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## Satellite-detected forest disturbance forecasts American marten population decline: The case for supportive space-based monitoring

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### ABSTRACT

Limited monitoring resources often constrain rigorous monitoring practices to species or populations of conservation concern. Insufficient monitoring can induce a tautology as lack of monitoring resources makes it difficult to determine whether a species or population deserves additional monitoring resources. When in-situ monitoring resources are limited, remote habitat monitoring could be a useful supplementary tool, as linking parameterized species distribution models to spatially explicit time-series of environmental correlates allows iterative prediction of population change. Yet the performance of predictive forecasts or hindcasts has been difficult to evaluate. We paired contemporary field data, historic population estimates, and a remotely-sensed archive of landscape change to evaluate predictions of American marten (*Martes americana*) population decline owing to habitat loss in Maine, USA. We estimated contemporary spatial patterns in marten density relative to landscape disturbance with spatial capture-recapture models. We compared current density estimates to historical density calculations to evaluate population decline, and compared historical calculations to habitat-based model predictions to evaluate the efficacy of habitat monitoring as a proxy for direct monitoring. Marten density was negatively associated with the proportion of surrounding regenerating forest, and point estimates within focal townships were 50–80% lower than historical calculations. Habitat-based hindcasts of marten density across our entire focal area interest suggested a smaller population decline (roughly 50%) within our focal area. Thus, although habitat-based predictions underpredicted marten decline, they provided correct directional inference. Habitat monitoring and predictions from species distribution models may provide useful inference about population changes given trends in habitat at limited expense when in-situ information is lacking.

### 1. Introduction

Changes in population size and distribution are fundamental metrics used for making wildlife conservation or management decisions. Yet it often is challenging to evaluate population dynamics at scales relevant to decision-making, and the resources needed for thorough long-term monitoring that can rigorously evaluate population responses to different population drivers or management actions typically are allocated only to species of concern (Lindenmayer and Likens, 2010). Species that are either presumed to be more common or for which there is no existing mandate are often monitored using imperfect measures collected conveniently or at low intensity and with limited power to detect population trends (Yoccoz et al., 2001; Lindenmayer and Likens, 2010;

Skalski et al., 2011). Many taxonomic groups are scarcely monitored at all (McKinney, 1999). This can lead to tautological monitoring: species are more likely to be effectively monitored when rare, but only effective monitoring can determine rarity. The fundamental risk is that species presumed to be relatively common can potentially fall into deep decline and become worthy of protection without detection, while monitoring resources are allocated to species of concern that may be recovering because they are also the focus of targeted conservation action (Leon-Cortes et al., 1999; Inger et al., 2015). This risk may be particularly pronounced for species distributed across several managerial jurisdictions, where existing monitoring of common resources is commonly uncoordinated and inefficient (Jantke and Schneider, 2010).

Given that biodiversity monitoring is resource-constrained, cost-

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efficient tools for supplementing or improving the power of existing practices are essential, particularly for species lacking monitoring mandates. Broad-scale habitat loss linked to anthropogenic changes to land cover, and climate is a primary contemporary cause of biodiversity loss and projected future losses (Sala et al., 2000); paradoxically, the scale these forces operate at also makes habitat loss easier to detect across relevant spatial extents and timeframes using existing sensor networks or remote sensing (Pettorelli et al., 2014a; Turner, 2014; Turner et al., 2015). Spatially explicit environmental products derived from local sensors or satellite imagery already have wide use in applied ecology, perhaps most commonly as sources of predictor variables for species distribution models (SDMs, Elith and Leathwick, 2009) that relate population state variables such as occurrence or abundance to environmental measurements. Such models can elucidate important population correlates, but may be used more widely to predict population status into non-sampled domains to inform alterations to existing management delineations (Fuller et al., 2016), identify regions of conservation priority (Hebblewhite et al., 2011), or leverage modeled associations to forecast future population trajectories given projected environmental change (Araujo et al., 2005; Simons-Legaard et al., 2016).

One largely untapped potential use of SDMs in support of biodiversity monitoring is to implement predictions across time-series of spatial environmental products in order to evaluate population growth or decline. In other words, space or sensor-based monitoring of important population predictors could be used to supplement existing monitoring practices or indirectly infer population trend when no other information is available. Such space-based monitoring could be achieved using either SDM forecasts (i.e., making predictions into the present using a previously-built SDM) or hindcasts (i.e., making predictions into the past using a model built in the present); both provide information regarding potential population change strongly congruent with the needs of many monitoring programs. However, few studies make such predictions (e.g., Barrows et al., 2008; Sillett et al., 2012). This is unfortunate, because space-based monitoring is a potentially extremely cost-effective means to indirectly monitor population change and to prioritize follow up field-based sampling to confirm, refute, or refine model predictions (Pettorelli et al., 2014b).

Yet clearly, the value that space-based monitoring provides depends upon how reliably SDMs can predict population change. Here, we use American martens (*Martes americana*) in Maine, USA, as a focal organism to evaluate space-based monitoring as a supplementary population monitoring tool. Martens are overwhelmingly recognized as being sensitive to conditions created by timber harvest (Thompson et al., 2012), as they select against regenerating forest and exhibit reduced density, survival, and dispersal and increased home-range size as the landscape is increasingly harvested (Thompson, 1994; Chapin et al., 1998; Potvin et al., 2000; Johnson et al., 2009). Forest change is readily observed from space-based sensors, and since 1973, satellite imagery suggests that > 40% of northwestern Maine's mature forest that provides primary habitat for martens has been lost to high-intensity timber harvest (Legaard et al., 2015). This may understate habitat loss associated with predominant contemporary partial harvest practices (e.g., less intensive silviculture such as shelterwood or selection; Legaard et al., 2015), although partially harvested stands have previously exhibited mixed habitat value for martens (Fuller and Harrison, 2005; Godbout and Ouellet, 2008). Given landscape changes in northern Maine over the previous 40 years, marten population decline is a reasonable baseline expectation.

Indeed, previous research related marten home range characteristics to changes in forest disturbance using a Landsat-derived time-series, and predicted that habitat loss had led to a > 50% decline in the proportion of occupied marten home ranges across northern Maine between 1975 and 2007 (Simons, 2009). Here, we directly evaluate this prediction. We consider three focal questions. 1) What are the attributes of forest harvest that best describe variability in contemporary marten

density? 2) Has marten density declined over previous decades as predicted? 3) To what degree does decline appear linked to forest changes (i.e., how well do SDM predictions built in the present effectively hindcast past density estimates)? To address the first question, we develop models of present-day marten density in relation to timber harvest legacy. To address the second, we compare contemporary density estimates to historical estimates. To address the third, we evaluate how well the model built with contemporary data back-predicts historical density. This third component evaluates the linkage between satellite-derived measurements of forest disturbance and marten population size, and how effectively habitat changes serve as a proxy for population changes.

