

Enhancing species distribution modeling by characterizing predator–prey interactions

ANNE M. TRAINOR,^{1,4} OSWALD J. SCHMITZ,¹ JACOB S. IVAN,² AND TANYA M. SHENK³

¹*School of Forestry and Environmental Studies, Yale University, New Haven, Connecticut 06511 USA*

²*Colorado Parks and Wildlife, Fort Collins, Colorado 80526 USA*

³*National Park Service, Fort Collins, Colorado 80525 USA*

Abstract. Niche theory is a well-established concept integrating a diverse array of environmental variables and multispecies interactions used to describe species geographic distribution. It is now customary to employ species distribution models (SDMs) that use environmental variables in conjunction with species location information to characterize species' niches and map their geographic ranges. The challenge remains, however, to account for the biotic interactions of species with other community members on which they depend. We show here how to connect species spatial distribution and their dependence with other species by modeling spatially explicit predator–prey interactions, which we call a trophic interaction distribution model (TIDM). To develop the principles, we capitalized on data from Canada lynx (*Lynx canadensis*) reintroduced into Colorado. Spatial location information for lynx obtained from telemetry was used in conjunction with environmental data to construct an SDM. The spatial locations of lynx–snowshoe hare encounters obtained from snow-tracking in conjunction with environmental data were used to construct a TIDM. The environmental conditions associated with lynx locations and lynx–hare encounters identified through both SDM and TIDM revealed an initial transient phase in habitat use that settled into a steady state. Nevertheless, despite the potential for the SDM to broadly encompass all lynx hunting and nonhunting spatial locations, the spatial extents of the SDM and TIDM differed; about 40% of important lynx–snowshoe hare locations identified in the TIDM were not identified in the lynx-only SDM. Our results encourage greater effort to quantify spatial locations of trophic interactions among species in a community and the associated environmental conditions when attempting to construct models aimed at projecting current and future species geographic distributions.

Key words: biotic interactions; Canada lynx; *Lepus americanus*; *Lynx canadensis*; niche theory; predator–prey system; snowshoe hare; species distribution modeling; trophic interaction distribution model.

INTRODUCTION

Accurate descriptions of species geographic range distributions are fundamental to developing effective biodiversity conservation actions and natural resource management strategies. Currently, many efforts to identify these ranges employ species distribution models (SDMs) that statistically associate the geographic locations of species with a set of environmental variables that are presumed to facilitate or constrain their persistence (Guisan and Zimmermann 2000, Peterson et al. 2011). Multiple abiotic and biotic variables affect and interact throughout the life cycle of a species to govern its long-term presence across geographic space. Typically, SDMs represent this complexity by using variables such as soil condition, climate, topography, hydrology, and dominant vegetation as predictor variables to identify a species range (Meier et al. 2010, Zimmermann et al. 2010). As such, SDM (a.k.a. niche

modeling) approaches most often consider just one facet of species' ecologies, namely the environmental conditions within which species live (Soberón 2007), akin to the early Grinnellian niche concept (Guisan and Thuiller 2005, Araújo and Guisan 2006). Furthermore, under the typical SDM implementation, species observation data are treated as general occurrences. Even when high-quality telemetry data are available, there is typically little or no specificity regarding the behavior or type of activity associated with each location. Each location is simply treated as a place where the species of interest was known to occur (Peterson et al. 2011).

Species geographic distributions are not, however, determined solely by environmental variables (Paine 2010). Species regularly interact with other species through predation and competition (Austin 1980, Austin and Smith 1989), a.k.a. the Eltonian niche concept (Elton 1927). Indeed, the Grinnellian and Eltonian niche concepts were long ago combined to provide a greater understanding of where species exist and where species impact other species in their environment (*sensu* Hutchinsonian *n*-dimensional niche

Manuscript received 20 February 2013; revised 21 May 2013; accepted 20 June 2013. Corresponding Editor: J. Franklin.

⁴ E-mail: anne.trainor@yale.edu

concept; Hutchinson 1957, Holt 2009). Yet, the explicit inclusion of species interactions, in addition to environmental conditions, has yet to be widely quantified and included in modern SDM approaches (Sexton et al. 2009, Paine 2010, Zarnetske et al. 2012).

Typically, SDM approaches consider species interactions by using the geographic ranges of prey or host plant species as covariates to constrain the focal species distribution model (Leathwick and Austin 2001, Araújo and Luoto 2007, Heikkinen et al. 2007, Schweiger et al. 2008, Meier et al. 2010, Ettinger et al. 2011). The strength of this approach is that it can characterize species geographic distributions and biotic relations based on quantifiable, multivariate, n -dimensional attributes. But often the coarseness in the spatial resolution (e.g., 1–50 km²) of the environmental variables and the lack of geospatial data of observed interactions limit the ability of the models to explicitly capture the fine-resolution spatial nature of species interactions. For example, intraspecific competition or predator–prey interactions may arise from variation in local habitat conditions across landscapes (Araújo and Guisan 2006).

A parallel, but independent, approach to modeling species interactions employs finer-resolution (e.g., 30–1 km²) observations to describe environmental conditions where focal species directly interact with their resources, known as resource selection theory, RST (Manly et al. 2002, Warton and Aarts 2013). RST approaches implicitly include a spatial component to relate species resource use and availability (Manly et al. 2002). The increased availability of remotely sensed data and spatial modeling capabilities now allows a generation of more spatially explicit representations of used resources. These advances are offering much promise to integrate spatial information of biotic interactions between species and their resources into species distribution models (Marzluff et al. 2004, Kertson et al. 2011, Kamler et al. 2012).

Here, we show how embedding concepts from RST into SDM can enhance understanding of environmental conditions that determine species presence across geographic space. A priori, one would expect the SDM to encompass a wide range of activities and behaviors (i.e., hunting, defending territory, shelter, and perhaps exploring). Thus location data from an RST that focuses primarily on acquiring resources from a single activity (i.e., hunting) should be geographically nested within the more general SDM distribution model. We show, however, that this expectation was not supported in a case study of the predator–prey interactions between the Canada lynx (*Lynx canadensis*) and its primary prey, snowshoe hare (*Lepus americanus*). Our data were obtained from a long-term monitoring program following the establishment of reintroduced lynx into their historical range in Colorado, USA (Devineau et al. 2010). We also demonstrate how species distributions vary temporally to produce different annual winter habitat associations for lynx, a phenomenon that would

have been missed by pooling the data across years as per the standard SDM approach. We discuss the implications of this for distribution modeling of species interactions.

