

ARTICLE

Effects of forest disturbance, snow depth, and intraguild dynamics on American marten and fisher occupancy in Maine, USA

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Funding information

Maine Department of Inland Fisheries and Wildlife; University of Maine Cooperative Forestry Research Unit; USDA National Institute of Food and Agriculture, Grant/Award Number: #ME0-41913; Center for Undergraduate Research at the University of Maine; Honors College Charlie Slavin Research Fund

Handling Editor: Elizabeth A. Flaherty

Abstract

Human land use is a driving force of habitat loss and modification globally, with consequences for wildlife species. The American marten (*Martes americana*) and fisher (*Pekania pennanti*) are forest-dependent carnivores native to North America. Both species suffered population declines due to loss of forested habitat and overharvest for furs, and continued habitat modification is an ongoing threat. Furthermore, the smaller marten may be susceptible to intraguild exclusion where the larger fisher are abundant, and both habitat modification and climate change may reduce spatial refugia available to marten. A detailed understanding of co-occurrence patterns of marten and fisher in landscapes subjected to intense forest disturbance represents a key knowledge gap for wildlife ecology and management. Maine, in the northeastern United States, supports populations of both these species. It is an extensively forested state, and the vast majority is managed as commercial timberland. We designed a large-scale field study to understand the relative importance of three sets of predictions for marten and fisher occupancy patterns where commercial silviculture is widespread: (1) The intensity of forest disturbance primarily determined both marten and fisher occupancy rates, (2) fisher occupancy was limited to areas of shallower snow and marten limited by fisher presence, or (3) both species responded to the composition of tree species within forested habitat. We collected data to test these nonmutually exclusive hypotheses via camera-trap surveys, using an experimental design balanced across a gradient of forest disturbance intensity. We deployed 197 camera stations in both summer and winter over 3 years (2017–2020). We tagged over 800,000 images and found marten at 124 (63%) and fisher at 168 (85%) of the stations. By fitting multiseason occupancy models to the data, we found that the degree of habitat disturbance negatively influenced detection, occupancy, and temporal turnover for both species. Contrary to our expectations, however, we found no evidence of interspecific competition and instead support for positive associations with detection

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probabilities both spatially and temporally. Both species were positively associated with forest stands containing deciduous trees. Our findings further illustrate the impact that land use has on the occupancy dynamics for these forest-dependent carnivores.

KEYWORDS

camera trap, forest management, habitat modification, interspecific competition, land use, *Martes americana*, mesocarnivores, multiseason occupancy, *Pekania pennanti*, wildlife management

INTRODUCTION

American marten (*Martes americana*) and fisher (*Pekania pennanti*) are mustelid predators native to forests in Canada and the northern United States (Aubry et al., 2012; Powell et al., 2003). Following European colonization of North America, unregulated trapping for pelts and the clearing or logging of vast areas of forest led to population declines and local extirpations (MacCleery, 2011; Maser, 1989; White et al., 2015). As silvicultural techniques advanced toward sustainability (Puettmann et al., 2008) and states implemented trapping regulations (and in some cases, active reintroduction efforts), both species began to recover across much of their historic range (Aubry & Lewis, 2003; Lancaster et al., 2008; Williams et al., 2007). However, habitat disturbance, often resulting from timber extraction, is still a major threat to these species: activities that reduce forest patch size, remove large and senescent trees, and simplify forest structure may severely compromise the long-term viability of their populations (Bridger et al., 2016; Harrison et al., 2004; Moriarty et al., 2011; Patton, 1992; Sauder & Rachlow, 2014).

Marten and fisher are taxonomically close (Koepfli et al., 2008; Sato et al., 2012; Stone & Cook, 2002) with similar life history traits and hunting strategies, but they differ in body size (marten 0.5–2 kg and fisher 2–7 kg; Zielinski & Duncan, 2004). Their geographic ranges overlap, though marten extend farther north than fisher (Clark et al., 1987; Powell, 1993) (Figure 1). Both species are dependent on forested habitat, and although the effects of land use change on each individual species have been studied and suggest certain effects are consistent across their ranges, others may be highly variable. As an example for fisher, logging activity that removes snags and decaying trees from the landscape is likely incompatible with successful reproduction (Paragi et al., 1996; Weir et al., 2012). Although large trees and connectivity between stands are still required to sustain populations in managed forests, fisher do tolerate more disturbance than previously thought (Matthews et al., 2013; Zielinski

et al., 2013). For marten, even partial harvest activities can diminish the canopy cover, structural complexity and overall basal area they require and thus reduce habitat suitability (Chapin et al., 1998; Fuller & Harrison, 2005). Although home ranges can overlap areas of cut forest and edge habitat, harvest practices that maintain forest cover by retaining larger patches of uncut trees, reducing edges, and keeping total cut areas below 20%–30% of the landscape are more viable (Hargis et al., 1999; Potvin et al., 2000).

A critical knowledge gap in the study of marten and fisher response to landscape change is the role of intraguild competition between these two species (Lesmeister et al., 2015; Ritchie & Johnson, 2009; Sévêque et al., 2020). Because of the similarities in their ecological niches, marten and fisher may experience intraguild competition in areas of sympatry (Donadio & Buskirk, 2006; Palomares & Caro, 1999; Polis & Holt, 1992). The disparity in body size between fisher and marten may allow fisher to suppress marten populations, due to either direct predation (Jensen & Humphries, 2019; McCann et al., 2010) or competition (Fisher et al., 2013; Manlick et al., 2017). However, there are also many parts of their range where the species do co-occur, suggesting that some form of niche partitioning facilitates coexistence (Hardin, 1960; Schoener, 1974). One hypothesis is that the larger, heavier fisher is limited to areas of shallower, wetter snow in winter, providing a spatial refuge for marten at higher elevations or other areas with deeper snowpack (Krohn et al., 1995; Raine, 1983). This may be an important component of the species' geographic distributions, where marten benefit from both increased subnivean hunting access in winter and reduced competition from fisher in regions of deeper snow. It does also explain spatial segregation in some areas of sympatry, such as along the elevation gradient in the Sierra Nevada mountains (Sweitzer & Furnas, 2016). However, there are many areas where the species do overlap in space and time, even in winter seasons (Croose et al., 2019; Williams et al., 2009).