## 2. Methods

### 2.1. Study area

Northern Maine (45.5° to 47.5° N) is typical of the Acadian/Laurentian ecoregion, with cold winters (average January temperature -11 °C, NOAA, 2015) and mixed coniferous/deciduous forests dominated by species in the genera *Picea*, *Abies*, *Acer*, *Betula*, *Fagus*, *Fraxinus*, and *Populus*. The area is predominantly (95%) privately-owned and managed as commercial forest (Maine Forest Service, 2010), and in the late 1970s and 1980s much of the state was subject to an outbreak of spruce budworm (*Choristoneura fumiferana*) that resulted in broad scale clear-cutting for salvage purposes. Contemporary timber harvest is dominated by selection or shelterwood operations collectively referred to as partial harvest (Maine Forest Service, 1995) or small clear-cuts (< 50 ha). Forest composition shifted during the same time period, as an estimated 20% of existing coniferous forest in 1974 transitioned into deciduous-dominated or mixed stands by 2004 (Legaard et al., 2015).

We defined our study area as completely encompassing six contiguous townships (each a 93 km<sup>2</sup> survey unit) that we either directly sampled or had previously been sites of marten-based sampling (T4R11, T5R11, T6R11, T5R10, T6R10, T7R10), and including some overlap with surrounding townships (Fig. 1). The focal townships within the study area were managed as privately-owned industrial forest open to trapping (T4R11, T5R11, T7R10), publicly-owned forest also subject to silviculture and trapping (T6R11, T6R10), and a publicly-owned forest reserve closed to forestry operations and trapping (T5R10). The study area was selected to have some overlap with previous field-based research focusing on marten density (Phillips, 1994; Payer, 1999; Fig. 1) that could be used to evaluate previous predictions of decline: Simons (2009) predicted that marten population size in our focal region had declined by roughly 30% between 1975 and 2007. The townships we directly sampled were all open to fur-trapping and logging (T5R11, T6R11, T6R10, T7R10).

### 2.2. Marten sampling

We surveyed for martens between 7 January and 4 April 2015 at 238 baited detection stations (Fig. 1) that paired a hair-catch constructed from glue-strips (Tomcat Indoor Rodent Trap, Madison, USA) with a remote camera (Bushnell Trophy Cam, Overland Park, USA) facing the bait station. We rotated stations across the study area, sequentially sampling between 55 and 63 stations in T5R11, T6R10, T6R11, and T7R10. Each specific station location was active for 9–31 nights and checked 3–9 times (every 3–4 days) to replace bait, camera batteries, and glue-strips as needed. Realized mean nearest neighbor distance between stations was 602 m. Individual martens were identified photographically by two observers following Siren et al. (2016), and identified genetically using genotypes from 9 microsatellite loci and one sex-specific marker. For the analysis presented, we pooled detection histories to estimate density given that there was a single shared underlying encounter process (Clare et al., 2017 contains further description of the sampling scheme and justification for the pooled

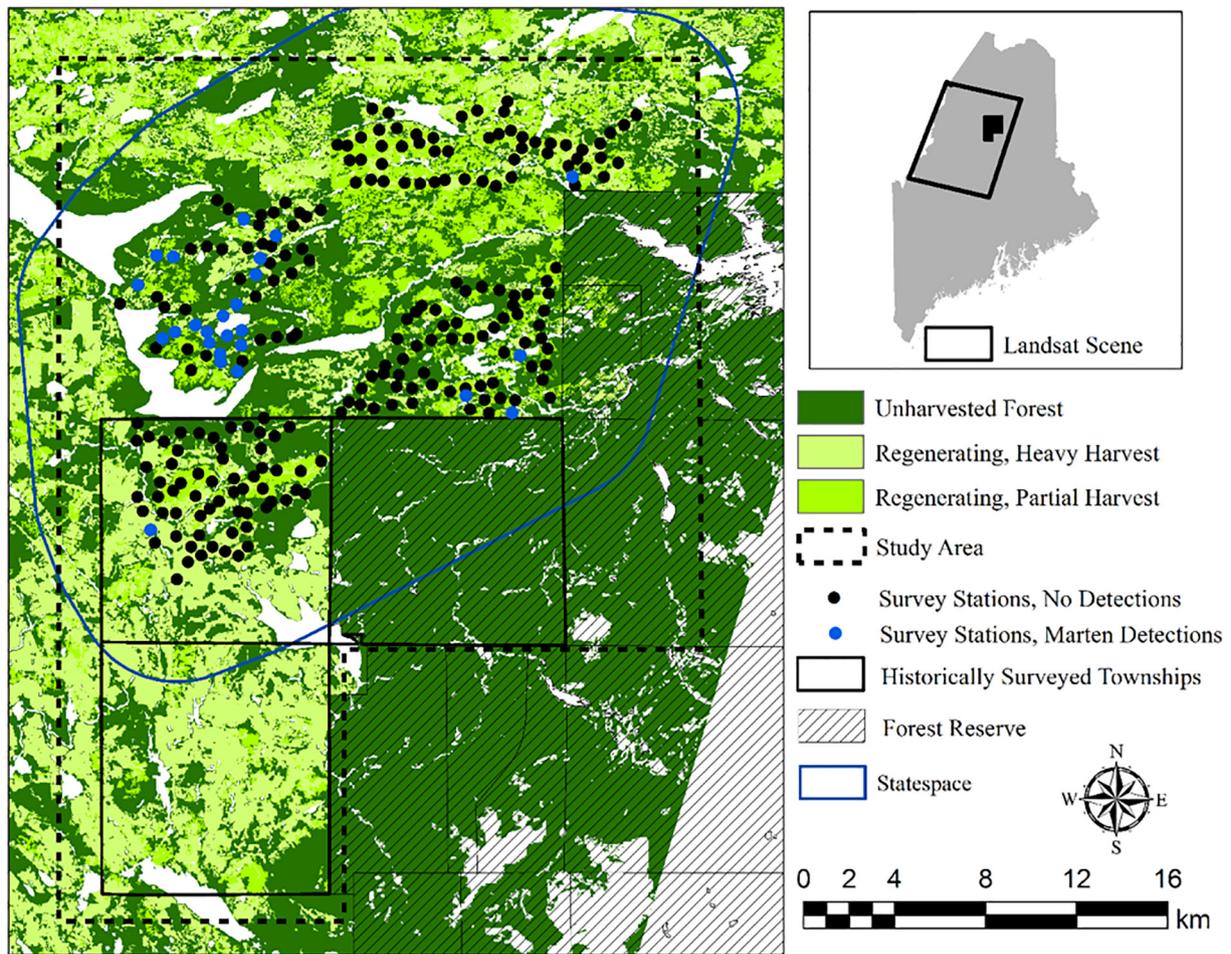


Fig. 1. Location of study area, state-space used for model fitting, and detection stations used to sample American martens in Maine, USA, during 2015, in relation to townships previously surveyed during 1988–1989 and 1996–1997.

model).

