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Forest and snow rather than food or foe limit the distribution of a generalist mesocarnivore in winter

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Abstract

Investigating species responses to trophic interactions and abiotic factors is crucial to better understanding their ecology and creating effective management strategies. In carnivore communities, smaller species are often regulated by larger ones via top-down interference competition. Smaller subordinate carnivores can also be regulated by bottom-up and abiotic factors, such as the availability of important prey, habitat features, and climatic conditions. However, substantial ambiguity remains regarding the relative roles these complex factors play in shaping subordinate carnivore populations, especially during winter. To investigate this issue, we conducted a large-scale camera-trapping study ($n = 197$ sites distributed across a ~60,000 km^2 landscape) using a balanced study design that sampled a gradient of forest disturbance and climatic conditions. We used dynamic occupancy modeling to examine the influences of top-down (interference competition), bottom-up (prey and habitat), and abiotic (climate) factors on a widespread, generalist subordinate carnivore, the red fox (*Vulpes vulpes*), in Maine, USA. Across three winters, we collected 107 red fox and 185 coyote (*Canis latrans*) daily detections, and 3875 snowshoe hare (*Lepus americanus*) detections. We found evidence for the top-down effects of coyotes on red fox detection probability and site colonization. However, contrary to theoretical expectations, the association between coyotes and red foxes was positive rather than negative. Snowshoe hares had a positive association with local extinction by red foxes, which also contrasts with prevailing theory given that snowshoe hares are an important winter prey of red foxes in this ecosystem. The intensity of forest disturbance and the proportion of conifer forest had negative effects on red fox occurrence and detection probability, while snow depth had a strong negative effect on site colonization. Together, these results suggest red foxes are limited more by abiotic and bottom-up factors related to habitat than by the top-down interference competition or primary prey availability in winter. Our study supports recent findings that bottom-up factors may shape carnivore distributions

during less productive times of year. Our work also highlights how caution is needed when extrapolating previous results from summer studies to winter, as the role of top-down and bottom-up factors may change seasonally.

INTRODUCTION

Evaluating how wildlife respond to variation in top-down and bottom-up factors is critical to understanding their ecology and informing management and conservation actions (Krausman & Cain, 2013; Leopold, 1933). Given this importance, ecologists have long debated the relative roles of top-down and bottom-up factors in regulating populations (Hairston et al., 1960; McQueen et al., 1986; Power, 1992; White, 1978). More recent work has lent support for a holistic view that avoids a strict top-down or bottom-up dichotomy and instead seeks to understand the relative strength of multiple, concurrent factors (Burkepile & Hay, 2006; Hunter & Price, 1992; McCary et al., 2021; McLaughlin & Zavaleta, 2013; Meserve et al., 2003). While there have been recent investigations into the simultaneous influences of top-down and bottom-up effects in various communities (Bruce, 2012; Gigliotti et al., 2020; Meserve et al., 2003; Michel et al., 2016; Sergio et al., 2007; Smith et al., 2010), relatively few studies have investigated these factors in carnivore communities (Gigliotti et al., 2020; Lonsinger et al., 2017; Schuette et al., 2013). Understanding the magnitude and direction of influence that top-down and bottom-up factors exert on carnivore populations is important given these species' diverse ecological roles (Ripple et al., 2014; Roemer et al., 2009).

Carnivore communities are typically made up of one or more dominant large carnivores and one or more smaller subordinate carnivores. These species often have partially overlapping niches (e.g., shared dietary or habitat preferences) and therefore compete with one another for resources (Holt & Polis, 1997; Palomares & Caro, 1999; Polis et al., 1989). Competition often results in agonistic interactions and intraguild predation, and both factors can result in top-down regulation of smaller, subordinate carnivore populations (Palomares & Caro, 1999; Polis & Holt, 1992). Subordinate carnivore populations may also be regulated by bottom-up factors, especially prey availability, that can outweigh or modify the magnitude of top-down effects (Elmhagen & Rushton, 2007; Greenville et al., 2014). Other bottom-up factors beyond prey, such as changes in land use or habitat composition and configuration, can modulate populations as well (Gigliotti et al., 2020; Pasanen-Mortensen et al., 2017). Finally, abiotic factors such as snow conditions and temperature can influence carnivore populations directly (Bartoń & Zalewski, 2007; Pozzanghera et al., 2016; Woodroffe et al., 2017) or indirectly by modifying biotic interactions (Jensen & Humphries, 2019; Moll et al., 2021; Sirén et al., 2021). Simultaneously investigating top-down and bottom-up factors across time will improve our understanding of the drivers of carnivore populations.