Understanding the mechanisms allowing marten and fisher to coexist is essential for the long-term

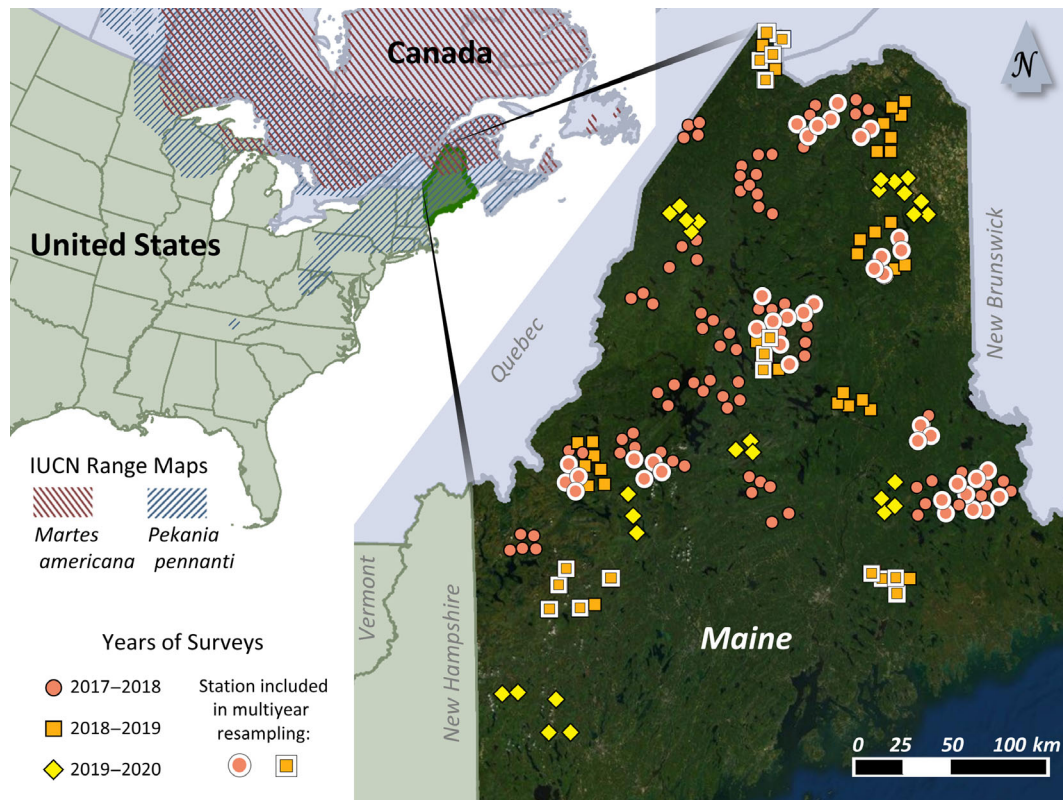


FIGURE 1 Camera-trap survey stations ($n = 197$) deployed in Maine, northeastern United States, at the border of overlapping marten (*Martes americana*) and fisher (*Pekania pennanti*) geographic ranges (IUCN, 2021). Each station was deployed for at minimum one summer and the following winter season, and a subset (highlighted in white) was resampled for up to seven total seasons

conservation of both species. This is undoubtedly a dynamic process, involving local climate, habitat characteristics, prey and predator species (Zielinski & Duncan, 2004), and direct and indirect human perturbations (Gabriel et al., 2012). The overarching goal of our study was to investigate the interacting roles of forest disturbance, habitat, and local climate on marten and fisher co-occurrence patterns in Maine, USA. Specifically, we aimed to test the relative support for three, nonmutually exclusive hypotheses: *H1: Habitat disturbance, resulting from timber harvest, is the main driver of the distributions of marten and fisher.* Based on this hypothesis, we would expect to see occupancy patterns for both species restricted to areas of low- to moderate-intensity disturbance and that co-occurrence would be most common in areas of lowest forest disturbance (Lewis et al., 2016; Sauder & Rachlow, 2014; Simons, 2009; Thompson, 1988). *H2: Species-specific climate limitations and intraguild dynamics drive distributions in Maine.* In this case, we expect fisher to be limited to areas of shallower winter snow, and marten limited to areas with deeper snow and low fisher probability of presence (following Krohn et al., 1995). *H3: Habitat characteristics, as captured by the composition of forest stands, drive marten and*

fisher distribution. If traits such as forest structure, deciduousness in winter, and food available for prey species are most important, we will expect to see relationships between the predictors for composition (deciduous vs. coniferous tree species, which we are using as an index for multiple facets of forest habitat) and the occupancy patterns of marten and fisher, with occasional co-occurrence in areas where habitat preferences overlap (Aubry et al., 2012; Powell et al., 2003).

To achieve our goal, we established a field study across the northern two-thirds of Maine, wherein we balanced survey effort for terrestrial wildlife across a gradient of forest disturbance intensity and latitude. Marten and fisher occupancy data were collected through transects of camera traps optimized for these species (Evans et al., 2019) across 197 survey sites, sampled over a 4-year period (Boitani et al., 2012; Kays et al., 2011; Kays & Slauson, 2008; Rowcliffe, 2017; Steenweg et al., 2017). By comparing the relative importance of forest management, snow depth, and species dynamics in an information theoretic framework, we aim to contribute to filling important knowledge gaps in the basic ecology of marten and fisher and inform optimal conservation strategies.

METHODS

Study area

Our research was conducted in the state of Maine, in the northeastern United States (Figure 1). Maine is primarily forested, with 89% of the state (17.6 million acres) covered by forest land (Butler, 2018), and located along the transition zone from Eastern Deciduous in the south of the state to Boreal Forest in the north (Gawler et al., 1996; McWilliams et al., 2005). Common tree species include maple (*Acer* sp.), birch (*Betula* sp.), American beech (*Fagus grandifolia*), balsam fir (*Abies balsamea*), spruce (*Picea* spp.), and white pine (*Pinus strobus*) (Butler, 2018). Forests are structurally diverse with predominantly mixed-age stands resulting from both natural disturbance (insect outbreaks and storm damage; Fraver et al., 2009) and anthropogenic disturbance (typically partial harvesting; Seymour et al., 2002). Our 197 sampling sites were distributed across the majority of the state, except for areas outside of the marten geographic range (down east and southern regions, which are influenced by coastal habitat and human development, and the far eastern border, which is predominately open, agricultural land) (geographic coverage: 44.15968°N to 47.42166°N and -70.55842°W to -67.62582°W). Mean temperatures in July, the hottest month in Maine, are 18.5°C (average low of 12°C to a high of 25°C). Winter temperatures in January, the coldest month, average -10°C (-16 to -4.5°C). From May to October, roughly 55 cm of precipitation fall as rain, and another 51-cm fall from November to April predominately as snow (NOAA, 2020).

Study design

We established a large-scale field study (Garton et al., 2011) to collect data on wild carnivore occupancy patterns across the range of forest disturbance regimes characteristic of Maine. We stratified our sampling based on the following factors: (1) low to high intensities of forest disturbance, (2) latitude, and (3) reported furbearer take by trappers for marten and fisher (Appendix S1: Figures S1–S3).