### 2.3. Modeling variation in marten density

To estimate contemporary marten density and identify important environmental predictors of its variability, we used spatial capture-recapture (SCR) models (Borchers & Efford, 2008; Royle et al., 2014). Individual animals  $i$  ( $i = 1, 2, \dots, N$  unknown total animals) are assumed to have fixed centers of activity ( $s_i$ ) during a sampling period, and the location of these activity centers is assumed to follow a spatial point process across a defined region of inference,  $S$  (Borchers & Efford, 2008; Royle et al., 2014). The intensity of this spatial point process,  $\mu(s)$ , is a measure of expected animal density within  $S$ . In the simplest form,  $\mu(s)$  is constant across  $S$ . Alternatively, density can be modeled as spatially varying such that the expected density within gridded regions (pixels)  $g$  changes in relation to spatially explicit covariates: e.g.,  $\log(\mu_g(s)) = \beta_0 + \beta_1 X_{1,g}$ . The centroid of each cell  $g$  represents a possible location for  $s_i$ .

Neither  $s_i$  nor  $\mu(s)$  can be directly observed; instead, individual animals  $i$  ( $i = 1, 2, n$  observed animals) are encountered at a discrete number of locations representing detectors  $j$ . Spatial capture-recapture models treat the probability of observing an individual animal  $i$  at a specific detector  $j$  during a discrete interval  $k$  ( $p_{i,j,k}$ ) as conditional upon the location of  $s_i$  and the location of  $j$ , and typically assume that  $p_{i,j,k}$  shrinks as a function of the distance between an animal's activity center and a trap increases. The functional form we use is a half-normal decay where  $p_{i,j,k} = p_0 \times \exp(-d_{i,j}^2/2\sigma^2)$ ,  $p_0$  is an estimated parameter equal to the probability of detecting an individual during a sampling occasion

at a detector placed directly at an animal's activity center,  $d_{i,j}$  reflects the Euclidean distance between  $s_i$  and the location of a detector, and  $\sigma$  is an estimated parameter that describes how quickly detection probability decays with distance. Observed detection or non-detection of existing animals  $y_{i,j,k} \sim \text{Bernoulli}(p_{i,j,k})$ . Additional variation in the detection parameters can be modeled in relation to individual, occasion, or detector-specific covariates, e.g.,  $\text{logit}(p_0) = \beta_0 + \beta_1 X_{1,j}$ . Although estimation details differ between classical and Bayesian approaches, both generally produce equivalent results, and we use each to either leverage the speed of MLE or the ease with which Bayesian analysis permits proper estimation of uncertainty intervals for derived quantities.

We defined  $S$  to include all land within 4.5 km of the outer boundaries of our trap array, and we masked out large bodies of water. We restricted our predictions to within the study area described above. We defined  $g$  as  $500 \text{ m} \times 500 \text{ m}$  pixels, because exploratory model-fitting suggested that this pixel size provided better fit than  $250 \text{ m} \times 250 \text{ m}$  pixels or  $750 \text{ m} \times 750 \text{ m}$  pixels. We considered the proportion of forest regenerating from previous heavy harvest (defined as  $> 70\%$  reduction in existing stand basal area; Legaard et al., 2015), light or partial harvest ( $< 70\%$  reduction), any harvest (the combination of light and heavy harvest), and the mean proximity index (3 pixel or 90 m search radius) of mature (unharvested) forest within a 1 km radius around the pixel centroid as predictors for marten density. That the spatial extent of the circular window used to define covariates for  $g$  differs from the size of the  $g$  itself reflects a distinction between the parametric assumptions of the model and marten ecology. The 1 km buffer was selected to reflect previous research on the spatial scale of

marten habitat selection and roughly corresponds to the size of marten home range in highly suitable habitat (Phillips et al., 1998; Simons, 2009; Wasserman et al., 2012; Siren et al., 2015), whereas the search radius used for proximity index reflects a grain at which martens may avoid moving across regenerating forest (Broquet et al., 2006; Planckaert and Desrochers, 2012). Although this means that values associated with  $g$  were drawn from overlapping landscapes, such overlap rarely substantially affects inference in habitat-association studies (Zuckerberg et al., 2012).

Cell-specific attributes were extracted using FRAGSTATS v4.3 (McGarrigal et al., 2012) from a spatially explicit time-series quantifying forest harvest across Maine during 1973–2010 within 2 or 3 year intervals (15 temporally distinct layers, Legaard et al., 2015). Identified harvests were classified as “stand-replacing” (here, called heavy) or “partial” (here, called light) based on the relative magnitude of change in vegetation indices (normalized differential vegetation index, normalized differential moisture index) derived from Landsat imagery using an unsupervised ISODATA clustering classification algorithm (Legaard et al., 2015). Although categorizing harvests on the basis of a proportional reduction suggests that a class will include a range of absolute changes in canopy opening, the economics of timber harvesting require a fairly substantial timber removal to make the effort viable, and comparison to plot data from the U.S. Forest Service Forest Inventory and Analysis program indicated that classification of heavy (90%), light (79%), or any harvest (95%) was extremely accurate (Legaard et al., 2015). We did not model any harvested pixels as having regenerated during a later time step. This is because marten selection against regenerating forests may last up to 40 years (e.g., Thompson and Harestad, 1994), and also because we wanted our predictors to capture variability reflecting changes in forest composition associated with harvest that were more difficult to derive directly from satellite imagery (Legaard et al., 2015).