The red fox (*Vulpes vulpes*) is a generalist mesocarnivore that serves as a useful model species for investigating the relative effects of top-down, bottom-up, and abiotic factors on carnivore populations. In North America, the regional extirpation of gray wolves (*Canis lupus*) facilitated the dramatic expansion of coyotes (*Canis latrans*), which is hypothesized to have resulted in declines in red fox populations through interference competition (Gosselink et al., 2007; Levi & Wilmers, 2012). Like many other species, winter is a critical time of year for red foxes because they face the simultaneous challenges of higher energetic demands due to increased metabolism and costs of locomotion as well as reduced food resource availability (Bartoń & Zalewski, 2007; Crête & Larivière, 2003; Prestrud, 1991). Moreover, how red foxes simultaneously respond to competition and the availability of snowshoe hare (*Lepus americanus*), which is an important winter prey item of the red fox throughout much of their northern range (Major & Sherburne, 1987; Theberge & Wedeles, 1989), is not clear. Further, little is known about how red foxes respond to forest characteristics such as disturbance (Fisher & Wilkinson, 2005). For example, one study found that red fox tracks were most abundant in boreal forests that were 20 years post timber harvest, potentially due to the higher occurrence of potential prey (Thompson, 1988), but the extent to which such associations are generalizable is unknown. In addition to top-down and bottom-up factors, abiotic factors can directly influence the occurrence of red foxes, but these relationships are not always consistent. For instance, snow depth has been found to have both a negative and positive influence on red fox occurrence (Pozzanghera et al., 2016; Sirén et al., 2021). Given the strong ecological effects of climate change on snow levels

across northern latitudes (Burakowski et al., 2022), examining the effect of this abiotic factor relative to the top-down and bottom-up factors is critical not only for understanding red fox ecology but also for informing its conservation and management in light of future climatic conditions.

In this study, we evaluated the influences of top-down (interference competition), bottom-up (prey and habitat), and abiotic (climate) factors on red fox occurrence and persistence in the Northeastern United States. We assessed the relative roles of these variables using a Bayesian dynamic occupancy model fit to three years of data from a large camera trap array. Our analysis helps illuminate the relative influence of these factors on our focal species in particular and their role in potentially structuring carnivore communities more generally. Our results also highlight how caution is needed when extrapolating previous results from summer studies to winter, as the role of top-down and bottom-up factors may change seasonally.

METHODS

Study area

We conducted our study across central and northern Maine, USA (Figure 1). The study area spanned >60,000 km² and approximates the geographic range of American marten (*Martes americana*), which was the focal species of concurrent projects (Evans & Mortelliti, 2022a; Mortelliti et al., 2022). The area was characterized by spruce (*Picea* spp.)-fir (*Abies balsamea*), northern hardwood (predominately *Acer* spp., *Fagus grandifolia*, *Betula* spp., *Quercus* spp.), mixed forest types, and below freezing temperatures with consistent snowpack (average January temperature −10°C and average winter snowfall 0.5 m; NOAA, 2020). Most of the land was privately owned and managed for commercial timber harvest and after a spruce budworm (*Choristoneura fumiferana*) outbreak in the 1970s and 1980s had seen a regime shift
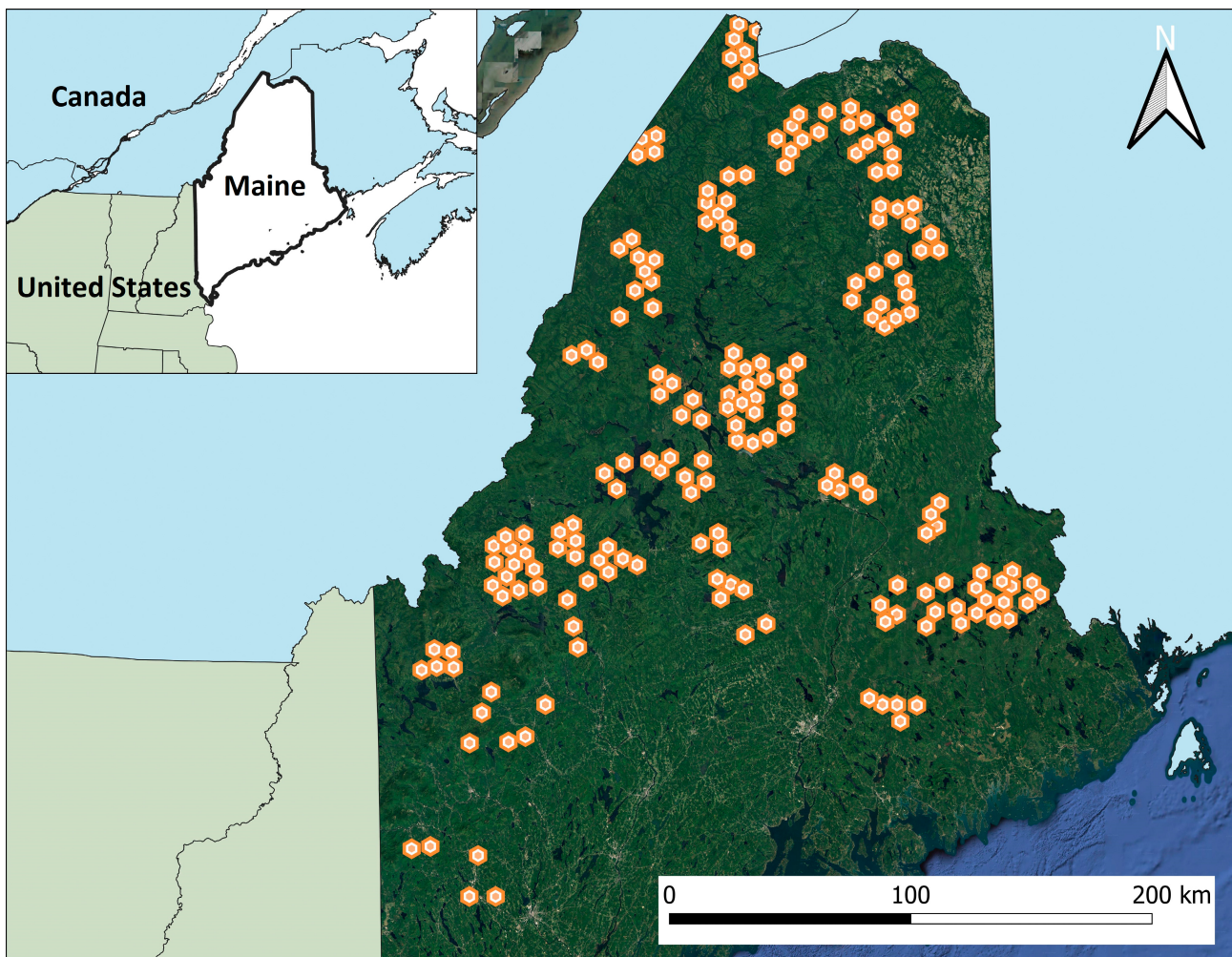
FIGURE 1 A map of survey sites (hexagons) deployed in Maine, USA, 2017–2020. All survey sites consisted of three camera traps located on a transect 100 m apart.