Forest disturbance intensity was obtained from remote sensed Landsat image data (Wulder et al., 2019) that were processed using a novel method to combine multiple individual change detection algorithms (Kilbride, 2018). Image layers from 1948 to 2017 provided continuous raster indices describing the magnitude, year, and duration of the most recent disturbance event modeled at each 30-m pixel, calibrated specifically to northeastern forests. We categorized each pixel by the year of most recent disturbance (none or prior to 1989 = 1, 1989–2000 = 2,

2001–2012 = 3, and 2013–2017 = 4) and the magnitude of that disturbance (0–199 = 1, 200–639 = 2, 640–1278 = 3, and 1279–10,185 = 4). We used raster math to multiply these, giving a discrete score from 1 to 16 for each pixel across the state of Maine. From this layer, we calculated the mean *disturbance index* at multiple spatial scales: townships (for initial course-scale selection of survey locations), and circular buffers around each surveyed site once established (300-m and 1-k radius “local” disturbance, and 3-k and 6-k radius “landscape” disturbance scores, the maximum area around each station while maintaining independence).

We used a *balanced study design* to distribute our survey effort along a continuum of forest disturbance. We prioritized townships where high, moderate, and low forest disturbance regimes were present in both large, continuous blocks (3+ townships of a similar value) and smaller, isolated blocks (1–2 townships) surrounded by differing disturbance history. We replicated each of these at least once in both the northern half and southern half of our survey extent to ensure no systematic bias was introduced. We further confirmed this by checking for correlation between our predictor variables and found that only latitude and snow had correlation coefficient greater than 0.1 and were therefore never included in additive models (Appendix S1: Figure S4).

To *maximize spatial coverage* while also collecting multiple-season data, we used a rotating panel design (MacKenzie et al., 2017, p. 218) in which a “permanent” subset of our sites were deployed from five to seven seasons, while other sites were deployed for only two seasons. We selected “permanent” sites, which were representative of the broader study design (e.g., sites in areas of low disturbance in large blocks and sites in areas of high disturbance surrounded by only moderate disturbance), and we replicated these in both northern and southern portions of the overall study area (Figure 1).

Furbearer trapping intensity was accounted for with additional survey stations deployed in townships with the highest reported fur trapping harvest (based on the 2014–2018 trapping season reports for marten and fisher; MDIFW, 2019) to augment the survey effort already expended in townships of low and moderate reported harvest (Appendix S1: Figure S2).

Survey stations were placed at randomly generated points within high priority townships as described above, maintaining a minimum distance of 6 km between stations. This spacing meets the assumption of independence between our detections for martens (home ranges 6–18 km²; Gosse et al., 2005; Shirk et al., 2014; Simons, 2009) and fishers (home ranges up to 10 km² for females and up to 38 km² for males; Clark, 1986; Furnas et al., 2017; Powell et al., 2003).

Snow depth data were obtained from the National Snow and Ice Data Center Snow Data Assimilation System data products (NOHRSC, 2004). We took the daily mean snow depth value of estimates within 1 km of each survey site for a duration of 2 months in the peak of each winter season that surveys were conducted (15 January to 15 March).

Habitat data were collected once at each survey station for stand-level tree species composition (living trees within two, 20-factor variable radius plots), and we used LANDFIRE vegetation type raster data for 300-m and 1-km buffers at larger spatial scales (LANDFIRE, 2016).

Camera trapping was conducted by placing three Bushnell Trophy Cam E2/E3 passive infrared cameras (Overland Park, KS, USA) at each survey station, spaced 100 m apart in a linear transect perpendicular to the access road/trail: We found from prior research that this configuration would maximize the probability of detection for marten and fisher (Evans et al., 2019, see also Mann et al., 2015; Mata et al., 2017; Pease et al., 2016). Each camera was set approximately 40 cm above the ground (or packed snow), facing toward a suet cage with a piece of beaver (*Castor canadensis*) meat, bait which served as a local attractant (Stewart et al., 2019) (Appendix S1: Figure S5). Scent lure designed for furbearers (skunk essence and Vaseline-based, private seller in Kenduskeag, ME, USA) was applied at the base of the bait tree and at >2 m height, to act as a long-distance attractant (Schlexer, 2008; Stewart et al., 2019). A previous study in this region demonstrated that the combined use of bait and lure increased the detection probability of carnivore species without impacting noncarnivore mammals (Buyaskas et al., 2020). Each year of our surveys, stations were first deployed in a summer season for 15+ days, then revisited in the following winter season for 15+ days to collect two seasons of detection data. Each following year, a subset of previously surveyed sites were redeployed to increase the total number of contiguous seasons of data (up to seven), while the remaining effort was allocated to new sites to increase total sample size. Seasons ran from June to September in summer and January to April in winter, for the years 2017–2018, 2018–2019, 2019–2020, and summer 2020. Our methods adhere to ethical research standards for free ranging wild mammals (Sikes, 2016) and were approved by the University of Maine Institutional Animal Care and Use Committee, Protocol #A2018-05-06.

Occupancy models

We analyzed species detection data in two phases: using multiseason, single-species occupancy models in R unmarked (Fiske & Chandler, 2011; MacKenzie

et al., 2003; R Core Team, 2020) and then multiseason, two-species models in program Presence 2.13.12 (Hines, 2006; MacKenzie et al., 2017). Occupancy modeling accounts for the potential bias introduced with imperfect detection (MacKenzie et al., 2002; White, 2005) and allows inclusion of habitat-level and observation-level variables that may influence the probability of an animal being observed at a survey station separately from the occupancy process itself.

We constructed detection histories by pooling images from all three cameras within each station, for each 24-h period that the station was active in summer and in winter. We incorporated the following covariates: latitude; year and season of surveys; forest disturbance within 300-m, 1-km, 3-k, and 6-km radius buffers around each station, to account for the scale of effect of local, home-range, and landscape-level roles of disturbance on detection, occupancy, and turnover; and the proportion of deciduous trees within the immediate stand, as well as 300-m and 1-km radius buffers. We ran two phases of sequential models: (1) single-species, multiseason models to determine key landscape variables affecting marten alone and fisher alone. We first ranked models with all parameters held constant except the one of interest, beginning with detection. We then retained the top model for the detection process as we repeated this step for the initial occupancy probability, then colonization, and finally extinction. We ranked models via Akaike information criterion (AIC) corrected for small sample sizes (Burnham & Anderson, 2002). If one or more model ranked within 2 Δ AIC of the top model and was not modeling the same covariate at a different spatial scale (e.g., disturbance at 1 km followed by disturbance at 300 m), additive models were also tested. (2) After models with habitat covariates were fully parameterized, we ran two-species, multiseason models for marten and fisher to explicitly test for the importance of interaction between species. We used the ψ , p , and r parameterization for the two-species models, which allow for initial occupancy probabilities to be modeled by whether or not the other species is present; for colonization and extinction between seasons to be modeled by the presence or absence of the other species; and for detection to vary both at sites where the other species is present, as well as at the observation occasion, if the other species is simultaneously detected. This modeling requires one species to be considered “dominant,” that is, driving the dynamics of the other species, and thus, we ran models twice to include all the possible directional interactions between marten and fisher. We tested for the impact of interspecific dynamics on initial occupancy, colonization, extinction, and detection with an a priori set of models, shown in Appendix S2: Tables S1 and S2.