METHODS

Study system

Canada lynx in Colorado were extirpated, or reduced to a few individuals, by the late 1970s, most likely due to predator control efforts (McKelvey et al. 2000, Meaney 2002). From 1999 to 2006, the Colorado Division of Wildlife (CDOW) reintroduced 218 wild-caught lynx into southwestern Colorado in an effort to establish a viable population of the species in the state (Devineau et al. 2010). Data used here are part of the post-release monitoring research project conducted during winters 2001–2006 (Shenk 2010).

The study area was characterized by wide plateaus, river valleys that bottom at ~1500 m, and rugged mountains reaching elevations over 4200 m. Consequently, there are strong gradients in physical attributes of the landscape that created heavily dissected vegetation types and, hence different habitat conditions. For instance, alpine tundra dominated the study area above treeline (~3300–4200 m). Below treeline, Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) forests were the dominant vegetation at the higher elevations, but also occurred on north-facing slopes at mid-elevations. The coniferous forest in areas below ~2800 m elevation were dominated by lodgepole pine (*Pinus contorta*) and Douglas-fir (*Pseudotsuga menziesii*) intermingled with aspen (*Populus tremuloides*) groves. Riparian areas at all elevations contained willow species (*Salix* spp.).

Overall analysis approach

We conducted a systematic series of analyses to characterize habitat conditions determining the lynx SDM and the lynx–hare TIDM. Because the data come from a lynx reintroduction, there was a chance that the lynx locations in each of six years had not reached equilibrium with environmental conditions, thus violating a key assumption of SDM (Guisan and Thuiller 2005). We therefore began our analyses to evaluate this assumption. We used multidimensional ordination to characterize the annual winter environmental conditions related to lynx locations and lynx–hare encounter locations (Hik 1995, Tolon et al. 2012). Furthermore, we postulated that hare response to reintroduced lynx, and thus the spatial characteristics of lynx–hare encounters, would be a function of predation pressure. So, in addition to conducting analyses separately for each year, we estimated individual utilization distributions (UD) to examine how predator–prey encounters differed for areas of high and low lynx activity. The variables most associated with these locations were then implemented in MaxEnt (maximum entropy modeling)

to generate SDM and TIDM for each year individually and all years in the aggregate.

Location data

Lynx locations.—Aerial and satellite telemetry provided coarse-resolution (1.5-km²) data on lynx locations during the course of their daily activities (Devineau et al. 2010, Shenk 2010). Reintroduced lynx were generally released during spring. Only winter (November–April) locations were used for analyses to match the snow-tracking data. Moreover, locations obtained during the first six months post-release were removed in order to exclude atypical movements while individuals were initially exploring their new landscape. Data were grouped by winter rather than calendar year such that telemetry or snow-tracking locations obtained November 2001–April 2002, for example, were grouped into “2001.”

Released lynx were equipped with two types of telemetry devices. All lynx released in 1999 were fitted with VHF radio collars (Telonics, Mesa, Arizona, USA). Except for five males released in 2000, lynx released after 1999 were fitted with dual satellite/VHF radio collars (Sirtrack, Havelock North, New Zealand). The satellite locations were obtained using conventional Argos tracking whereby the transmitter locations are collected by measuring the Doppler Shift on its transmit frequency (Collecte Localisation Satellites 2011). The satellite collar’s platform transmitter terminal was programmed to be active for 12 hours during one day per week, and locations were obtained via Argos, National Aeronautics and Space Administration, and National Oceanic and Atmospheric Administration satellites (Collecte Localisation Satellites 2011). Aerial VHF locations were typically collected weekly during winter months. Only the single most precise location (e.g., in descending order, Argos location code 3, VHF, Argos location code 2, 1) obtained within a 24-hour period was retained for each individual to maintain independence between locations. The error distribution (1 standard deviation) for satellite locations retained for analysis was ≤ 1.5 km (Theobald and Shenk 2011).

Lynx–snowshoe hare locations.—Lynx encounters with prey were identified from snow-tracking surveys and the prey species was identified by either tracks or animal remains (Shenk 2005). Snow-tracking data revealed that ~80% of the lynx–prey encounters involved snowshoe hares. Moreover, complementary scat analysis confirmed that snowshoe hares comprise the majority (65–90%) of the winter diet of the reintroduced lynx (Colorado Division of Wildlife, unpublished data). An average of 1.7 lynx–snowshoe hare encounters were recorded during individual snow-tracking surveys that typically spanned 2.8 km (range 0.5–5 km). We recognize that there may be nonindependence of multiple lynx–snowshoe hare encounters in a single tracking survey at our modeling resolution of 1.5 km² if the encounter locations fell into adjacent data

raster cells (i.e., $n = 2$ cells would be used by $n = 1$ lynx). For modeling purposes, independence can be achieved by removing observations that cross into an adjacent cell. However, fewer than 8% of the snow-tracking data had this property. We felt that this small number of dependencies would not significantly bias our distribution model. Thus we retained all data to ensure that the TIDM would be as representative of lynx–snowshoe hare spatial encounter distributions as possible.

Environmental data

Coarse-resolution environmental data.—We selected vegetation, topographic, and landscape characteristics previously identified as important to Canada lynx in Colorado (Ivan et al. 2011, Theobald and Shenk 2011) for our analyses (Table 1). We extracted seven vegetation classes from the 114 land-cover classes in the Colorado Vegetation Classification Project (CVCP) data set, a land-cover layer derived from 30-m² resolution 1993–1995 Landsat images (available online).⁵ Using Geospatial Modeling Environment function “Intersect polygons with raster” (Beyer 2012), percent cover was calculated for each of the seven vegetation classes at a 1.5-km² resolution to correspond to the accuracy of the lynx telemetry data. A 30-m² resolution digital elevation model (DEM; Gesch et al. 2002) was used to calculate the following topographic parameters at 1.5-km² resolution: mean slope, elevation, and topographic wetness plus (TWI+). The topographic wetness index metric was originally presented by Beven and Kirkby (1979) to predict soil moisture based on slope. Theobald (2007) adjusted the topographic wetness metric into TWI+ by including aspect into the soil moisture equation and developed a GIS toolset (LCaP) to implement the calculations. The effect of forest fragmentation was included by calculating distance from each 30-m² pixel (the resolution of the Colorado Vegetation Classification Project data set) to the nearest contiguous forest patch larger than 50 ha with the Spatial Analyst regional grouping tool in ArcGIS (version 10.1, ESRI 2012), then averaged all 30-m² pixels to upscale the metric to 1.5 km².