from primarily clear cutting to partial and shelterwood harvesting since the 1990s (McWilliams et al., 2005). Thus, forest disturbance due to timber harvest was a major source of habitat variation across this study area.

Data collection and model covariates

We stratified research sites (hereafter "sites") by forest disturbance, latitude, and fur harvest levels. We chose these strata because they represent the predominant sources of landscape-level habitat, climate, and human-use variation across this study area. Within each stratum, we established research sites at random locations and enforced a 6 km minimum distance between sites to help meet model assumptions of closure and independence. Each site consisted of three Bushnell Essential E2 camera traps (Overland Park, KS, USA) spaced 100 m apart and all cameras were baited with beaver meat and skunk-based scent lure (private vendor,

J. Braley, ME, USA). We deployed cameras in a combination of permanent sites that were active in all three winters (January–April, $n = 38$ sites) and sites that were sampled over one or two winters ($n = 159$ sites). We sampled 118 sites in winter one, 85 in winter two, and 78 in winter three (Appendix S1: Table S1). At a given site, cameras were operational for a maximum of 33 days during any given winter. For additional details on the study design, see Mortelliti et al. (2022).

We modeled red fox site occurrence and persistence using daily detection histories by aggregating images from all camera traps at each site within a 24-h period during each winter. We defined a site as the area within a 2.2-km buffer around cameras, which approximates the average red fox home range size in our study area (Harrison et al., 1989). Given the model's complexity (see below), we selected a relatively small ($n = 5$) set of a priori hypotheses related to factors limiting or supporting red fox distribution during winter in this study area (Table 1). Briefly, we evaluated the influence

TABLE 1 Hypothesis, covariate, covariate description, predicted relationship, references, data source, and data summary for hypotheses used to model the distribution of red foxes in Maine, USA, 2017–2020.

Hypothesis	Covariate	Description	Predicted relationship	References	Data source and details
Coyotes limit red foxes through interference competition	Coyote relative abundance	The no. coyote detection days per active station days	−	Gosselink et al. (2007), Levi and Wilmers (2012), Moll et al. (2018)	Cameras Mean = 0.03; SD = 0.04 Range = 0.00–0.31
Important winter prey shapes red fox space use and distribution	Snowshoe hare site visitation rate	The no. independent snowshoe hare observations per active station days multiplied by 100	+	Major and Sherburne (1987)	Cameras Mean = 17.8; SD = 15.2 Range = 0.0–115.2
Conifers provide cover and reduce deep snow, which enhances red fox mobility and decreases energetic demand	Conifer forest	Proportion conifer forest within a red fox home range buffer around sites	+	Ozoga (1968), Halpin and Bissonette (1988), Thibault and Ouellet (2005)	Homer et al. (2020) Mean = 0.3; SD = 0.1 Range = 0.0–0.8 Raster resolution: 30 m
Young forests contain more red fox potential prey than mature forests	Disturbance	Mean forest disturbance index within a red fox home range buffer around sites	+	Thompson (1988), Theberge and Wedeles (1989)	Kilbride (2018) Mean = 42.8; SD = 31.8 Range = 0.0–159.5 Raster resolution: 30 m
Deep snow impedes red fox mobility, increases energetic demands, and decreases small mammal catchability	Snow depth	Mean snow depth (m) within a red fox home range buffer around sites	−	Halpin and Bissonette (1988), Lindstrom and Hornfeldt (1994), Crête and Larivière (2003), Bartoń and Zalewski (2007)	SNODAS (2004) Mean = 0.6; SD = 0.2 Range = 0.0–1.6 Raster resolution: 1 km