RESULTS

We obtained image data from 197 independent survey stations across seven seasons, for a total of 632 station/seasons. Each station was deployed for a minimum of 15 consecutive days (33-day maximum survey period analyzed, 26.2 ± 4.6 [mean \pm SD]) in one summer season and all but four stations again in the following winter season, from 2017 to 2020. A subset of stations were redeployed for additional summers and winters, with three stations out for 3–4 seasons total, 18 stations out for 5 seasons total, and 38 for 6–7 seasons total (Appendix S3: Table S1). Attrition in the number of camera stations was due to access issues (some areas were impossible to reach in winter), changes in landowner, or unforeseen equipment failures. In total, we recorded over 800,000 images of which 12,000 contained identifiable martens and 67,000 contained fishers (Appendix S3: Figure S1). After collapsing images into 24-h survey periods, our data set contained 1086 independent marten visits and 1112 fisher visits, and of those, 123 were visits by both species to the same station within a single day. Marten were detected at 35%–61% of stations deployed in each of the seven seasons (naïve occupancy), and fisher were detected at 26%–86%, with consistently greater detection rates in winter than in summer seasons (Appendix S3: Table S2). After accounting for imperfect detection, the estimated seasonal occupancy rates for marten across the survey extent ranged from 0.41 to 0.59 and fisher occupancy ranged from 0.54 to 0.73, with both species detected across the entire spatial extent of our surveys (Appendix S3: Figure S2).

The top-ranking single-species, multiseason model for marten included the intensity of disturbance, with negative effects on initial occupancy ($\beta = -0.64 \pm 0.19$) and colonization ($\beta = -0.51 \pm 0.18$), and a positive effect on extinction probability ($\beta = -0.52 \pm 0.20$). The percentage of deciduous trees had a positive effect on initial occupancy ($\beta = 0.84 \pm 0.18$), and the average depth of winter snow was positive with colonization and negative with extinction ($\beta = 3.02 \pm 1.11$ and $\beta = -3.00 \pm 1.21$). Detection probability for marten decreased with the number of days in the survey and also decreased with more disturbance ($\beta = -0.025 \pm 0.004$ and $\beta = -0.23 \pm 0.032$) (Table 1) (Figure 2) (Appendix S3: Table S3).

For fisher, no covariate ranked above null for initial occupancy, while the probability of turnover between seasons negatively affected by disturbance (colonization $\beta = -0.47 \pm 0.25$, and extinction $\beta = -0.23 \pm 0.17$). The proportion of deciduous trees had a positive effect on colonization ($\beta = 1.25 \pm 0.57$), and snow depth had a negative effect on extinction ($\beta = -2.64 \pm 1.13$). Detection probability for fisher varied with survey session, with

higher detection rates in the winter seasons than in the summer seasons (see Appendix S3: Table S3).

Results of the two-species, multiseason models indicate that for marten, the occupancy status of fisher was not included in any of top models, but it was included in the top model sets (within 2 Δ AIC) as a predictor for initial occupancy (positive), colonization (negative), and extinction (positive) (Table 2). However, the top-ranked detection model included positive associations for both species. For marten, detection probability during a given survey period was higher if a fisher was also detected ($r^{FF} < r^{FF}$). For fisher, both the overall occupancy status of marten at a site and the detection of a marten in a period increased detection probability ($p^m < r^{Mm} < r^{MM}$). For fisher, the probability of marten presence was also included in models ranked within 2 Δ AIC as a predictor of initial occupancy (positive), colonization (positive), and extinction (positive).

DISCUSSION

Through a large-scale field study conducted in Maine, USA, over a 4-year period, we found that marten and fisher dynamic occupancy patterns were driven primarily by the intensity of forest disturbance (caused by forest management), followed by other habitat features (proportion of deciduous trees) and, to a limited extent, by interspecific dynamics. We did not find a negative influence of fisher presence on marten, but rather a positive relationship between detection events for both species.

Effects of forest disturbance on marten and fisher occupancy patterns

The effects of disturbance were always negative: Models indicated that survey stations in areas that had more recent, or more intense, timber removal activities had lower probability of initial occupancy (marten), lower colonization probability (marten and fisher), and higher probability of extinction (marten and fisher). This is consistent with literature, indicating that forest modification is detrimental to habitat quality for marten and fisher (Chapin et al., 1998; Fuller & Harrison, 2005; Zielinski et al., 2013) and supports our first hypothesis that it is a driver of occupancy patterns in Maine. Marten especially showed lower initial occupancy probability in areas of increasingly disturbed forest and had both higher extinction rates and lower colonization rates in these areas. This suggests that marten have a lower tolerance for intense forest harvest than fisher, and may be more impacted by continued silviculture practices in the state.

TABLE 1 Ranking of single-species, multiseason occupancy models within 2 ΔAIC of the top model for American marten (*Martes americana*) and fisher (*Pekania pennanti*) derived from 197 camera-trap stations in Maine, USA, over four summer and three winter seasons, 2017–2020