Fine-resolution environmental data.—Fine-resolution environmental variables were measured at 25 sampling points equally spaced 3 m apart (5 × 5 grid) within a 12 m² area centered at each lynx–snowshoe encounter location (Shenk 2005). Environmental variables measured at each sampling point were: (1) the understory percent cover in a 3 cm radius column at three height classes above snow cover (0–0.5 m, 0.51–1.0 m, 1.01–1.5 m); (2) an ocular estimate of canopy cover over each point (Ganey and Block 1994); and (3) snow depth. Within the 12 m² area, the number and species of all conifer and deciduous trees were recorded by size class

⁵ www.ndis.nrel.colostate.edu/coveg

TABLE 1. Coarse-resolution (1.5-km²) environmental variables used to develop the species distribution model (SDM) and trophic interaction distribution model (TIDM) for Canada lynx (*Lynx canadensis*) in Colorado for winters 2001–2006.

Type and parameter	Description
Topography†	
Elevation	average elevation
Slope	average slope
Topographic wetness+‡	indicator of soil moisture based on aspect and slope
Landscape	
Dist. forest patch	distance (km) to nearest contiguous forest patch > 50 ha
Percent vegetation cover§	
Spruce–fir	Engelmann spruce (<i>Picea engelmannii</i>) and subalpine fir (<i>Abies lasiocarpa</i>)
Lodgepole pine	<i>Pinus contorta</i>
Aspen	<i>Populus tremuloides</i>
Willow	<i>Salix</i> spp.
Mixed spruce–fir	Engelmann spruce/subalpine fir with Douglas-fir (<i>Pseudotsuga menziesii</i>), aspen, and lodgepole pine
Montane shrubs	Gambel oak (<i>Quercus gambelii</i>), serviceberry (<i>Amelanchier utahensis</i>), and snowberry (<i>Symphoricarpos</i> spp.)
Montane forest	Douglas-fir, ponderosa pine (<i>Pinus ponderosa</i>), and mixed Douglas-fir/ponderosa pine

† Digital elevation model, USGS DEM (Gesch et al. 2002).

‡ Abbreviated TW+ (Theobald 2007).

§ Colorado Vegetation Classification Project (www.ndis.nrel.colostate.edu/coveg).

(diameter at breast height [dbh] = 0–15, 15.1–30, 30.1–45, 45.1–60, and >60 cm).

Analysis

Distribution of predator activity.—We investigated whether the environmental conditions surrounding lynx–hare encounters varied in relation to lynx predation pressure. Following Kauffman et al. (2007, 2010) and Kertson et al. (2011), lynx telemetry locations were used to estimate utilization distributions (UD) for each lynx during each winter. We defined areas most intensely used by lynx (i.e., within the 50% isopleth of the UD) as high-activity areas in which lynx concentrated their daily activities, such as hunting and resting. Presumably these areas presented relatively high risk of lynx predation to hares residing in them. Areas less intensely used by lynx (i.e., beyond the 50% isopleth diffusing outward to the 95% isopleth) were defined as low-activity areas. We used data from individual lynx that had at least 20 locations per winter (mean = 28.6 locations, SE = 0.4) to estimate the 50% and 95% UD. Lynx space-use patterns may change annually due to resource availability and territory vacancies (Ward and Krebs 1985, Vashon et al. 2008; Colorado Division of Wildlife, unpublished data). For lynx monitored over multiple winters, we assumed that each winter's UD was independent. UD were estimated using the adaptive local convex-hull approach (a-LoCoH), which is a nonparametric home-range estimator (Getz and Wilmsers 2004, Getz et al. 2007). Thus, for a given telemetry location, minimum convex polygons (i.e., local hulls) were constructed using all other locations within a preselected distance, a , from that location. Following Getz et al. (2007), we defined a as the maximum distance between all locations collected for a given individual. The union of all possible local hulls formed the UD for each individual, along with

isopleths of intensity of use. We estimated the UD for each individual using the AdehabitatR package in R statistical software (Calenge 2006) and then projected the UD for all individuals in a single raster. A cell size of 1.5 km² was selected to match the accuracy of the telemetry locations. Only lynx–snowshoe hare encounters that occurred within the estimated high- or low-lynx-activity areas were used for the TIDM analysis.

Ordination.—Species distribution models are based on the assumption that species are at equilibrium with their environment (Guisan and Thuiller 2005). We used nonmetric multidimensional scaling (NMS; Kruskal 1964, Mather 1976, Kenkel and Orloci 1986) to test whether the environmental conditions associated with lynx locations and lynx–hare encounter locations were indeed in equilibrium. This analysis also provided insight into which of the candidate variables best described differences in environmental conditions where lynx occurred or encountered hares among years. The advantage of NMS is that it requires no assumptions about the nature of a species response to underlying environmental gradients; further, the algorithm seems robust to variability and nonlinearities in the data (Minchin 1987, McCune and Grace 2002). Prior to analysis, these data were standardized by dividing the value of each location-specific environmental variable by the maximum value observed for that variable across all locations. The Mahalanobis distance measure (McCune and Grace 2002) was used to account for the minor collinearity among the variables (average $r^2 = 0.028$, range = 0.000064–0.563). NMS iteratively searches for the solution that characterizes relationships among the original variables with the greatest fit and the lowest “stress,” the inverse measure of fit (McCune and Grace 2002). We performed a step-down procedure (3000 runs of a Monte Carlo test and a maximum of six possible

axes) to identify the number of axes (i.e., dimensionality) needed to define the environmental conditions for each model containing fine- and coarse-resolution data. We plotted stress values in relation to the number of dimensions to identify the optimal number of axes needed to represent the environmental conditions at sites used by lynx and at lynx–snowshoe hare encounter locations. The optimum was defined as the number of axes present when the stress value started decreasing as the number of dimensions increased (McCune and Grace 2002). NMS analyses were conducted using the *nmds* function of the *ecodist* package (version 1.2.7, Goslee and Urban 2007) in R (version 2.15, R Development Core Team 2012).

Predator distribution modeling.—Many statistical approaches are available to estimate SDMs (Elith et al. 2006, Peterson et al. 2011), and multiple approaches are often used to compare SDMs and determine congruency among models. Our goal here was to evaluate how detailed information about where encounters occur between a predator and its primary prey could further enhance the development of the predator SDM. We therefore elected to use only one modeling approach, maximum entropy in MaxEnt software (ver. 3.3.1; Phillips et al. 2006), to generate our SDM and TIDM. MaxEnt performs well in comparison with other distribution models, and is recognized as particularly effective when species occurrence data consist of presence-only records and small samples (Elith et al. 2006, Phillips and Dudík 2008).