We initially fit 19 models with combinations of input variables (total harvest, heavy harvest, light harvest, landscape proximity index of ‘unharvested’ forest) with several different functional forms using ‘secr’ (Efford, 2014): linear and quadratic terms were considered using log or identity links (as density cannot be negative, ‘secr’ truncates estimates at 0; Table S1 provides a complete list of models). For all models, we considered  $p_{i,j,k} = p_{0,i,j,k} \times \exp(-d_{i,j}^2/2\sigma^2)$ , where  $\text{logit}(p_{0,i,j,k}) = \beta_0 + \beta_1 \times \text{EARLY}_j + \beta_2 \times C_{i,j,k}$ , to accommodate lower rates of marten detection during early periods (January and February) of our survey and a trap-happy bait response (Clare et al., 2017). Although we previously had found sex-specific differences in detection decay and baseline encounter probability (Clare et al., 2017), we ignored this source of variability during initial model fitting, because compensatory sex-specific detection heterogeneity is not expected to lead to biased density estimation (Efford and Mowat, 2014). We compared models using second-order Akaike's Information Criterion (AIC<sub>c</sub>, Burnham and Anderson, 2002), and we selected the model with the greatest AIC<sub>c</sub> weight ( $w_i$ ) for subsequent analysis.

#### 2.4. Hindcasting density and evaluating marten decline

After having fitted and selected a candidate model (or averaged between several candidates), we evaluated linkages between the forest disturbance time-series developed by Legaard et al. (2015) and previous empirical estimates of marten density in parts of our study area (Phillips, 1994; Payer, 1999) to evaluate how effectively a spatial time-series of forest harvest aligned with estimates of changes in marten density derived directly. We refit the SCR model with greatest  $w_i$  using Markov Chain Monte Carlo (MCMC) simulation in JAGS (Plummer, 2003) through the R library ‘jagsUI’ (Kellner, 2015). We modeled individual detection probability as  $p_{i,j,k} = p_{0,i,j,k} \times \exp(-d_{i,j}^2/2\sigma_{\text{sex}[j]}^2)$  and  $\text{logit}(p_{0,i,j,k}) = \beta_{0,\text{sex}[j]} + \beta_1 \times \text{EARLY}_j + \beta_2 \times C_{i,j,k}$  based upon previously determined important terms (Clare et al., 2017). Simulations were conducted over five chains, with each chain burned in for 10,000

iterations and 25,000 posterior iterations used for inference. Convergence was assessed via visual inspection of trace-plots and standard diagnostic tests (e.g., Gelman and Rubin, 1992).

We used beta coefficients associated with density post-hoc to produce posterior predictive distributions of expected historical density and derive predictive distributions of expected population decline across the study area. To evaluate whether our predictions appeared reasonable or at least directionally correct, we compared township level predictions based upon spatial layers through 1988 to results reported by Phillips (1994) based upon sampling during 1989 and 1990, and predictions based upon layers through 1995 to results reported by Payer (1999) based upon sampling from 1996 and 1997. These represent the closest temporal matches between the available spatial layers and sampling times that maintained an appropriate temporal structure (i.e., marten response to forests, and not vice versa).

Both historical studies annually live-trapped martens for 2.5 months within 3 township-scale treatment units, with 390 total stationary trap locations spaced 250–650 m apart and active for 10 days (Payer, 1999). All trapped martens were fitted with radio-collars. Historical marten density was previously presented as the number of radio-collared martens located > 10 (Payer, 1999) or 25 (Phillips, 1994) times with at least 50% of locations falling within the land-area of each treatment. The land-area used as the denominator for density calculation initially was defined as the minimum concave polygon that encompassed trap locations, 95% minimum convex polygons associated with home ranges, or the bounds of all individual locations for martens for which home ranges could not be estimated (e.g., captured marten died before its home range could be fully defined, Payer, 1999). Phillips (1994) lumped T4R11 and T5R11 into a single ‘industrial forest’ treatment for comparison with T5R10 (‘forest reserve’ treatment), and estimated density during the years 1989 and 1990. Payer (1999) sampled the same townships during 1996 through 1997, but enacted an experimental trapping closure within T5R11 and considered this an additional treatment level (‘industrial forest, no trapping’). Within the forest reserve treatment, trap locations did not expose all martens to detection due to holes in the trapping array, and the calculated size of the land-area sampled was further reduced to exclude land that was not within at least one home range radius of a trap (Payer, 1999).

Both previous studies effectively report minimum density within specific treatment, as they assumed all animals living within each study site's effective sampling area were captured. More specifically, these reported densities are closer to the product of density ( $\mu_g$ ) and the cumulative probability of capture across the sampling duration integrated across possible locations for  $s_i$ . We viewed this assumption as fairly stringent, and took measures to attempt to correct for imperfect detection. Lacking both the study-specific estimates of detection parameters  $p_0$  and  $\sigma$  and knowledge of the trap locations for each study, we used simulation to estimate how many individual animals may have eluded capture so that we could correct the reported estimates post-hoc to account for imperfect detection (code and additional detail provided in Supporting information S1) to increase congruency with our own estimation process and limit the degree that deviance from prediction derived from our own SCR hindcasts were sampling/estimator artifacts. We defined a square 100 km<sup>2</sup> region (analogous to a township) as the spatial unit for simulation. Within each simulation, we randomly located 60 individual activity centers across the region, gridded the region into cells of size 250 m × 250 m (the minimum trap spacing reported by these studies), and randomly placed simulated trap locations at the centroids of 130 cells (equivalent to the average trapping intensity across treatments in the 1990s). We modeled detection parameters as varying across simulations as  $p_0 \sim \text{Uniform}(0.03, 0.25)$  and  $\sigma \sim \text{Uniform}(0.5, 1.5)$ , distributions derived from the live-trapping SCR analysis of Siren et al. (2016) and local estimates of marten detection parameters (Clare et al., 2017). Within each simulation, we generated detection histories over 10 sampling occasions using a multinomial detection likelihood (Borchers & Efford, 2008) and calculated the

proportion of individuals that were detected. Thus, we incorporate uncertainty in the locations of traps and  $s_i$ , and uncertainty in the detection parameters when correcting historical estimates to align with our own predictions, although we assume the true parameter values fall within the intervals used. Using our simulated calculations of the number of individuals that were not captured, we generated adjusted estimates of historical density by dividing reported minimum density by the simulated distribution of the proportion of individuals that were detected. Throughout, we use the mean of the posterior distribution as a point estimate for parameters either directly considered within the likelihood (e.g., contemporary marten density and detection parameters) or derived after the fact (e.g., changes in marten density across time).