| Species | Model formula | ΔAIC | AIC | W_i | k | R^2 |
|-------------------------|---|-------|---------|-------|-----|-------|
| <i>Martes americana</i> | $\psi(\text{DI}_{3k} + \text{DC}_{300m}) \gamma(\text{DI}_{300m} + \text{Snow}) \epsilon(\text{DI}_{300m} + \text{Snow}) p(\text{DI}_{3k} + \text{Days})$ | 0 | 6875.46 | 0.579 | 12 | 0.58 |
| | $\psi(\text{DI}_{3k} + \text{DC}_{300m}) \gamma(\text{DI}_{300m} + \text{Snow}) \epsilon(\text{DI}_{300m} + \text{Lat}) p(\text{DI}_{3k} + \text{Days})$ | 2.071 | 6877.53 | 0.206 | 12 | 0.58 |
| | $\psi(\text{DI}_{3k} + \text{DC}_{300m}) \gamma(\text{DI}_{300m} + \text{Snow}) \epsilon(\text{DI}_{300m}) p(\text{DI}_{3k} + \text{Days})$ | 4.171 | 6879.63 | 0.072 | 11 | 0.57 |
| | $\psi(\text{DI}_{3k} + \text{DC}_{300m}) \gamma(\text{DI}_{300m} + \text{Snow}) \epsilon(\text{Snow}) p(\text{DI}_{3k} + \text{Days})$ | 4.564 | 6880.02 | 0.059 | 11 | 0.57 |
| | $\psi(\text{DI}_{3k} + \text{DC}_{300m}) \gamma(\text{DI}_{300m} + \text{Snow}) \epsilon(\text{Lat}) p(\text{DI}_{3k} + \text{Days})$ | 5.955 | 6881.42 | 0.029 | 11 | 0.57 |
| | $\psi(\text{DI}_{3k} + \text{DC}_{300m}) \gamma(\text{DI}_{300m} + \text{Snow}) \epsilon(\text{DI}_{1k}) p(\text{DI}_{3k} + \text{Days})$ | 7.259 | 6882.72 | 0.015 | 11 | 0.56 |
| | $\psi(\text{DI}_{3k} + \text{DC}_{300m}) \gamma(\text{DI}_{300m} + \text{Snow}) \epsilon(.) p(\text{DI}_{3k} + \text{Days})$ | 7.982 | 6883.44 | 0.010 | 10 | 0.56 |
| | $\psi(\text{DI}_{3k} + \text{DC}_{300m}) \gamma(\text{DI}_{300m} + \text{Snow}) \epsilon(\text{DI}_{6k}) p(\text{DI}_{3k} + \text{Days})$ | 8.752 | 6884.21 | 0.007 | 11 | 0.56 |
| | $\psi(\text{DI}_{3k} + \text{DC}_{300m}) \gamma(\text{DI}_{300m} + \text{Snow}) \epsilon(\text{DI}_{6k}) p(\text{DI}_{3k} + \text{Days})$ | 8.765 | 6884.23 | 0.007 | 11 | 0.56 |
| | $\psi(\text{DI}_{3k} + \text{DC}_{300m}) \gamma(\text{DI}_{300m} + \text{Snow}) \epsilon(\text{DC}_{300m}) p(\text{DI}_{3k} + \text{Days})$ | 9.445 | 6884.91 | 0.005 | 11 | 0.56 |
| | $\psi(\text{DI}_{3k} + \text{DC}_{300m}) \gamma(\text{DI}_{300m} + \text{Snow}) \epsilon(\text{DC}_{\text{Stand}}) p(\text{DI}_{3k} + \text{Days})$ | 9.605 | 6885.07 | 0.005 | 11 | 0.56 |
| | $\psi(\text{DI}_{3k} + \text{DC}_{300m}) \gamma(\text{DI}_{300m} + \text{Snow}) \epsilon(\text{DC}_{1k}) p(\text{DI}_{3k} + \text{Days})$ | 9.895 | 6885.36 | 0.004 | 11 | 0.56 |
| <i>Pekania pennanti</i> | $\psi(.) \gamma(\text{DC}_{300m} + \text{DI}_{6k}) \epsilon(\text{Snow} + \text{DI}_{6k}) p(\text{Survey})$ | 0.000 | 7257.44 | 0.207 | 15 | 0.67 |
| | $\psi(.) \gamma(\text{DC}_{300m} + \text{DI}_{6k}) \epsilon(\text{Snow}) p(\text{Survey})$ | 0.042 | 7257.48 | 0.202 | 14 | 0.67 |
| | $\psi(.) \gamma(\text{DC}_{300m} + \text{DI}_{6k}) \epsilon(\text{Snow} + \text{DC}_{1k}) p(\text{Survey})$ | 1.111 | 7258.55 | 0.119 | 15 | 0.67 |
| | $\psi(.) \gamma(\text{DC}_{300m} + \text{DI}_{6k}) \epsilon(\text{Snow} + \text{DC}_{1k} + \text{DI}_{6k}) p(\text{Survey})$ | 1.460 | 7258.90 | 0.099 | 16 | 0.67 |
| | $\psi(.) \gamma(\text{DC}_{300m} + \text{DI}_{6k}) \epsilon(\text{DI}_{6k}) p(\text{Survey})$ | 3.401 | 7260.84 | 0.037 | 14 | 0.66 |
| | $\psi(.) \gamma(\text{DC}_{300m} + \text{DI}_{6k}) \epsilon(\text{DC}_{1k}) p(\text{Survey})$ | 3.976 | 7261.42 | 0.028 | 14 | 0.66 |
| | $\psi(.) \gamma(\text{DC}_{300m} + \text{DI}_{6k}) \epsilon(\text{DC}_{300m}) p(\text{Survey})$ | 4.422 | 7261.86 | 0.023 | 14 | 0.66 |
| | $\psi(.) \gamma(\text{DC}_{300m} + \text{DI}_{6k}) \epsilon(.) p(\text{Survey})$ | 4.597 | 7262.04 | 0.021 | 13 | 0.66 |
| | $\psi(.) \gamma(\text{DC}_{300m} + \text{DI}_{6k}) \epsilon(\text{DC}_{\text{Stand}}) p(\text{Survey})$ | 4.701 | 7262.14 | 0.020 | 14 | 0.66 |
| | $\psi(.) \gamma(\text{DC}_{300m} + \text{DI}_{6k}) \epsilon(\text{DI}_{3k}) p(\text{Survey})$ | 5.529 | 7262.97 | 0.013 | 14 | 0.66 |
| | $\psi(.) \gamma(\text{DC}_{300m} + \text{DI}_{6k}) \epsilon(\text{Lat}) p(\text{Survey})$ | 5.831 | 7263.27 | 0.011 | 14 | 0.66 |
| | $\psi(.) \gamma(\text{DC}_{300m} + \text{DI}_{6k}) \epsilon(\text{DI}_{300m}) p(\text{Survey})$ | 6.389 | 7263.83 | 0.008 | 14 | 0.66 |

Note: ψ is the probability of occupancy in the first season; γ is the probability of a colonization (a station that was unoccupied becoming occupied from one season to the next); ϵ is the probability of extinction (an occupied station becoming unoccupied); and p is the detection probability given that a station is occupied. W_i is the individual model, and k is the number of parameters. DI: disturbance intensity, at the most influential spatial scale. DC: percentage of living trees that were deciduous species, at the most influential scale. Snow: daily values recorded within a 1-k radius buffer by National Snow and Ice Data Center (NSIDC) Snow Data Assimilation System (SNODAS), averaged over all winters the stations were active (date range held constant, 15 January to 15 March). Survey: the season (summer or winter) and year (2017–2020) of data collection. Abbreviations: AIC, Akaike information criterion; Lat, The latitude of the camera station.

The need for both cover from predators and structural complexity to access small mammal prey could be more limiting for marten, where fisher are able to take advantage of increased snowshoe hare in many areas (Fuller &

Harrison, 2005; Sirén et al., 2021). For both species, our data support our first hypothesis that the degree of disturbance is a key factor in explaining the occupancy patterns of marten and fisher in Maine.