of top-down interspecific competition on red foxes using coyote relative abundance, which we quantified as the number of coyote detection days per active station days in each winter. To model the influence of prey, we estimated the site visitation rate of snowshoe hare as the number of independent (>30 min apart) snowshoe hare detections per active station days multiplied by 100. We chose to use a different index for red fox, coyote, and snowshoe hare to provide the best "resolution" given the differences in the number of detections among species. We used these indices as covariates, rather than running a co-occurrence model, to discern the effects of varying local abundance and visitation rate of predators and prey, respectively, on red foxes. We evaluated the influence of two forest habitat characteristics on red foxes. First, we used the National Land Cover Database (Homer et al., 2020) to quantify the proportion of conifer forest around a site to test the hypothesis that increased cover and reduced snow depth in conifer stands positively affect red foxes. Second, we used a recently developed forest disturbance index (Kilbride, 2018) to test the hypothesis that red foxes would more likely occur in younger, more disturbed forest due to higher overall (non-hare) prey availability. The disturbance index not only consisted of a multiplicative combination of the year of the last disturbance of any kind (typically timber harvest) and its magnitude but also included events such as fire or insect damage. The forest disturbance index was specifically created for northeastern North America using Landsat data from 1947 to 2017 (Kilbride, 2018). Finally, we evaluated the hypothesis that climate limits red foxes via increased snow depth, which decreases their movement efficiency and prey catchability. We calculated the mean annual snow depth at each site during each week using data from the Snow Data Assimilation System (SNODAS, 2004). We quantified forest covariates and snow depth by averaging values across the spatial scale of a typical red fox home range (2.2-km buffer) using QGIS v3.26.1. Prior to modeling, we standardized all covariates to have a mean = 0 and SD = 1, which facilitated model convergence and enabled a direct comparison of relative effect sizes. To avoid multicollinearity, we ensured that no covariates had pairwise Spearman correlations >0.6 (Dormann et al., 2013).

Red fox dynamic occupancy

We modeled the effects of the covariates on red foxes using a dynamic occupancy model. The model estimates initial red fox occurrence in the first year as well as the probability of site local extinction (i.e., a site where foxes occurred in one year but not in the following year) and site colonization (i.e., a site where foxes did not occur in one year but colonized the site the following year) in subsequent years (Kéry & Schaub, 2012; MacKenzie et al., 2003). The model estimates these parameters while accounting for imperfect detection (i.e., a red fox occurred at a site but was not detected on camera). The initial occurrence submodel took the following form:

$$Z_{i,k=1} \sim \text{Bernoulli}(\Psi_{i,k=1}), \tag{1}$$

$$\text{logit}(\Psi_{i,k=1}) = x_{i,k=1} \times \boldsymbol{\alpha}, \tag{2}$$

where $Z_{i,k}$ is a binary latent variable indicating red fox occurrence at the ith site in the kth winter (here, $k = 1$ indicates the first winter) as determined and Ψ is the probability of red fox occurrence. We estimated the effects of covariates ($x_{i,k=1}$) on Ψ using a logit link and $\boldsymbol{\alpha}$ is a conformable vector of parameters indicating covariate effect magnitude and direction. For winters two and three, the local extinction and colonization submodels took the following form:

$$Z_{i,k+1}, \mid Z_{i,k} \sim \text{Bernoulli}\big(Z_{i,k} \times (1 - \varepsilon_{i,k}) + (1 - Z_{i,k}) \times \gamma_{i,k}\big), \tag{3}$$

$$\text{logit}(\varepsilon_{i,k}) = x_{i,k} \times \boldsymbol{\beta}, \tag{4}$$

$$\text{logit}(\gamma_{i,k}) = x_{i,k} \times \boldsymbol{\delta}, \tag{5}$$

where ε is the probability of local extinction, γ is the probability of site colonization, $x_{i,k}$ are the covariates hypothesized to affect these processes, and $\boldsymbol{\beta}$ and $\boldsymbol{\delta}$ are conformable vectors of parameters indicating covariate effects. Note that the colonization and local extinction processes are affected by covariate values in the previous time step (e.g., snow depth in year k impacts red fox occurrence in the year $k + 1$ by influencing colonization and local extinction probabilities). Finally, the detection model took the following form:

$$y_{i,j,k} \sim \text{Bernoulli}\big(P_{i,j,k} \times Z_{i,k}\big), \tag{6}$$

$$\text{logit}(P_{i,j,k}) = x_{i,j,k} \times \boldsymbol{\theta}, \tag{7}$$

where $y_{i,j,k}$ are detection and non-detection data at the ith site during the jth replicate in year k, P is the probability of detecting a red fox, given site occurrence, $x_{i,j,k}$ are covariates hypothesized to affect detection probability, and $\boldsymbol{\theta}$ is a conformable vector of parameters indicating the effects of these covariates.