MaxEnt requires two types of input data: a grid depicting environmental variables (i.e., raster of environmental variables) and the point coordinates of species occurrences. Coarse-resolution (1.5-km²) environmental variables were used for all distribution models. We used the lynx occurrences provided by presence-only telemetry data ($n = 493$ locations, range = 11–156 locations per lynx per winter; range = 31–80 lynx per winter) to generate the SDM. We used presence-only lynx–snowshoe hare encounters that were collected during snow-tracking ($n = 493$, range = 11–156 lynx–snowshoe hare encounters per winter, range = 6–22 lynx per winter) to generate the TIDM.

To generate SDM estimates, we obtained subsamples of lynx locations that matched the sample size for the TIDM (which had fewer location points). We ensured that each individual lynx monitored contributed equal information to the analysis by using a bootstrapping procedure to randomly select a fixed number of records from each animal within a winter. This approach also removed any spatial and temporal autocorrelation that could diminish the reliability of the SDM. We also conducted a resampling procedure to verify that our results were robust to the subsampling. Each set of presence-only data (i.e., SDM and TIDM) was randomly assigned to training (75% of locations) and testing (25% locations) data sets, and this process was

repeated 10 times using bootstrap sampling from each set of occurrence data.

We used 10 000 random background points for each model. Background samples in MaxEnt are considered random samples in the study region where the species could be present or absent, as opposed to “pseudo-absences” (Phillips and Dudík 2008). Predictions from the 10 models were averaged to produce final maps that represent the mean probability of lynx presence at a site, conditioned on environmental variables (Phillips and Elith 2013). Probability values near 1 indicated areas with the most suitable environmental conditions, whereas values close to 0 represented unsuitable environmental conditions (Phillips and Dudík 2008). We also conducted a jackknife test to estimate the relative contribution of each predictor variable in explaining the geographic distribution of lynx.

Model performance was evaluated using a testing data set to estimate area under the curve (AUC) of a receiver operating characteristic (ROC) plot (Elith et al. 2006). The AUC in MaxEnt evaluates the performance of the model based on a true-positive accuracy assessment, which is the ratio of cells correctly classified to the total number of cells classified. AUC values range from 0 (distribution estimates worse than random) to 1 (a perfect estimate of distribution), with 0.5 indicating random classification.

We evaluated whether or not the SDM and TIDM were more different than expected by chance using Schoener’s D similarity metric (Schoener 1968, Warren et al. 2008, 2010, Veloz et al. 2012). Schoener’s D ranges from 0 (species’ estimated niches do not overlap) to 1 (estimated niches completely overlap at all grid cells). A randomization test was used to generate an expected null distribution of similarities and we compared the similarity from our observed SDM and TIDM to this null. Implementing the randomization test required pooling lynx telemetry locations and lynx–snowshoe hare encounter locations into a single data set. Pooled locations were then randomly assigned to either of two arbitrary groups. Each of the new groups contained the same number of locations as the two original empirical data sets (Warren et al. 2010). We repeated this sampling procedure to create 10 random data sets of two groups each. We used MaxEnt to produce models for each group in a sample pair and subsequently to conduct the niche-identity test by estimating Schoener’s D in ENMTools (ver. 1.3; Warren et al. 2008, 2010). The null distribution generated by the 10 Schoener’s D estimates was then compared with the similarity value for the observed SDM and TIDM. The hypothesis of niche similarity is rejected when the empirically observed value for Schoener’s D falls outside of the 95% confidence limit for the null distribution.

RESULTS

Ordination of fine- and coarse-resolution environmental data.—Our results confirmed that annual lynx–snow-

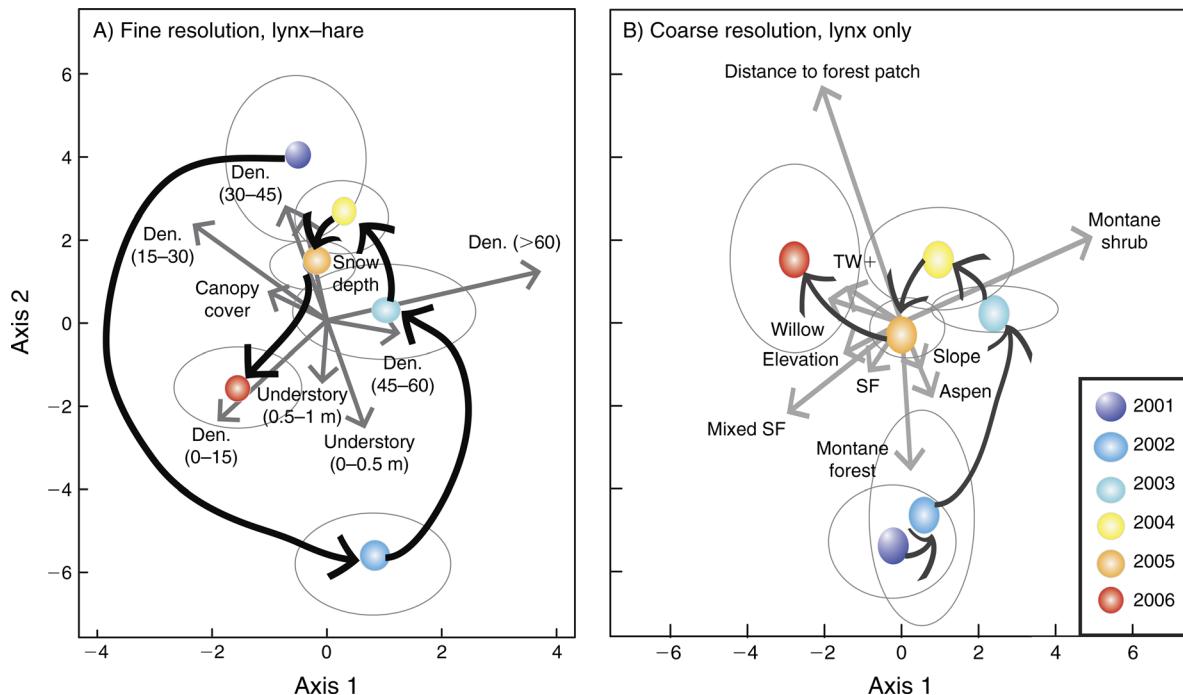


FIG. 1. (A) The best nonmetric multidimensional scaling (NMS) ordination created with fine-resolution environmental conditions where lynx encountered snowshoe hares. (B) The best NMS ordination created with coarse-resolution environmental conditions from the telemetry data used in the lynx-only species distribution model. For each plot, the markers and associated ellipses represent the mean scores \pm SE. Smaller distances between consecutive winters, as indicated by curved arrows, represent years where lynx use had similar environmental characteristics. The angle and length of the vector lines indicate the direction and relative strength of the relationship between environmental variables and the ordination axes. Abbreviations are: Den., stem density for each diameter at breast height (dbh); SF, spruce-fir forest; TW+, topographic wetness.

shoe hare encounters and lynx-only telemetry observations were not in equilibrium with the environment (Fig. 1). The best ordination for the fine-resolution environmental conditions measured at lynx-snowshoe hare encounters was described by a three-dimensional solution that yielded a stress value of 0.21 and a cumulative r^2 of 0.901. After inspecting all three axes, we determined that the first two accounted for the highest proportion of the variation and thus we present results using the first two axes only. Although the specific locations of points along the ordination axes are arbitrary, the spacing of points on the plot relative to one another offers meaning, especially when presented in conjunction with vectors describing the important environmental variables along the ordination axes.