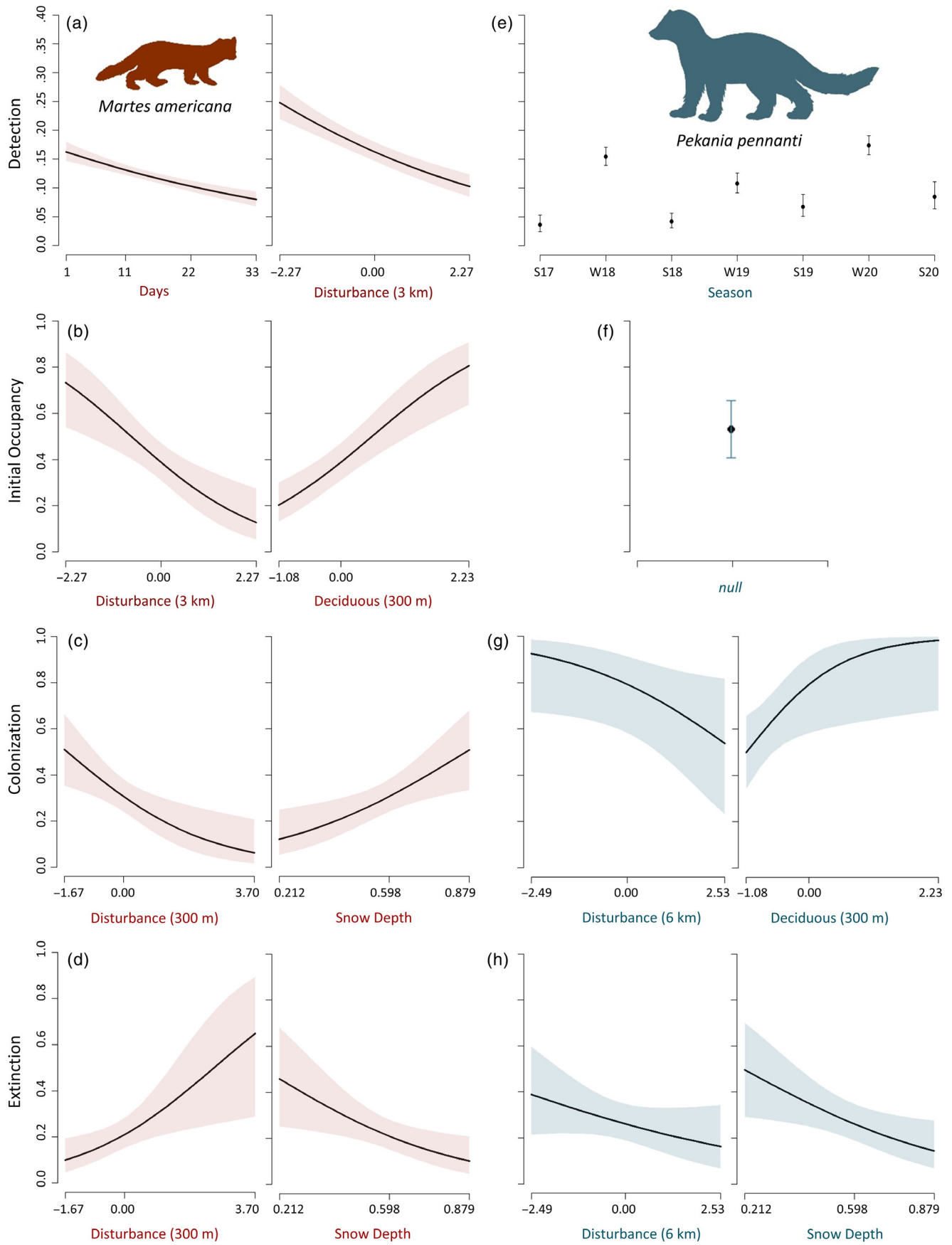


FIGURE 2 Legend on next page.

Effects of snow depth on marten and fisher occupancy patterns

Snow depth positively affected both species and indicated by higher colonization and lower extinction rates for marten, and lower extinction rates for fisher, in areas of deeper winter snow. Although the historic literature suggests fisher are limited by deep snow (Krohn et al., 1995), we found they were widely distributed, occupying over 70% of our survey stations regardless of either snow or latitude predictors. The positive association between snow depth and mustelid predators may be linked to access to “subnivean” resources, both for prey and for thermal shelter, during winter (Aubry et al., 2012). We included only one factor of the many that can describe snow quality, and research into new modeling techniques including sinking depths and formation of icy crusts may provide valuable insight (W. Jakubas, personal communication, 2021). Overall our results, which failed to detect a negative impact on snow depth on fisher, mirror recent trends documented in the northeast, suggesting that warming winters and abundant prey such as snowshoe hare may be expanding the areas available to fisher (Sirén et al., 2021; Suffice et al., 2017, 2020). To what extent this trend may continue is unclear, and it is also possible that had our surveys extended farther north (into Canada) we may have captured an inflection point where winter conditions still limit fisher.

Intraguild effects on occupancy patterns

We documented co-occurrence between the two species at 98 stations (50%)—these detected both marten and fisher within the same season—while another 13 (6%) detected both species, though only in different seasons. We modeled marten occupancy based on the presence or the absence of fisher to assess the potential risk of intraguild predation (Manlick et al., 2017; McCann et al., 2010), and we modeled fisher by including marten occupancy and detection not because we suspect they act as a dominant predator, but to examine whether habitat preferred by marten was used more-than-chance by fisher.

Detection probability was higher for both species at sites where the other was present, and even on individual survey occasions (24-h periods) when the other species was also detected. This indicates a greater-than-random overlap in the spatial and temporal use of their habitat, as represented by the probability of daily detections in the same location, and perhaps, indicating both species respond to weather conditions favorable for hunting.

Because the inclusion of fisher occupancy probability failed to outrank the habitat-only models for marten, we do not find evidence that competition is a limiting factor for the smaller species. Sévêque et al. (2020) recently proposed a conceptual framework for three potential ways human disturbance may influence niche partitioning among carnivores: Disturbance can reduce total available resources and thus increase competition; it can modify resources and destabilize community dynamics; or it can increase the abundance or diversity of resources, and so facilitate greater niche partitioning. This third scenario may be facilitating the overlap, both in space and time, we observed between these species: They are taking advantage of the heterogeneous landscape resulting from forest disturbance, rather than avoiding potential competitors as expected in our second hypothesis, though these are speculative explanations.