We note that there are imperfections in the model inputs and the comparison. We did not sample in areas closed to trapping and thus could not incorporate this potentially important source of variation (Hodgman et al., 1994) into any analysis. Furthermore, we did not sample the same specific locations as Phillips (1994) or Payer (1999), and their historic density estimates were derived using different sampling methods and analyses. Ideally, we would have fit a comparable SCR model to the raw capture data. Lacking information about individual encounters and trap locations, we attempted to adjust their calculations to be as comparable to our estimates as possible.

Furthermore, we could not perfectly pair sampling years with the remotely-sensed time-series, and in particular, the contemporary marten capture-recapture data were modeled based upon the disturbance state five years previous. However, because the vast majority of the study area open to timber harvest was already disturbed by 2010 (Legaard et al., 2015), we suspect that we did not greatly understate contemporary disturbance. In contrast, because forest harvest classification layers were not available prior to 1973, it is possible that we overestimate the proportion of mature forest on the landscape during earlier time periods (i.e., pixels we assume were mature forest were harvested recently before 1973). However, Legaard et al. (2015) simultaneously mapped forest types during 1975, and found limited prevalence (< 10%) of indeterminate pixels (i.e., pixels that were impossible to classify as forest due to a high proportion of bare soil or very young plant growth resulting from recent harvest or natural vegetation states), so we expect that any overestimation of mature forest is not substantial.

### 3. Results

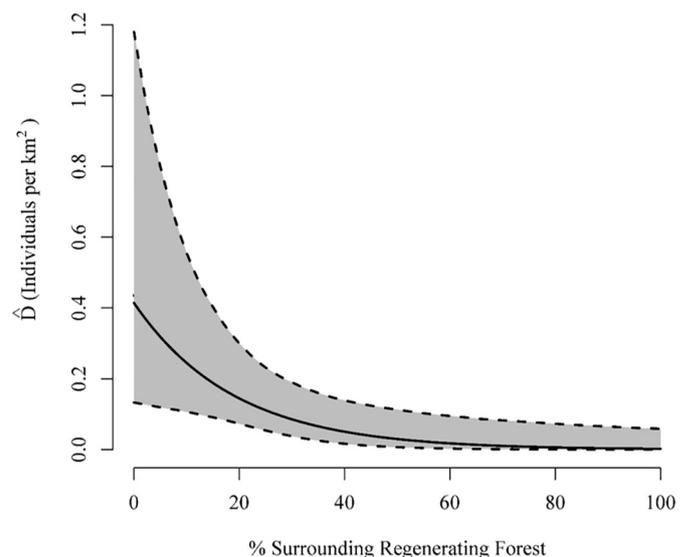
We detected 16 distinct martens during 55 of 1296 station checks, and individuals were detected 1–15 times. Individuals were detected at an average of 2.06 stations (range 1–7), with 5 individuals detected at > 1 station and most of the remaining individuals detected near the edges of the detector array. Several models of marten density were moderately competitive ( $\Delta\text{AIC}_c < 7$ , Burnham and Anderson, 2002; Table 1), but most suggested the same general effect of forest harvest, and more complex models often carried uninformative parameters (Arnold, 2010). When terms for the effects of both light and heavy harvest were included, point estimates and confidence intervals were nearly equivalent. The most supported model ( $w_i = 0.53$ ) suggested a log-linear association between marten density and the proportion of the surrounding landscape regenerating from any sort of harvest (Table 1).

MCMC diagnostics suggested convergence for all parameters ( $\hat{r} \approx 1.0$ ). We predicted marten density across the study area in 2015 as 0.18 individuals per  $\text{km}^2$  (posterior mean; 95% CRI = 0.05, 0.40). In general, marten density quickly declined as the proportion of harvested landscape increased ( $\hat{\beta} = -6.33$ , 95% CRI =  $-9.33, -1.09$ , Fig. 2), resulting in substantial spatial heterogeneity in marten density, as most individuals were predicted to live within areas closed to timber harvest ( $\hat{D}$  outside townships associated with the forest reserve = 0.06; 95% CRI = 0.02, 0.15; Fig. 3A). The predicted decline in density across the study area since 1988 based upon the mean of the posterior predictive

**Table 1**

Candidate models for American marten density in Maine, USA, in 2015, their fitted link function, number of estimated parameters (K), Deviance, and weight of evidential support ( $w_i$ ). Only models with non-negligible support ( $\Delta\text{AIC}_c < 7$ ) are displayed.

Density model	Link Function	-2 Log $\mathcal{L}$	K	AIC <sub>c</sub>	$\Delta\text{AIC}_c$	$w_i$
Total harvest	Log	397.99	6	419.33	0	0.54
Uncut proximity index	Log	400.26	6	421.60	2.27	0.17
Null	Log	405.99	5	421.99	2.66	0.14
Heavy harvest	Log	401.73	5	423.06	3.73	0.08
Heavy harvest + heavy harvest <sup>2</sup>	Log	396.47	7	424.48	5.15	0.04
Total harvest + total harvest <sup>2</sup>	Log	397.68	7	425.68	6.35	0.02
Heavy harvest + light harvest	Log	397.78	7	425.79	6.46	0.02