The most important fine-scale environmental variables associated with lynx-snowshoe hare encounters were density of medium-sized trees (30–60 cm dbh), snow depth, and understory vegetation percent cover from the snow surface to 0.5 m (Appendix A), but their importance varied over time (Fig. 1A), with the largest differences being observed among the first three years of data. After that, differences in fine-scale attributes of hare encounters were more similar among years. The environmental conditions associated with lynx-snowshoe hare encounters also varied with the intensity of

lynx activity (Appendix A). There was also interannual variability between areas of high and low lynx activity (Appendix A). In 2001, lynx-snowshoe hare encounters in both high and low lynx activity density areas were relatively similar and characterized by higher snow depth and increased density of medium-sized trees. There were large differences between high and low lynx activity density areas in 2002 and 2006. The environmental variables describing snowshoe hare-lynx encounter locations within high and low lynx activity density areas were similar in the intervening years (Appendix A).

The best ordination for the lynx telemetry data using coarse-resolution (1.5-km²) environmental variables was a three-dimensional solution that contained a stress value of 0.13 and a cumulative r^2 of 0.976. Again, we present the results for the first two axes because they explain the greatest variation. We found that vegetation (percentage of mixed spruce-fir, montane forest, and montane shrub) and landscape composition (proximity to forest patches larger than 50 ha) were important factors explaining variation in annual lynx spatial locations (Appendix A). The coarse-resolution environmental variables at lynx-only locations during the first two winters were relatively constant and strongly influenced by the presence of montane forest. The

TABLE 2. Number of observations, area under the curve (AUC), and percentage contribution of the three top-ranked environmental variables for each SDM and TIDM for all winters combined ("Overall" row) and each winter.

Winter	<i>n</i>	Lynx-only SDM				Lynx-SSH TIDM			
		AUC	Rank 1	Rank 2	Rank 3	AUC	Rank 1	Rank 2	Rank 3
Overall	493	0.92	elevation (43%)	spruce-fir (34%)	willow (9%)	0.96	spruce-fir (55%)	elevation (13%)	willow (12%)
2001	11	0.91	spruce-fir (79%)	dist. forest patch (7%)	elevation (5%)	0.92	spruce-fir (43%)	dist. forest patch (35%)	aspen (10%)
2002	72	0.91	spruce-fir (64%)	willow (16%)	lodgepole (5%)	0.97	spruce-fir (62%)	willow (16%)	slope (5%)
2003	120	0.94	spruce-fir (41%)	elevation (23%)	slope (7%)	0.98	spruce-fir (59%)	willow (13%)	TW+ (7%)
2004	88	0.93	spruce-fir (56%)	willow (17%)	mixed SF (6%)	0.97	spruce-fir (61%)	willow (12%)	TW+ (7%)
2005	134	0.94	elevation (51%)	spruce-fir (11%)	dist. forest patch (10%)	0.96	spruce-fir (62%)	willow (19%)	slope (6%)
2006	156	0.93	spruce-fir (48%)	elevation (32%)	willow (6%)	0.97	spruce-fir (59%)	willow (10%)	dist. forest patch (9%)

Note: Observations were telemetry locations for the lynx-only species distribution model (SDM) and lynx-snowshoe hare (SSH) encounters for the trophic interaction distribution model (TIDM).

environmental conditions associated with lynx observations shifted toward moist, high-elevation spruce-fir and willow vegetation cover in 2003–2006. Thus temporal shifts in environmental conditions used by lynx were similar to those observed using fine-resolution attributes.

Comparison of SDM and TIDM.—When all years were aggregated, MaxEnt produced a good fit for both distribution models (mean AUC for SDM = 0.923, SE = 0.004; mean AUC for TIDM = 0.964, SE = 0.002). The jackknife procedure showed that elevation, percent cover of spruce-fir, and percent cover of willow were the variables most associated with lynx-only or lynx-snowshoe hare distributions (Table 2); each variable was positively associated with the probability of lynx locations or lynx-hare encounters. Because the environmental conditions associated with the location data varied over the winters (Fig. 1B), we created a SDM and a TIDM for each year. Spruce-fir (>40% contribution) was the most highly associated variable for the SDM for each winter, except in 2005, but the importance of the other variables changed annually (Table 2). In contrast, after 2001, presence of subalpine spruce-fir and willow were consistently the most highly associated variables of the TIDM (Table 2).

The niche-identity test revealed large disparities between the lynx-only SDM and lynx-snowshoe hare encounter TIDM across years (except for 2001) and when all the years were aggregated (Fig. 2). The SDM and TIDM spatial extents for each year almost completely overlapped when the probability of lynx presence was <75%. But, at high (>75%) probability of lynx presence (areas likely to be identified as most used by lynx), the SDM and TIDM matched at only 60% of cells; mismatches included areas identified by SDM but not TIDM, as well as areas identified by TIDM but not SDM. The SDM represented the lynx winter distribution over all lynx activities. The TIDM constrained the lynx winter distribution to lynx-snowshoe hare interactions and predation (Fig. 2).

DISCUSSION

We found that a trophic interaction distribution model (TIDM) bridges two scientific cultures that use altogether different approaches to modeling species distribution by characterizing the nuanced temporal and spatial interactions of a predator and prey species. This refinement can be used to highlight important spatial locations and habitat attributes that improve niche modeling beyond standard SDM. For instance, predators and prey may engage in temporally dynamic behavioral games (e.g., Lima and Dill 1990, Lima 2002). This behavior may cast doubt about the assumption of most SDM approaches; environmental variables deemed important for building the SDM are invariant (are at steady state) over the time horizon that the SDM data were collected. Our TIDM approach offers a flexible way to consider not only the spatially explicit and dynamic biotic interactions, but also information on temporal variation and spatial heterogeneity of the environment and community composition to refine the niche space of a predator species in relation to its prey.

