Agricultural fields are open areas where marten could be more vulnerable to predation.	Agriculture cover	Agriculture cover + (agriculture cover) ^{2} + null model	+	−
Fisher movements are limited in areas where snow is abundant. Crust increases snow lift and therefore the probability that a fisher can use a territory. More crust during the previous winter would favor fisher movements, survival and reproductive success. Marten use subnival environments to hunt and as protection against winter weather (Taylor and Buskirk 1994). Crust on the snowpack compromises subnival access (Berteaux et al. 2017).	Rain during previous winter	Number of rain days during previous winter + rain amount during previous winter + null model	+ +	− −
Cold spring rainfall during the first few weeks of life of young mustelids can affect survival potential, and thus recruitment and number of captures by trappers the following year.	Cold rain during previous spring	Number of rain days during previous spring + null model	−	−

Ice crust during the trapping season (15 Nov–1 Mar) may favor fisher movements and increase the likelihood of encountering a trap.	Rain during trapping season	Number of rain days during trapping season	+	+
		+ rain amount during trapping season	+	+
		+ null model		

Table 2. Model-averaged estimates of variables for which the 95% confidence interval excluded 0 (βi [lower confidence limit, upper confidence limit]) in models explaining fisher yield per year per fur-bearing animal management unit in Quebec, Canada, 1984–2015.

Variable	Predicted response	Hardwood forest zone	Mixed forest zone	Coniferous forest zone
Year	+	0.11 [0, 0.22]	0.19 [0.14, 0.24]	0.05 [0.01, 0.08]
Number of trappers in given year	+	0.76 [0.65, 0.87]	0.27 [0.23, 0.31]	0.05 [0.03, 0.07]
Pelt price of previous year	+	−0.05[−0.09, −0.01]	−0.04 [−0.06, −0.02]	−0.02 [−0.02, −0.01]
Deciduous 4–12 m cover	+			
Mixedwood 4–12 m cover	+			
Coniferous 4–12 m cover	+			
Deciduous >12 m cover	+	−0.38 [−0.60, −0.16]		−0.11 [−0.20, −0.02]
Mixedwood >12 m cover	+	0.31 [0.04, 0.56]		0.07 [0.01, 0.13]
Coniferous >12 m cover	+			
Quadratic effect of agriculture cover	+			
Number of rain days during previous winter	+			
Rain amount during previous winter	+			
Number of cold rain days during previous spring	−		−0.02 [−0.04, 0]	−0.01 [−0.02, 0]
Number of rain days during trapping season	+			
Rain amount during trapping season	+			

Table 3. Model-averaged estimates of variables for which the 95% confidence interval excluded 0 (βi [lower confidence limit, upper confidence limit]) in models explaining marten yield per year per fur-bearing animal management unit in Quebec, Canada, 1984–2015.

Variable	Prediction	Hardwood forest zone	Mixed forest zone	Coniferous forest zone
Year	−	−0.37 [−0.52, −0.21]	−0.14 [−0.22, −0.05]	
Number of trappers in given year	+	0.45 [0.27, 0.63]	0.65 [0.58, 0.71]	0.67 [0.60, 0.70]
Pelt price of previous year	+		−0.06 [−0.09, −0.03]	−0.05 [−0.08, −0.02]
Deciduous 4–12 m cover	−			
Mixedwood 4–12 m cover	−			
Coniferous 4–12 m cover	−			
Deciduous >12 m cover	+			
Mixedwood >12 m cover	+			
Coniferous >12 m cover	+			
Quadratic effect of agriculture cover	−		0.51 [0.02, 0.99]	
Number of rain days during previous winter	−		−0.03 [−0.06, 0]	
Rain amount during previous winter	−		−0.09 [−0.12, −0.06]	
Number of cold rain days during previous spring	−			
Number of rain days during trapping season	+			
Rain amount during trapping season	+			0.04 [0.01, 0.08]

Summary for online Table of Contents

In areas where fisher and marten habitats overlap in Quebec, Canada, fishers benefit from increased abundance of mixedwood forests taller than 12 m, whereas martens are negatively affected by increased rainfall in winter. Results of this study support hypotheses made by local trappers about fisher and marten habitat use. Managers should strive to maintain mixedwood stands taller than 12 m to maintain habitat for fishers.

APPENDIX A. FISHER MODEL SELECTION

Table A1. Selection based on the Akaike's Information Criterion for small samples (AIC_c) among linear mixed models explaining fisher yields in Quebec, Canada, 1984–2015. All models included a random intercept and a random slope of year for each fur-bearing animal management unit, a continuous first-order autocorrelation structure, and fixed effects for the number of trappers who sold ≥1 marten or fisher pelt and marten pelt price of the previous year. We present the number of model parameters (K), difference in AIC_c between the top-ranked model and other candidate models (ΔAIC_c), Akaike weight (ω_i), and log-likelihood (LL). Only models with $\Delta AIC_c < 4$ are presented.

Zone	Fisher model	K	AIC_c	ΔAIC_c	ω_i	LL
Hardwood forest	Stands >12 m cover + rain during previous winter	14	62.62	0.00	0.62	−16.59
	Stands >12 m cover + cold rain during previous spring	13	64.54	1.92	0.24	−18.64
	Stands >12 m cover + rain during trapping season	14	66.43	3.81	0.09	−18.49
Mixed forest	Cold rain during previous spring	10	−266.20	0.00	0.46	143.21
	Agriculture cover + cold rain during previous spring	12	−264.90	1.30	0.24	144.61
	Stands 4–12 m cover + cold rain during previous spring	13	−263.32	2.89	0.11	144.84
	Stands >12 m cover + cold rain during previous spring	13	−262.96	3.24	0.09	144.67
Coniferous forest	Stands >12 m cover + cold rain during previous spring	13	−1338.44	0.00	0.84	682.47

APPENDIX B. MARTEN MODEL SELECTION

Table B1. Selection based on the Akaike's Information Criterion for small samples (AIC$_c$) among linear mixed models explaining marten yields in Quebec, Canada, 1984–2015. All models included a random intercept and a random slope of year for each fur-bearing animal management unit, a continuous first-order autocorrelation structure, and fixed effects for the number of trappers who sold ≥1 marten or fisher pelt and marten pelt price of the previous year. We present the number of model parameters (K), difference in AIC$_c$ between the top-ranked model and other candidate models (ΔAIC$_c$), Akaike weight (ω_i), and log-likelihood (LL). Only models with $\Delta\text{AIC}_c < 4$ are presented.

Zone	Marten model	K	AIC$_c$	ΔAIC$_c$	ω_i	LL
Hardwood forest	Null	9	438.00	0.00	0.25	−209.69
	Cold rain during previous spring	10	438.50	0.50	0.19	−208.88
	Stands 4–12 m cover	12	438.93	0.94	0.16	−206.93
	Stands 4–12 m cover + cold rain during previous spring	13	439.78	1.78	0.10	−206.26
	Stands >12 m cover	12	441.23	3.23	0.05	−208.08
	Agriculture cover	11	441.61	3.61	0.04	−209.35
	Rain during previous winter	11	441.63	3.63	0.04	−209.36
Mixed forest	Agriculture cover + rain during previous winter	13	749.98	0.00	1	−361.81
Coniferous forest	Stands 4–12 m cover + rain during trapping season	14	588.61	0.00	0.57	−280.02
	Rain during trapping season	11	591.55	2.94	0.13	−284.60
	Agriculture cover + rain during trapping season	13	591.70	3.08	0.12	−282.60