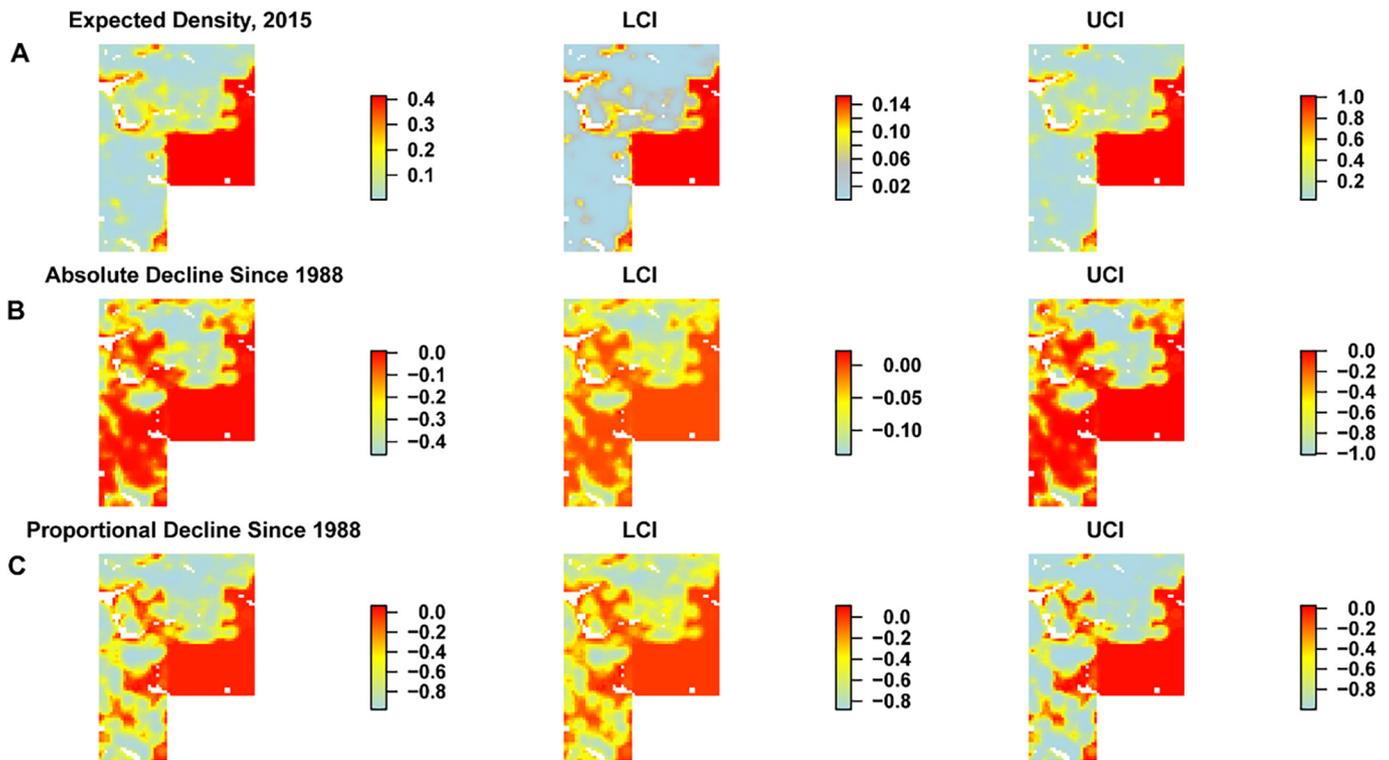


**Fig. 2.** Predicted American marten density declines as the proportion of surrounding area (within 1 km radius) subject to timber harvest within the previous 40 years increases. Dashed lines represent 95% credible intervals.

distribution associated with the contemporary model was  $-0.16$  individuals per  $\text{km}^2$  (95% CRI  $-0.02, -0.39$ ), corresponding to an overall decline of 48% (95% CRI 20%, 60%) from 1988 to 2015. Reductions in marten density were also predicted to be spatially heterogeneous, and the extent of decline was less certain within areas of limited disturbance (Fig. 2; Fig. 3B). When townships within the study area closed to timber harvest were excluded from the analysis, the predicted overall population decline was estimated as  $-0.23$  individuals per  $\text{km}^2$  (95% CRI  $-0.05, -0.51$ ), a 67% decrease (95% CRI 38%, 79%, Fig. 3C).

We predicted contemporary marten density across the industrial forest treatments of the historical studies as 0.05 individuals per  $\text{km}^2$  (95% CRI = 0.01, 0.13), which barely overlapped the lowest minimum density reported by Phillips (1994) and Payer (1999) within defined industrial treatments (0.12). In the one previously-sampled treatment (T5R11) for which we could directly estimate realized density (e.g., the finite-sample rather than expected density), 95% CRI fell far beneath historical minimum calculations ( $\hat{D} = 0.01$ ; 95% CRI = 0.01, 0.03). Thus, evidence suggested overall marten population decline. Parameter estimates and uncertainty intervals are summarized in Table 2.

Seventy-five percent (9 of 12) of the minimum density calculations reported by Phillips (1994) and Payer (1999) during 1989, 1990, 1996, and 1997 fell within the 95% credible intervals of our habitat-based model predictions (Fig. 4), and in each case that the predictive interval



**Fig. 3.** Spatially explicit predictions of American marten density (individuals/km<sup>2</sup>) in northern Maine, USA, during 2015 (A), predictions of differences in marten density (individuals/km<sup>2</sup>) between 2015 and 1988 (B), and predictions of proportional reductions in marten density (% decline) between 2015 and 1988 (C): center and right panels depict lower and upper 95% credible intervals.

**Table 2**

Beta parameter estimates and 95% Credible Intervals associated with spatial capture-recapture models fit to American marten detection data in Maine, USA, 2015. Beta parameters are associated with density (individuals per km<sup>2</sup>),  $\sigma$  (the rate of detection decline given a specific distance from an individual activity center), and  $p_0$  (the probability of detecting an individual during a sampling occasion directly at its activity center). Estimates are presented as effects or intercepts on the log-scale (Density) or logit-scale ( $p_0$ ), except for  $\sigma$  (presented in km units).

Parameter	Posterior mean	LCRI	UCRI
Density, intercept	-0.83	-2.02	0.17
Density, effect of harvest	-6.08	-9.33	-1.09
$\sigma$ , male	1.58	1.05	2.46
$\sigma$ , female	1.07	0.57	1.98
Proportion of females in population	0.56	0.18	0.87
$p_0$ , male intercept	-2.47	-3.43	-1.60
$p_0$ , female intercept	-2.03	-3.26	-0.79
$p_0$ , effect of previous capture	3.22	2.05	4.65
$p_0$ , effect of early winter	-2.46	-3.66	-1.26