Understanding the dynamic nature of the system can offer greater biological realism when characterizing the geographic distribution of a species. We found that lynx did indeed reach a steady state with their environment after they gradually shifted their use of space over three winters post reintroduction (Fig. 1). However, the steady state was only observed for environmental characteristics most important to predicting lynx-snowshoe hare TIDM. Environmental characteristics identified as important in the lynx-only SDM continued to fluctuate annually (Table 2). The mismatch between the SDM and TIDM became even more evident when we compared the predicted geographic locations for each distribution model. The SDM probably encompasses a wider range of activities and behaviors (i.e., hunting, defending territory, and shelter) than a TIDM focusing solely on lynx hunting for snowshoe hare. Therefore, locations in which lynx encounter a snowshoe hare should presumably be geographically nested within the more general lynx-only SDM distribution model.

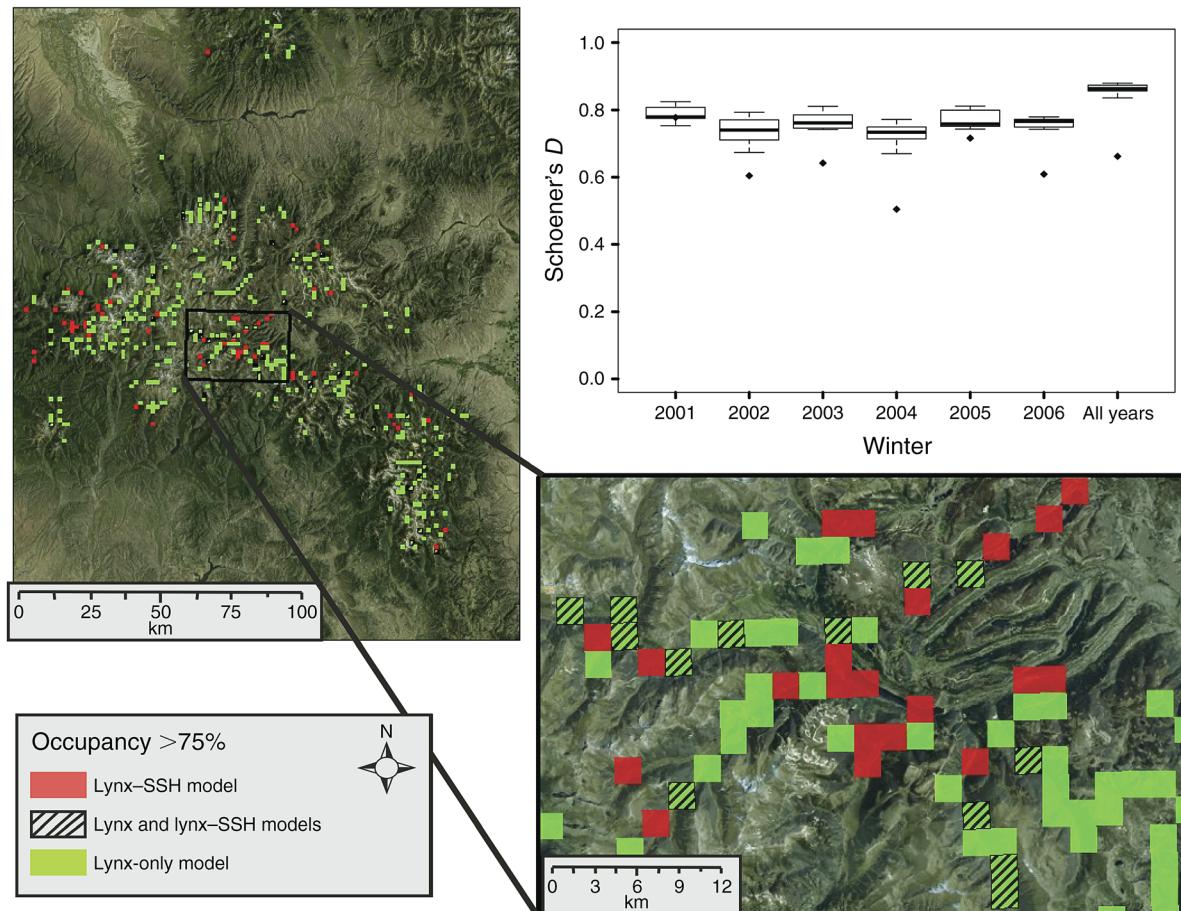


FIG. 2. The niche-identity test for comparing Schoener's D score (diamonds) from lynx-only and lynx-snowshoe hare (SSH) models to a null distribution with box plots (top right). For each year (and all years combined), the box plot shows the median (center line), 75th percentile (top of box), and 25th percentile (bottom of box); whiskers connect the largest and smallest values within 1.5 interquartile ranges. Similarity scores for the lynx-only and lynx-snowshoe hare encounter models were lower than the null hypothesis of niche equivalency, indicating that the niches were not equivalent. To illustrate, the 2004 distribution models are displayed (upper left), with a subset of locations enlarged (bottom right) showing probability of occurrence $>75\%$ from the lynx-only species distribution model derived from telemetry locations (green), trophic-niche distribution model generated from lynx-snowshoe hare encounters (red), and areas where the two distribution models agree (hatched).

However, this was not so: 40% of the areas important for the lynx-snowshoe hare encounters were not identified as areas highly important in the lynx-only model (Fig. 2). That is, SDMs may potentially under-represent the spatial extent and environmental conditions needed to support lynx-snowshoe hare trophic interactions.

We interpret the temporal shift in environmental conditions used by lynx to arise from a behavioral response of lynx and snowshoe hare as lynx become accustomed to their new environment and as hares adjust their use of space to adapt to a new predation threat. However, we cannot rule out hidden effects of sample size variation on our results. We were able to equalize sampling intensity by randomly selecting the same number of observations in lynx-only model to match the number of encounters in the lynx-snowshoe hare model to reduce effects of sampling bias. However,

we were unable to match sample size between years. Thus, the shift we attribute to behavior also could have arisen from a biased measure of space use in the original (2001) data set owing to small sample size. Although MaxEnt is deemed reliable for sample sizes as small as 10 (Hernandez et al. 2006, Guisan et al. 2007), and numerous studies build SDM with such low sample sizes (e.g., Kharouba et al. 2009, Vasconcelos et al. 2012), our results suggest caution in inferring mechanisms determining species geographic distributions when only few samples are available.