Model analysis, selection, and assessment

We analyzed the model above in a Bayesian framework using Markov chain Monte Carlo (MCMC) simulations. We used R version 4.0.4 and RStudio version 1.1.463 to run the model in the JAGS language via the packages R2jags (R Core Team, 2017; Su & Yajima, 2012). We ran three MCMC chains of 10,000 iterations each with a burn-in of 1000 and thinning rate of three. We used non-informative priors for all covariate parameters, which had a logistic distribution centered at 0 with a scale parameter of 1 (Hobbs & Hooten, 2015; Northrup & Gerber, 2018).

We performed model selection to test all combinations of the five covariates in each submodel (i.e., detection probability, initial occurrence, local extinction, and site colonization) using Bayesian indicator variables. Indicator variables were Bernoulli-distributed with non-informative priors of 0.5 (Kuo & Mallick, 1998). The posterior of these indicator variables represents the probability that a given covariate should be included in the best model out of all possible combinations (Royle & Dorazio, 2008). Following Barbieri and Berger (2004), we retained a covariate in the model if the posterior mean of its associated indicator variable was ≥0.5. We considered the retained covariates to be significantly influential. We first ran this model selection process on the detection probability submodel (keeping other submodels constant as null models), followed sequentially by the initial occurrence submodel and then the local extinction and colonization submodels (sensu Lesmeister et al., 2015). At each step, the best model from the previous step was retained and held constant. The result of this process was a single final model that retained only those covariates in each submodel that were more likely than not to be in the best model out of all combinations.

We evaluated model convergence by visually inspecting posterior traceplots and ensuring all R-hat statistics were <1.1 (Gelman & Hill, 2007). We assessed the fit of the final model using posterior predictive checks and calculating a Bayesian p value, where a value of $0.05 \leq p \leq 0.95$ indicates an acceptable model fit (Kéry & Royle, 2015).

RESULTS

Of the 197 sites, four failed to collect winter data for various logistical reasons. Of the remaining 193 sites, 34 recorded a full three years of winter data, and an additional 21 recorded two years of winter data (although not always in the same years, e.g., some sites were active in years 1 and 2, others in years 2 and 3). The remaining 138 sites recorded one year of winter data each, although this sampling spanned multiple years (see Appendix S1 for a detailed breakdown of camera site operation). Between 2018 and 2020, we recorded 107 red fox daily encounters (days with at least one fox detection) at 57 of the 197 sites. We detected red foxes at 25 sites in 2018 resulting in naïve occupancy estimates of 0.21, 18 sites in 2019 resulting in naïve occupancy estimates of 0.21, and 20 sites in 2020 resulting in naïve occupancy estimates of 0.26. In addition, we recorded 185 coyote daily encounters, and 3875 snowshoe hare detections. The final dynamic occupancy model fit the data well with a Bayesian p value of 0.71. Using this model to account for imperfect detection, we estimated that red foxes occupied 74.5 ± 16.1 (posterior mean $\pm$ SD) sites in 2018, 87.2 ± 11.7 sites in 2019, and 82.5 ± 11.6 sites out of 197 sites in 2020. Estimated detection probability was 0.08 (95% credible intervals [CI] = 0.06–0.11), local extinction was 0.68 (CI = 0.32–0.92), site colonization was 0.56 (CI = 0.25–0.85), and initial occurrence was 0.32 (CI = 0.14–0.58).

In the final model, each submodel contained a unique set of the covariates (Table 2). Proportion of conifer forest, coyote relative abundance, and forest disturbance were retained in the site-use intensity submodel; proportion of conifer forest and forest disturbance had negative effects, whereas coyote relative abundance had a weak positive effect (Figures 2 and 3). Proportion conifer forest and forest disturbance were retained in the initial occurrence submodel (Table 2), and both covariates had a negative effect (Figures 2 and 3). Snowshoe hare relative abundance was retained in the local extinction submodel (Table 2) and had a positive effect, albeit with considerable uncertainty as evidenced by a wide credible interval (Figures 2 and 3). Coyote relative abundance and snow depth were retained in the colonization submodel (Table 2) with coyote relative abundance having a strong positive effect and snow depth having a strong negative effect (Figures 2 and 3).

DISCUSSION

Using a large-scale camera-trapping study conducted over three winters, we found that the distribution of a generalist mesocarnivore, the red fox, was predominately limited by snow and forest characteristics rather than its primary competitor, coyote, or important prey, snowshoe hare. In contrast to theoretical and empirical predictions, red fox detection probability and colonization were positively associated with coyote relative abundance, and red fox local extinction was positively associated with snowshoe hare visitation rate. Our results suggest that the winter distribution of red foxes in the Northeastern United States is more limited by factors related to habitat

TABLE 2 Inclusion probabilities for covariates in each submodel of parameters from dynamic occupancy models for red foxes in Maine, USA, 2017–2020.