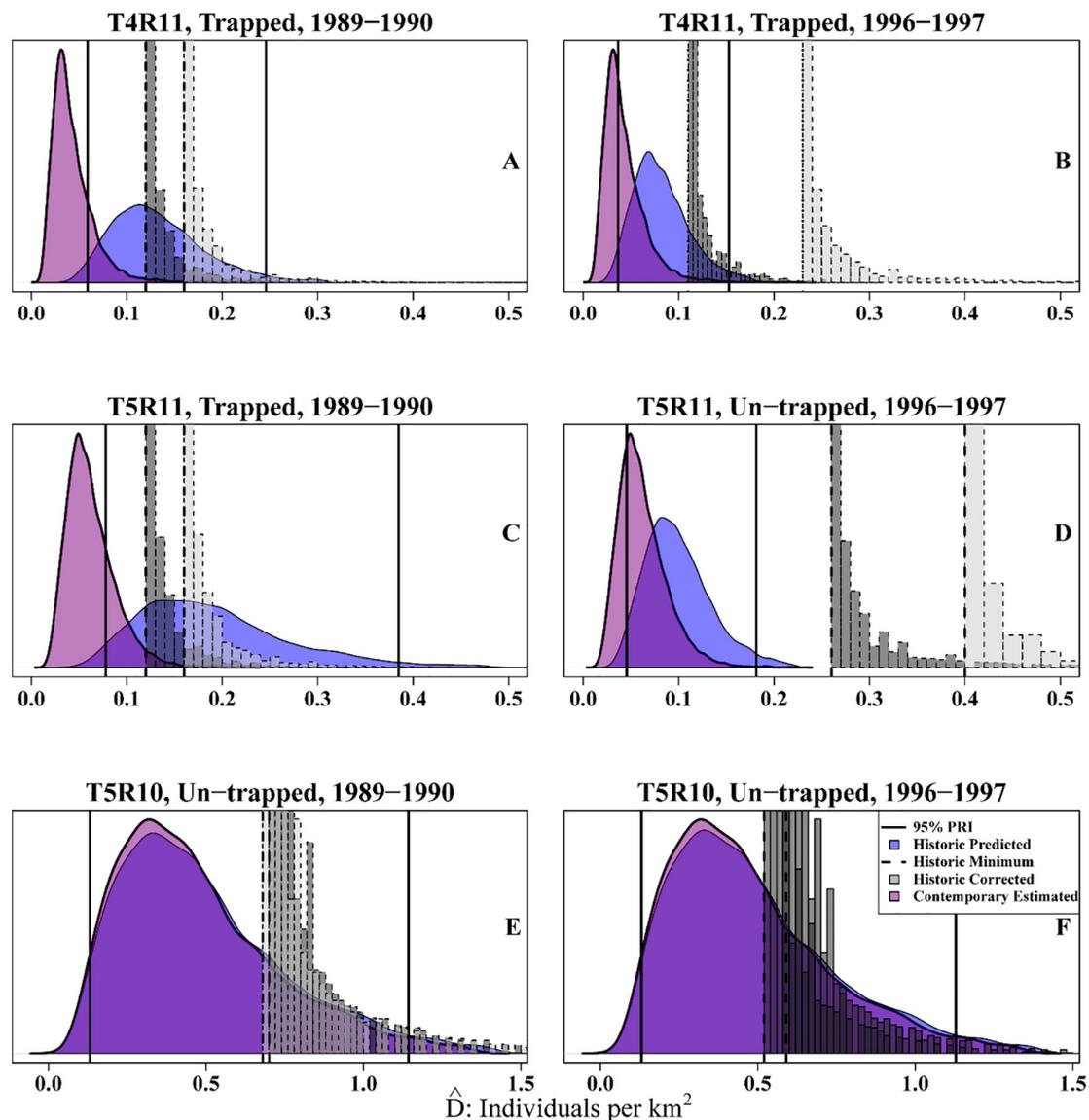
included the point calculation, it also encompassed the 95% highest density intervals associated with the detection-corrected calculation. Corrected estimates of density calculations reported by Payer (1999) from a township in which an experimental trapping closure was implemented during 1996 and 1997 were far greater than the habitat-based model projections (Fig. 4D), and corrected estimates of marten density within a trapped and logged township during 1997 also fell outside the predictive interval (Fig. 4B). Our predictions encompassed other reported and corrected calculations within trapped and logged treatments, and also calculations within an area without logging (4C, 4E) even though we did not directly sample any comparable region. Consequently, marten population decline appeared linked to habitat losses. However, all minimum and adjusted calculations fell above the regions of greatest posterior predictive density, indicating population

decline was generally underestimated by the contemporary habitat association.

#### 4. Discussion

To our knowledge, this is the first study that leverages a time-series of spatial environmental products derived from freely available imagery to produce estimates of changes in population size using hindcast SDM predictions and also evaluates hindcasts with empirical information. Our results highlight the potential value of space-based monitoring. Although our application primarily leverages inferred changes in land cover or disturbance, products associated with vegetation phenology, snow cover, or weather are often effective predictors within SDM, and could be increasingly cost-effective and efficient monitoring proxies as the archive of spatial data and the accuracy of derived products continues to grow (Turner et al., 2015).

We acknowledge that monitoring habitat proxies has clear limits. As with species distribution models as a collective, inferential or predictive capacity will be limited by the degree to which animal sampling is representative of the area of interest, the degree to which environmental predictors effectively measure proximal drivers of demography, the degree to which these associations hold over space or time (e.g., Elith and Leathwick, 2009; Guillera-Arroita et al., 2015). As with direct monitoring inferences made with SDM, limited data allow limited inference: predicted changes in distribution or abundance derived from presence-background models are more difficult to interpret than predicted changes derived from richer data types (Guillera-Arroita et al., 2015). Any of these errors are likely to compound over time, as we discuss further below. In short, species with poorly understood or measured habitat currencies are unlikely to be effectively monitored via indirect habitat proxies. Despite these concerns, for many species, the realistic extent or intensity of plausible monitoring effort is limited. We believe that even an imperfect monitoring metric is preferable to an explicit assumption of no change.



**Fig. 4.** Model-predicted estimates of American marten density in previously surveyed townships in northern Maine, USA. Density plots (blue) represent the posterior distributions of density hindcasts based upon forest cover in 1988 and 1995; pink density plots depict the posterior distribution of present-day density averaged across the same townships. Prediction intervals are the 95% credible intervals for hindcast density. Reported point calculations of marten density during the subsequent two years are represented as dashed vertical lines, and gray bars represent ad-hoc corrections to reported point estimates based upon simulations (light vs. dark gray used to differentiate specific years). Historic empirical results fall generally within habitat-based predictions, but suggest population decline was greater than expected.

Contemporary marten density appeared to be most strongly predicted by the extent of recent timber harvest (irrespective of harvest intensity). There was scant evidence that marten density responded differently to different surrounding harvest types, supporting previous in-state research that martens respond negatively to less intensive silvicultural practices as they are currently and locally implemented (Fuller and Harrison, 2005). The exponential decrease in marten density as harvest increased is consistent with previous assertions that martens are sensitive to small forest disturbance footprints (Hargis et al., 1999; Fuller, 2006; Cushman et al., 2011). Jointly, these results imply marten sensitivity to even small amounts of less-intensive disturbance, and that marten density in much of the study area is vastly suppressed at existing levels of disturbance.