Our approach was motivated by a conceptual understanding of the spatial habitat domain of predator-prey interactions driven by predator hunting behavior (Schmitz et al. 2004, Schmitz 2010). This theory holds that the spatial extent of predator and prey movement and habitat selection is largely influenced by predator hunting mode and prey mobility to avoid

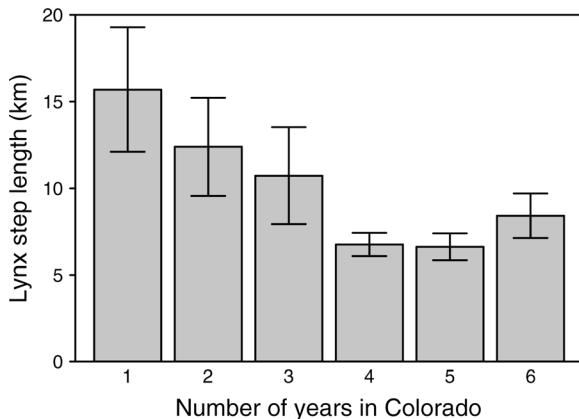


FIG. 3. Step length (mean \pm SE) for lynx during each winter since their release. See Appendix B for details on the calculation of step length.

predation. Experimental insights from predator–prey interactions indicate that steady states in habitat use and behavioral predator avoidance by prey follow a period of transient behavior, as the prey become accustomed to the nature and level of predation risk determined by the different hunting modes (Schmitz et al. 2004, Schmitz 2010). Hence, detailed understanding of the dynamic interplay between predators and prey requires characterizing temporal variation in predator and prey space use, as well as temporal variation in the environmental variables associated with the interactions. This has rarely been done for species across large landscapes with application of RST approaches, in part, because of the logistical difficulties of conducting the kinds of controlled experiments in geographically extensive and complex landscapes needed to resolve the important variables (Dray et al. 2012). We capitalized here on a quasi-experiment: a predator reintroduction in which predators and prey settle over time into steady-state space and habitat use following an initial “perturbation” represented by the predator reintroduction. This information allowed us to quantify how a potentially new risk factor for prey propagates across a landscape over time and influences spatial habitat use of the predator and/or the prey.

As the members of the community respond to each other’s presence, species adjust their behavioral traits to align resource intake against risk (Schmitz 2005). Our effort to characterize a species’ distribution in terms of its trophic interactions (TIDM) showed that lynx–snowshoe hare encounters changed temporally, suggesting a dynamic interplay between the environment and biotic interactions among the reestablished predator–prey populations. Thus, aggregating all of the observations (both transient and steady-state) into a single projection, as would customarily be done with SDM, would be likely to conceal key insights about temporal changes in environmental variables important to the predator species (Fig. 1). Likewise, if only data from the

initial transient period were used, one would arrive at a biased assessment of the intensity of the trade-off between predator avoidance and resource acquisition, and misidentify the spatial habitat characteristics needed for long-term persistence of the predator and prey.

By evaluating predator–prey interactions through the duration of the predator transient phase as well as the steady-state phase, we were able to identify the spatial conditions that sustain the newly established trophic interaction. Our results revealed that the duration of the transient phase might be attributed to the ability of lynx to adjust their hunting mode in response to prey. Maletzke et al. (2008) observed that lynx adjust their hunting strategies throughout the landscape to become more efficient hunters. In northern boreal forests, lynx are known to switch from an active-stalking hunting mode during high snowshoe hare densities to a more energetically efficient sit-and-ambush hunting mode during low snowshoe hare densities when they are more elusive (Murray et al. 1995, O’Donoghue et al. 1998, Maletzke et al. 2008). In our study, hares, like other prey species (Berger et al. 2001), may have been naïve about the predation threat from lynx immediately after the reintroduction, but then over time settled to a steady-state habitat choice that made them more elusive to lynx once they calibrated landscape-scale predation risk. Indeed, the time to steady state varied directly with the intensity at which lynx used particular spatial locations. Throughout most of steady-state phase, snowshoe hares had a 70% success rate escaping encounters with lynx (Colorado Division of Wildlife, unpublished data), supporting our contention that the spatiotemporal dynamics of the predator–prey interaction may have been driven by the hare’s ability to discern and respond to different predation threats. This dynamic may have been reflected in the temporally variable nature of the TIDM in the three years following the reintroduction, leading eventually to a steady state. Furthermore, analyses of lynx distribution across the landscape using step lengths collected during winter months (Fig. 3; see Appendix B for details) revealed that lynx roamed more widely in the early years after reintroduction, but average step lengths decreased by half in later years. This is consistent with the kind of movement one would expect if there were a shift in hunting behavior from active to more sedentary sit-and-wait stalking, as is observed for lynx populations in Canada. These observations may also suggest that lynx refined their use of space among years by learning to navigate in a new environment. During this adjustment, lynx were probably cueing into environments on the landscape that enabled successful kills of snowshoe hares, thus increasing their hunting efficiency.

Our study focused on one important prey of lynx and thus may not reflect the full TIDM if other prey species (e.g., red squirrel *Tamiasciurus hudsonicus*) were considered. Nevertheless, the same approach could be used to characterize lynx interactions with other potential prey

on the landscape to elaborate the TIDM across different prey species and additional behaviors (i.e., breeding and summer den sites) key to species persistence. Likewise, one can apply the TIDM approach to develop understanding of how a single prey such as hare responds to different predators, both singly and collectively. For example, before the lynx reintroduction, wintering snowshoe hares in Colorado faced primarily raptors and coyotes (*Canis latrans*) (Buskirk et al. 2000). Hares may have selected dense cover from medium-sized trees to optimize their ability to avoid avian predators, as reflected in the 2001 data set, and may have minimized coyote predation pressure by seeking refuge in deep snow (Murray et al. 1995, Buskirk et al. 2000). One year after lynx were reintroduced, snowshoe hares appeared to display heightened sensitivity to this particular predator, as revealed by behavior to select different habitat conditions in winter that probably reduced predation success by the lynx, but made them more vulnerable to avian predators. After several years, however, they seemed to settle into a suite of steady-state environmental conditions and spatial distributions that presumably balanced risk from their avian predators against risk from lynx.

Species distribution or niche models increasingly are becoming important analytical tools to support conservation planning for biodiversity, especially in the face of changing environmental conditions over multi-decadal time horizons (Peterson et al. 2011). Most SDMs are built by relating single-species observations to ecological gradients of environmental variables, which may be only indirectly related to species occurrences (e.g., land cover, vegetation, and thermal conditions) (Guisan and Zimmermann 2000). Yet, for effective conservation strategies reliant on understanding species interactions, models that accurately characterize current and future species distributions should include species interactions as well as environmental conditions (Chase and Leibold 2003, Schmitz et al. 2003, Kearney and Porter 2009, Paine 2010). Most approaches that do consider species interactions use focal species distributions merely as additional spatial covariates that constrain the SDM of the primary species of interest (Leathwick and Austin 2001, Araújo and Luoto 2007, Heikkinen et al. 2007, Schweiger et al. 2008, Meier et al. 2010, Ettinger et al. 2011).