Variable	Initial occurrence	Local extinction	Colonization	Detection probability
Conifer forest	**0.72**	0.38	0.47	**1.0**
Coyote relative abundance	0.26	0.42	**0.78**	**0.96**
Disturbance	**0.88**	0.39	0.28	**0.89**
Hare relative abundance	0.29	**0.54**	0.38	0.06
Snow	0.37	0.45	**0.85**	0.12

Note: Values in boldface indicate covariates with inclusion probabilities >0.5, which were retained for final model inference.
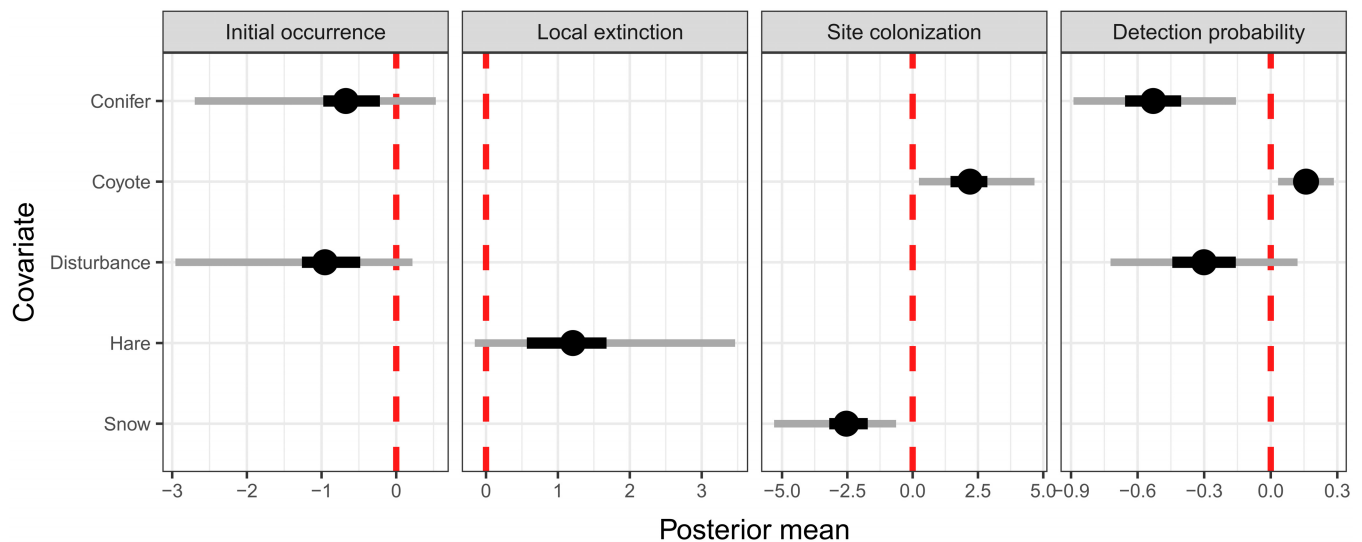

FIGURE 2 Posterior means (circle) and 50% (black line) and 95% (gray line) credible intervals of parameters from dynamic occupancy models for red foxes in Maine, USA, 2017–2020.

and climate than top-down factors associated with interference competition or the bottom-up influence of snowshoe hare. Surprisingly, the data repudiated four of our five hypotheses. We only found evidence of the expected relationship for one of these hypotheses, namely, that red fox occurrence would be limited by climatic conditions associated with greater snow depth. Together, these somewhat unexpected results shed light on the winter ecology of this widespread mesocarnivore species and have broader implications for the relative influence of top-down, bottom-up, and abiotic factors on carnivores inhabiting harsh landscapes.

Given that snowshoe hares are an important winter prey of red foxes in this ecosystem, it is surprising that there is some evidence to suggest that snowshoe hares had a positive association with red fox local extinction. We speculate that one mechanism behind this pattern may be that red foxes abandoned areas with high hare visitation because these areas might also have been characterized by high stem densities, making the hares inaccessible to the red foxes (Fuller et al., 2007), but additional work is

required to test this hypothesis. Alternatively, local extinction could have been caused by competition with Canada lynx (*Lynx canadensis*) as Eurasian lynx have been found to predate on and suppress red foxes (Helldin et al., 2006; Pasanen-Mortensen et al., 2017), but we did not have sufficient Canada lynx detections to test this hypothesis. We also note that the positive effect of hares on local extinction had relatively high uncertainty and a modest inclusion probability, underscoring a need for further clarification. We note that the spatial scale of this study was extensive and required trade-offs in the number of permanent sites surveyed all years and the number of rotating sites surveyed one or two years (see Appendix S1). We therefore acknowledge that the patterns of local extinction reported here should be further assessed in future work.