While we did not find that marten occurrence was suppressed by the presence of fishers, it is possible that either or both species are impacted by the risks posed by other mammalian predators (Bull & Heater, 2001; Feldhamer et al., 2003; Jensen & Humphries, 2019; Moriarty et al., 2015; Wengert et al., 2014). Exploratory analyses of our dataset indicate the potential for intraguild dynamics driven by coyote (*Canis latrans*), Canada lynx (*Lynx canadensis*), and bobcat (*Lynx rufus*) and warrant further investigations.

Effects of forest composition on occupancy patterns of marten and fisher

The species composition of trees as a predictor was included in top-ranked models, and the presence of deciduous trees was always positive, with higher

FIGURE 2 Predictions from the top-ranked multiseason occupancy models from 197 camera-trap survey stations deployed in Maine, USA. (a) American marten (*Martes americana*) detection decreases over the survey period and with increasing forest disturbance. (b) Marten initial occupancy is negatively affected by forest disturbance intensity and positively affected by the percentage of deciduous trees. (c) Marten colonization between seasons is also negatively related to disturbance and positively related to increasing snow depth. (d) Marten extinction is more likely with increased disturbance and less likely in areas of deeper snowpack. (e) Fisher (*Pekania pennanti*) detection varied with each survey, with a consistent trend of higher detection probabilities in the winter seasons. (f) Fisher initial occupancy was around 50% across sites, while (g) colonization was less likely in areas of large-scale disturbance and more likely in stands with more deciduous trees, and (h) extinction was negatively related to disturbance and snow depth

TABLE 2 Ranking of two-species, multiseason occupancy models for American marten (*Martes americana*) and fisher (*Pekania pennanti*)

| Species | Parameter | Model formula | Δ AIC | AIC | W_i | k |
|----------------------------|-------------------|--|--------------|-----------|-------|-----|
| <i>Martes americana</i> | Initial occupancy | $\psi^F = \psi^f$ | 0.00 | 14,157.64 | 0.791 | 26 |
| | | $\psi^F \neq \psi^f$ | 2.66 | 14,160.30 | 0.209 | 27 |
| | Colonization | $\gamma^{FF} = \gamma^{Ff} = \gamma^{ff} = \gamma^{ff}$ | 0.00 | 14,157.64 | 0.466 | 26 |
| | | $\gamma^{FF} = \gamma^{Ff} = \gamma^{ff} \neq \gamma^{ff}$ | 2.23 | 14,159.87 | 0.153 | 27 |
| | | $\gamma^{FF} = \gamma^{Ff} \neq \gamma^{ff} = \gamma^{ff}$ | 2.45 | 14,160.09 | 0.137 | 27 |
| | | $\gamma^{FF} = \gamma^{ff} \neq \gamma^{Ff} = \gamma^{ff}$ | 2.66 | 14,160.30 | 0.123 | 27 |
| | | $\gamma^{FF} = \gamma^{ff} \neq \gamma^{ff} = \gamma^{ff}$ | 2.67 | 14,160.31 | 0.122 | 27 |
| | | $\gamma^{FF} = \gamma^{Ff} \neq \gamma^{ff} = \gamma^{ff}$ | 2.67 | 14,160.31 | 0.122 | 27 |
| | Extinction | $\epsilon^{FF} = \epsilon^{Ff} = \epsilon^{ff} = \epsilon^{ff}$ | 0.00 | 14,157.64 | 0.442 | 26 |
| | | $\epsilon^{FF} = \epsilon^{Ff} \neq \epsilon^{ff} = \epsilon^{ff}$ | 1.94 | 14,159.58 | 0.168 | 27 |
| | | $\epsilon^{FF} = \epsilon^{ff} \neq \epsilon^{Ff} = \epsilon^{ff}$ | 2.35 | 14,159.99 | 0.136 | 27 |
| | | $\epsilon^{FF} = \epsilon^{Ff} = \epsilon^{ff} \neq \epsilon^{ff}$ | 2.38 | 14,160.02 | 0.134 | 27 |
| | | $\epsilon^{FF} = \epsilon^{ff} = \epsilon^{ff} \neq \epsilon^{Ff}$ | 2.61 | 14,160.25 | 0.120 | 27 |
| | | $\epsilon^{FF} = \epsilon^{Ff} = \epsilon^{ff} \neq \epsilon^{ff}$ | 2.61 | 14,160.25 | 0.120 | 27 |
| | Detection | $p^f = r^{Ff} \neq r^{FF}$ | 0.00 | 14,147.33 | 0.628 | 27 |
| | | $p^f \neq r^{FF} \neq r^{Ff}$ | 1.55 | 14,148.88 | 0.290 | 28 |
| $p^f = r^{Ff} = r^{FF}$ | | 10.31 | 14,157.64 | 0.001 | 26 | |
| $p^f \neq r^{FF} = r^{Ff}$ | | 12.96 | 14,160.29 | 0.001 | 27 | |
| <i>Pekania pennanti</i> | Initial occupancy | $\psi^M = \psi^m$ | 0.00 | 14,149.34 | 0.729 | 26 |
| | | $\psi^M \neq \psi^m$ | 1.98 | 14,151.32 | 0.271 | 27 |
| | Colonization | $\gamma^{MM} = \gamma^{Mm} = \gamma^{mM} = \gamma^{mm}$ | 0.00 | 14,149.34 | 0.304 | 26 |
| | | $\gamma^{MM} = \gamma^{Mm} \neq \gamma^{mM} = \gamma^{mm}$ | 0.39 | 14,149.73 | 0.250 | 27 |
| | | $\gamma^{MM} = \gamma^{Mm} = \gamma^{mm} \neq \gamma^{mM}$ | 0.66 | 14,150.00 | 0.218 | 27 |
| | | $\gamma^{MM} = \gamma^{Mm} = \gamma^{mM} \neq \gamma^{mm}$ | 1.91 | 14,151.25 | 0.117 | 27 |
| | | $\gamma^{MM} = \gamma^{mM} \neq \gamma^{Mm} = \gamma^{mm}$ | 2.00 | 14,151.34 | 0.112 | 27 |
| | | $\gamma^{MM} = \gamma^{mM} \neq \gamma^{mM} = \gamma^{mm}$ | 2.00 | 14,151.34 | 0.112 | 27 |
| | Extinction | $\epsilon^{MM} = \epsilon^{Mm} = \epsilon^{mM} = \epsilon^{mm}$ | 0.00 | 14,149.34 | 0.401 | 26 |
| | | $\epsilon^{MM} = \epsilon^{mM} = \epsilon^{mm} \neq \epsilon^{Mm}$ | 1.94 | 14,151.28 | 0.152 | 27 |
| | | $\epsilon^{MM} = \epsilon^{Mm} \neq \epsilon^{mM} = \epsilon^{mm}$ | 1.97 | 14,151.31 | 0.150 | 27 |
| | | $\epsilon^{MM} = \epsilon^{mM} \neq \epsilon^{Mm} = \epsilon^{mm}$ | 1.98 | 14,151.32 | 0.149 | 27 |
| | | $\epsilon^{MM} = \epsilon^{Mm} = \epsilon^{mM} \neq \epsilon^{mm}$ | 2.00 | 14,151.34 | 0.148 | 27 |
| | | $\epsilon^{MM} = \epsilon^{mM} = \epsilon^{mM} \neq \epsilon^{mm}$ | 2.00 | 14,151.34 | 0.148 | 27 |
| | Detection | $p^m \neq r^{Mm} \neq r^{MM}$ | 0.00 | 14,114.97 | 0.838 | 28 |
| | | $p^m \neq r^{MM} = r^{Mm}$ | 3.29 | 14,118.26 | 0.162 | 27 |
| $p^m = r^{Mm} \neq r^{MM}$ | | 17.42 | 14,132.39 | 0.000 | 27 | |
| $p^m = r^{MM} = r^{Mm}$ | | 34.37 | 14,149.34 | 0.000 | 26 | |