Direct evidence for marten population declines concurrent with an increase in regenerating forest stands is consistent with previous space-based population forecasts (Simons, 2009) and our own hindcasts. Thus, both predictive efforts produced reliable directional population

inference, the general goal of any population monitoring effort, without longitudinal field-based data, and accordingly, at limited cost. We expect that this is largely due to the strong proximal influence of silvicultural practices on marten demography. The reliability of SDM predictions across time is dependent upon how well important environmental associations with population status also reflect drivers of population change (Elith & Leafwick, 2009; Yackulic et al., 2015). Logging reduces marten survival and effective dispersal distance across eastern North America (e.g., Thompson, 1994; Payer, 1999; Johnson et al., 2009), and reductions in these demographic parameters would be expected to lead to population decline. Furthermore, previous studies have clarified individual-level mechanisms that might underpin demographic responses: increased predation risk and reduced foraging efficiency, as prey abundance, prey encounter rates, and marten hunting success may be reduced in regenerating forests (Hodgman et al., 1997; Fuller et al., 2004; Andruskiw et al., 2008).

However, our modeling effort did not appear to produce particularly

accurate estimates of historical marten density. Marten decline appears to have outpaced our predictions and also those of Simons (2009). We expect this largely relates to incomplete parameterization (i.e., missing covariates) within both models (Elith and Leathwick, 2009). The most extreme discrepancies were within logged forests experimentally closed to trapping, a well-understood population influence (e.g., Carroll, 2007). Failure within this specific treatment is not necessarily concerning because no such conditions exist in Maine today, but trapping effort across the state is both spatially and temporally variable and likely contributes to similar spatial and temporal variability in marten population size and trend. Additional non-modeled factors such as declines in prey density, the connectivity or extent of existing mature forest at scales larger than the home range, changing snow conditions associated with climate change, may have further contributed to population decline (Thompson and Colgan, 1987; Fredrickson, 1990; Hodgman et al., 1994; Flynn and Schumacher, 2009; Johnson et al., 2009; Krohn, 2012). Classification error associated with the forest disturbance product is another potential cause of under-prediction, because spatial error or thematic misclassification tends to shrink predictor coefficients towards zero (e.g., Johnson and Gillingham, 2008). Although ground-based validation indicated that disturbance events were very accurately predicted, it is possible that low rates of error may have compounded over time. Similarly, although we selected predictors based on forest harvest that we expect capture both changes in forest structure and composition associated with harvest, we effectively pooled these effects because it is difficult to distinguish between deciduous-dominated or mixed stands while they regenerate (Legaard et al., 2015). Martens respond differently to these stand types (Thompson et al., 2012), and an increase in the prevalence of deciduous cover across the study area (Legaard et al., 2015) may have accelerated marten decline beyond our predictions. As noted above, these issues collectively characterize the primary limitations of SDMs and spaced-based monitoring: predictive reliability depends upon how well important population drivers can be translated into spatial surfaces.

We expect that all SDMs are incompletely parameterized and include covariates subject to measurement error. It is likely unrealistic for any managerial or conservation effort to expect that solely using model predictions to infer population change represents sufficient monitoring (or lacking an SDM, using trends in the amount of important environmental features; Joshi et al., 2016). Instead, the most effective usage of spaced-based monitoring may well follow our implementation: use SDM predictions as an early warning system to identify species or spaces where additional field-based survey effort is warranted (Pettorelli et al., 2014b). Our own study was motivated by concerns regarding Simons' (2009) forecasts. Given evidence for local decline, two areas of subsequent focus suggested by our results include improving understanding of how additional population drivers (e.g., variability in trapping pressure and the configuration of forest disturbances across different spatial scales) influence marten populations and determining marten population status and the stability of marten population associations across a larger extent. Simons' (2009) model and extrapolations from our own model suggest low marten density and severe decline across much of northern Maine ( $\hat{D} = 0.06$ , 95% CRI = 0.02, 0.14;  $\widehat{\Delta D} = -72\%$ , 95% CRI =  $-52\%$ ,  $-83\%$ ; Fig. S3). Although we urge caution in interpreting these estimates given the limited extent of our sampling, pilot results did not suggest that population decline was strictly local (Fig. S3). The only comparably low marten density estimates across North America we are aware of are within Michigan (Williams et al., 2009; Skalski et al., 2011), where marten trapping is far more restrictive than in Maine (bag limit 1 vs. 25). These items are the focus of ongoing research.

The use of space-based monitoring as an early warning system can be particularly critical for escaping monitoring tautology due to political mandates. Had previous warnings of marten decline (Simons, 2009) not motivated our own follow-up research, it seems likely that marten decline locally (and potentially across a much larger extent)

may not have been recognized, even though this has been an explicit research concern in eastern North America for several decades (e.g., Thompson, 1991). While martens apparently declined, sympatric Canada lynx (*Lynx canadensis*) were targeted as a species of federal concern and subsequently protected, requiring agencies to allocate substantial resources to more intensive lynx research and monitoring. Results suggest lynx population growth is linked to widespread forest disturbance (Maine Department of Inland Fisheries and Wildlife, 2012; Simons-Legaard et al., 2016) associated with marten decline, and lynx have recently been suggested as a candidate for delisting given signs of recovery and landowner pledges to maintain suitable habitat. This is a noteworthy success, but reported density estimates for lynx in Maine (Vashon et al., 2008) generally overlap our own estimates of contemporary marten density, suggesting that a specific risk of tautological monitoring highlighted previously—i.e., the recovery of rare, monitored species, while unmonitored species assumed to be common decline—has been realized. Regionally, jointly conserving these species will likely require spatially-explicit planning to conserve their juxtaposed habitat needs, and space-based habitat projection and monitoring (e.g., Simons-Legaard et al., 2016) may be able to provide important insights into potential and realized population trajectories.

That available resources for in-situ monitoring are limited and tend to be shifted based upon political objectives or mandates that are likely an unavoidable reality in resource management and conservation. Inexpensive and easily implemented alternatives, such as space-based monitoring, appear to be useful means for bypassing monitoring tautology and may be particularly valuable for efficiently determining when and where species or populations deserve greater direct monitoring effort. Provided habitat associations have been properly evaluated, implementing space-based monitoring can require as little time and expense as downloading a set of openly available products as they are updated. As the resolution of local or remote sensors or their corresponding products improve, so too will the strength of inference and predictions derived from indirect habitat monitoring using sensor-based measurements.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2019.02.020>.

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