Contrary to our predictions regarding the association between predation risk from a larger carnivore on a smaller carnivore, coyote relative abundance and red fox detection and colonization probabilities were positive rather than negative. There is a large body of literature regarding the negative effects of coyotes on smaller canid
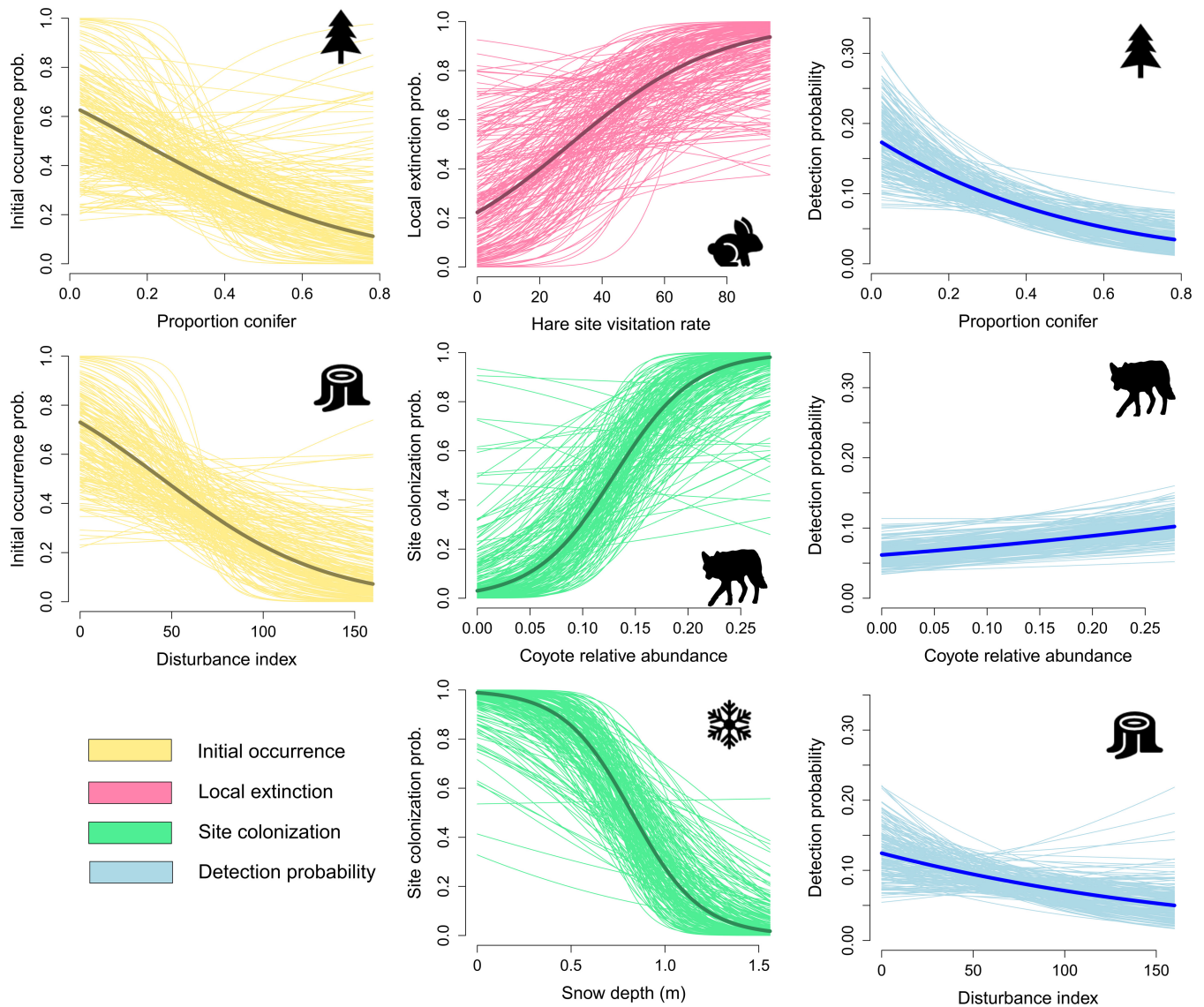
FIGURE 3 Predictive plots of covariates with inclusion probabilities greater than 0.5 from dynamic occupancy models for red foxes in Maine, USA, 2017–2020. Thick dark lines are model-predicted means and thin colored lines are a subset of model predictions from the Markov chain Monte Carlo simulations to depict uncertainty.

populations, including the red fox (Egan et al., 2021; Levi & Wilmers, 2012; Newsome & Ripple, 2015; Ralls & White, 1983; Sargeant et al., 1987). We hypothesize that in winter, red foxes may benefit from coyotes through providing scavenging opportunities, as coyotes in the region predate on white-tailed deer (*Odocoileus virginianus*; Patterson & Messier, 2000) and occasionally moose (*Alces alces*; Benson & Patterson, 2013). Given their relatively recent arrival (1950s; Hody & Kays, 2018), coyotes have become more abundant in Maine in the last several decades, so older information regarding the diet of red foxes (Major & Sherburne, 1987) might not still hold. For example, red fox diets may have shifted away from snowshoe hare and toward scavenging. In other temperate forests, red foxes are known to scavenge on

ungulates killed by large carnivores during winter and spring (Kidawa & Kowalczyk, 2011; Needham et al., 2014; Selva et al., 2005), especially when other food sources are low (Jędrzejewski & Jędrzejewska, 1992).