Note: Models for each species were parameterized to test how the occupancy and detection status of the other species would impact initial occupancy (ψ), colonization (γ), extinction (ϵ), and detection (p). All parameters included the top-ranked habitat covariates from the single-species models previously run (reported in Table 1). We tested ψ^A versus ψ^a (initial occupancy at a site where the other species was present vs. absent); the four possibilities of turnover between seasons, where the superscripts indicate the status of the other species at the first survey and at the second survey (e.g., γ^{aA} is the probability of colonization if the other species also colonizes the site); and for detection depending on p^a (detection at a site not occupied by the other species) and r^{aA} versus r^{AA} (detection probability at a site occupied by the other species, on an occasion when it is also detected vs. on an occasion when it is not detected). For marten occupancy models, F and f indicate the status of fisher, and for fisher models, M and m indicate the status of marten. See Appendix S2 for descriptions of the a priori models tested. Abbreviation: AIC, Akaike information criterion.

deciduous proportion linked to a higher probability of initial occupancy (marten) and colonization (fisher). This runs counter to some literature that indicates preference for conifers (Fuller et al., 2016; Powell et al., 2003; Wright, 1999), and does not offer support

for our third hypothesis that alternative habitat preferences segregated marten and fisher in Maine. The preference of both mustelid species for stands with a greater percentage of deciduous species is potentially linked to the availability of suitable trees for denning

and reproduction (Payer & Harrison, 2003; Weir, Harestad, & Wright, 2012). These stands may also offer increased availability and access to prey (Davis, 2009; Purcell et al., 2009; Yaeger, 2005), or the apparent role of hardwood may be a legacy of forest age itself. Given the commercial value for conifer trees, many conifer-dominated stands in Maine are also regenerating from harvest (McCaskill et al., 2016). However, we did not see any correlation between our predictor variables for deciduous and for forest disturbance, suggesting that the tree composition itself may influence habitat use for marten and fisher.

CONCLUSIONS

We found evidence that marten and fisher do respond negatively to heavily disturbed forests in Maine. Although both species were detected in a variety of forest types and ages, and across the entire spatial extent of our study, our occupancy models were primarily driven by the degree of forest disturbance. We note that interpretation of dynamic multiseason depends on many factors, and in our effort to collect widely spatially balanced data, we rotated through which areas were surveyed in successive seasons. We feel this presents the most holistic picture of both spatial and temporal dynamics for marten and fisher in this region, but acknowledge that no subset of data can capture all the information. We did not find that deeper snow limited the distribution of fishers, nor that fisher were an important limiting factor for martens. Both species had a positive relationship with the presence of deciduous trees in forest stands. In northeastern forests, preserving forest stands with only moderate timber harvest activities across both small and large scales, and ensuring that hardwood trees in particular are retained, is likely favorable for marten and fisher population persistence. The strength of our findings derives from the balanced natural experiment design of our study, which included replicated survey stations across all levels of silvicultural intensity. The history of forested habitat in Maine is representative of much of North America, from extensive clearing for agriculture and unsustainable timber extraction, followed by abandonment and young forest regeneration, and now experiencing the effects of climate change, pest outbreaks, and modern timber harvest practices (FPA, 2013). Further research designed specifically to unravel broader community interactions among carnivores would be helpful to understand the full array of factors driving marten and fisher distribution, and to better predict how these dynamics may be impacted by ongoing anthropogenic land use.

ACKNOWLEDGMENTS

We acknowledge the indigenous Wabanaki Tribal Nations on whose homeland we reside, and hope our research may help honor their legacy of stewardship for *apanakes* (marten), *wlanikw* (fisher), and the integrity of forests in Maine. Our research was funded by the Maine Department of Inland Fisheries and Wildlife, the USDA National Institute of Food and Agriculture (McIntire-Stennis Project #ME0-41913), and the Cooperative Forestry Research Unit. Special thanks to W. Jakubas, C. Mosby, S. Webb, and B. Roth. We appreciate additional funding awarded by the Honors College Charlie Slavin Research Fund, and the Center for Undergraduate Research at the University of Maine. We thank B. J. Cimpher, D. Nadjkovic, P. Detwiler, W. Thomas, and M. Hess for their work in the field, and especially G. Archambault for steadfast assistance. Innumerable volunteers gave their time to help tag image data, for which B. Evans is very grateful! Thank you to our reviewers for helpful critiques of earlier versions of this manuscript. Finally, this work would not have been possible without permission to access land across the state, generously granted by numerous public and private entities: American Forest Management, Inc.; Baxter State Park; BBC Land, LLC; Downeast Lakes Land Trust; Elliotsville Plantation, Inc.; Huber Resources Corporation; JD Irving Ltd.; Katahdin Forest Management, LLC; King and Bartlett Fish and Game Club; Maine Bureau of Parks and Land; Maine Department of Inland Fisheries and Wildlife; The Nature Conservancy; North Maine Woods, Inc.; Northwoods Management, LLC; Passamaquoddy Tribe of Indian Township; Seven Islands Land Company; Tall Timber Trust; Wagner Forest Management; and Weyerhaeuser Company. This is Maine Agricultural and Forest Experiment Station Publication Number 3669.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Evans, 2021) are available from Figshare: https://figshare.com/projects/Marten_and_fisher_occupancy_in_Maine_USA/121533.

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SUPPORTING INFORMATION

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How to cite this article: Evans, Bryn E., and Alessio Mortelliti. 2022. “Effects of Forest Disturbance, Snow Depth, and Intraguild Dynamics on American Marten and Fisher Occupancy in Maine, USA.” *Ecosphere* 13(4): e4027. <https://doi.org/10.1002/ecs2.4027>