There is some evidence to suggest that the intensity of forest disturbance, typically caused by timber harvest in this study area, had a negative effect on red fox site-use intensity and initial occurrence, which differed from our predictions. In their review of mammal responses to boreal forest disturbance, Fisher and Wilkinson (2005) noted a lack of information regarding mesocarnivore relationships with disturbance. Recent studies concurrent with our work on red foxes found that the intensity of forest disturbance had a negative effect on American marten (*M. americana*) and fisher (*Pekania pennanti*;

Evans & Mortelliti, 2022a), but a positive effect on weasels (Evans & Mortelliti, 2022b). Previous research has found that red foxes occur more in forested areas, especially those 20–30 years post clear cut, compared with regenerating (<5 years post clear cut) or uncut stands (Forsey & Baggs, 2001; Thompson, 1988). The exact mechanism to explain this negative effect of forest disturbance is unclear. For more arboreal mesocarnivores, the negative effect of disturbance may be the result of simplifying forest structure (Evans & Mortelliti, 2022a). For red foxes, we surmise that a decrease in forest cover would have a negative impact in environments with consistent snowpack during winter, discussed further below, and outweigh the access to increased small mammal abundance that can be found in recently harvested areas (Sullivan et al., 1999, 2008).

Of all the covariates we modeled on red fox occurrence state (i.e., initial occurrence) and processes (i.e., site colonization and local extinction), snow had the largest magnitude effect (posterior mean = −2.52), exhibiting a strong, negative association with site colonization. This finding suggests that the most limiting factor for red fox distribution in this study area is climactic, which has also been found across continental scales for red foxes in Eurasia (Bartoń & Zalewski, 2007). Increased snow depth can impede red fox movement and reduce the availability of small mammal prey (Halpin & Bissonette, 1988). For these reasons, some have hypothesized that conifer stands, which can have reduced snow depths, should be preferred by red fox in winter (Halpin & Bissonette, 1988; Ozoga, 1968; Thibault & Ouellet, 2005), but we found the opposite association. While our study focused on landscape-level patterns in red fox occurrence, foxes may still select for conifer stands with reduced snow cover at finer scales (e.g., daily movements within a home range), but at larger scales, this pattern fails to hold or even reverses. Such disparities between fine-scale selection and broad-scale occurrence patterns have also been recently reported for other mesocarnivores in the United States (e.g., gray fox [*Urocyon cinereoargenteus*]; Allen et al., 2022) and highlights the need to carefully align inference with scale. Our study provides evidence that, across the landscape, areas with average snowfalls of >1 m have a near-zero chance of red fox colonization, thereby acting as a predominate limiting factor to their spatial distribution in the northern portions of their range.

CONCLUSIONS

Taken together, our results suggest red foxes are limited in winter by bottom-up and abiotic factors related to

habitat and climate rather than by the top-down effect of interference competition or the bottom-up factor of prey abundance. Given the often-documented negative effects of coyotes on red fox populations, we expected to find a negative relationship between these two species but instead found a positive one. Therefore, interference competition between these species appeared to be dampened or absent during winter in our study area. The positive relationship between coyotes and red foxes suggests that shared prey (e.g., snowshoe hare; Major & Sherburne, 1987) may be at intermediate levels of abundance, which under traditional intraguild predation theory allows for the coexistence of an intraguild predator (coyote) and intraguild prey (red fox; Holt & Polis, 1997). Moreover, coexistence can occur when an alternative prey resource is available to the intraguild predator (Holt & Huxel, 2007). In our study area, white-tailed deer are consumed by coyotes, most often in winter (Major & Sherburne, 1987), and may serve as the alternative prey resource to allow coexistence. Such competition may be seasonal in nature as shared and alternative prey resources change in abundance and availability, which underscores the importance of considering intra-annual variation when examining the coexistence of competing species. Such variation has been long recognized as important in classical theory (e.g., Wiens, 1977) but is generally understudied in carnivore communities (Moll et al., 2021; Palmer et al., 2017). Similarly, our results support the long-held but often debated idea that interspecific competition at higher latitudes and in harsher environments is less limiting than in climactic conditions (MacArthur, 1972). This hypothesis has also found recent support in recent studies on mesocarnivores in Northern Europe (Elmhagen & Rushton, 2007; Stoessel et al., 2019), and they thus might be occurring in North America as well. Finally, this study highlights how care is required when interpreting the role of top-down and bottom-up factors in shaping species' distributions, as the relative influence of these factors in summer might not apply to winter and could change or even reverse across seasons.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Butler et al., 2023) are available from Figshare: https://doi.org/10.6084/m9.figshare.22110941.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.