Although these approaches offer some improvement in identifying where species might overlap, the coarseness in resolution of the data precludes characterizing the spatial nuances of the interactions, determined by factors such as species behavior (e.g., Lima and Dill 1990, Lima and Zollner 1996) that may be critically important for projecting future species distributions (Zarnetske et al. 2012). For example, predator-prey species interactions often involve spatial risk avoidance behavior by prey that can only be characterized by finer-resolution data (Lima and Zollner 1996, Brown et al. 1999, Thaker et al. 2011). We show here the added value

of including information on known species encounter locations to derive biologically richer insights about the environmental conditions in which species interactions occur.

All approaches used to characterize species distributions, RST, and SDM can benefit from further development to produce the kind of mechanistic insight needed to explicitly address hypotheses concerning species survival and reproduction across geographic ranges (Moorcroft et al. 1999, Buckley et al. 2010, Schurr et al. 2012). Mechanistic models require precise estimates of abundance and demography to characterize the relationship between species fitness and the environment. The TIDM approach that we describe here provides a step toward increased precision and mechanistic understanding of the environmental determinants of species range distributions. Using confirmed trophic interaction data in relation to resource availability at the appropriate scale helped to identify temporally dynamic mechanisms in habitat conditions that contributed to predator species niches and, hence, their presence across landscapes.

Conclusion

This study provides a cautionary tale for emerging conservation and management efforts that characterize species habitat needs based solely on SDM approaches (IUCN 1998). Data-sharing initiatives (museums, herbariums, surveys, and so forth) across the scientific community have dramatically increased the availability of point occurrence data for species distribution models. Although implications of the spatial accuracy of the locations used in species distribution models has been extensively evaluated (Graham et al. 2007), SDMs do not typically account for the temporal variation among locations or the potential change in community structure when locations were collected. Our results suggest that in a dynamic setting, such as a reestablished predator-prey interaction, a small time scale (i.e., years) can have a critical effect on the reliability of the species distribution model. Assessing habitat without consideration of how the spatiotemporal nature of interactions between focal species and their resources and predators constrains space use (akin to the difference between potential and realized niches) could lead one to mischaracterize the spatial domain needed to ensure persistent populations, especially in the face of global change in the form of habitat alteration and climate change.

Furthermore, climate change is shifting the spatial distribution of many species, and in turn stands to alter the structure and function of communities that these species comprise (Parmesan 2006, Zavaleta et al. 2009). The potential of altered community composition and ecosystem processes has increased the urgency of incorporating biotic interactions into species distribution models (Schmitz et al. 2003). If established predator-prey communities disassemble and reassemble

in a new region, it remains uncertain if the interactions will be reestablished to their original equilibrium as environmental conditions change (Menéndez et al. 2008). Here we showed the promise of using species encounter locations at fine resolution to provide the kind of insight needed to characterize how changing environmental conditions influence species distribution patterns in response to their biotic interactions. We encourage application of approaches such as RST to complement existing SDM approaches to develop more biologically accurate models of species geographic range distributions.

ACKNOWLEDGMENTS

The analyses presented here were completed at the Yale University School of Forestry and Environmental Studies. We are grateful to all the field technicians for countless hours of field data collection in harsh environments. We sincerely thank M. Strickland, Z. Cleveland, D. Tripp, H. Johnson, and J. Muehlbauer for insightful comments during the development of the paper. Funding for the Colorado lynx reintroduction program was provided by Colorado Division of Wildlife, Great Outdoors Colorado, Turner Foundation, USDA Forest Service, Vail Associates, and the Colorado Wildlife Heritage Foundation.

LITERATURE CITED

- Araújo, M. B., and A. Guisan. 2006. Five (or so) challenges for species distribution modelling. *Journal of Biogeography* 33:1677–1688.
- Araújo, M. B., and M. Luoto. 2007. The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology and Biogeography* 16:743–753.
- Austin, M. P. 1980. Searching for a model for use in vegetation analysis. *Vegetatio* 42:11–21.
- Austin, M. P., and T. M. Smith. 1989. A new model for the continuum concept. *Vegetatio* 83:35–47.
- Berger, J., J. E. Swenson, and I. Persson. 2001. Recolonizing carnivores and naive prey: Conservation lessons from Pleistocene extinctions. *Science* 291:1036–1039.
- Beven, K. J., and M. J. Kirkby. 1979. A physically based, variable contributing area model of basin hydrology. *Hydrological Sciences Bulletin* 24:43–69.
- Beyer, H. L. 2012. Geospatial modelling environment. Version 0.7.2.0. <http://www spatialecology.com/gme>
- Brown, J. S., J. W. Laundre, and M. Gurung. 1999. The ecology of fear: Optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy* 80:385–399.
- Buckley, L. B., M. C. Urban, M. J. Angilletta, L. G. Crozier, L. J. Rissler, and M. W. Sears. 2010. Can mechanism inform species' distribution models? *Ecology Letters* 13:1041–1054.
- Buskirk, S. W., L. F. Ruggiero, and C. J. Krebs. 2000. Habitat fragmentation and interspecific competition: implications for lynx conservation. Pages 83–100 in L. F. Ruggiero et al., editors. *Ecology and conservation of lynx in the contiguous United States*. University Press of Colorado, Boulder, Colorado, USA.
- Calenge, C. 2006. The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197:516–519.
- Chase, J. M., and M. A. Leibold. 2003. *Ecological niches linking classical and contemporary approaches*. University of Chicago Press, Chicago, Illinois, USA.
- Collecte Localisation Satellites. 2011. Argos user's manual. Pages 1–68. <http://www.argos-system.org/web/en/76-user-s-manual.php>
- Devineau, O., T. M. Shenk, G. C. White, P. F. Doherty, Jr., P. M. Lukacs, and R. H. Kahn. 2010. Evaluating the Canada lynx reintroduction programme in Colorado: patterns in mortality. *Journal of Applied Ecology* 47:524–531.
- Dray, S., et al. 2012. Community ecology in the age of multivariate multiscale spatial analysis. *Ecological Monographs* 82:257–275.
- Elith, J., et al. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29:129–151.
- Elton, C. 1927. *Animal ecology*. Macmillan, New York, New York, USA.
- ESRI. 2012. ArcGIS version 10.1. Environmental Systems Research Institute, Redlands, California, USA.
- Ettinger, A. K., K. R. Ford, and J. HilleRisLambers. 2011. Climate determines upper, but not lower, altitudinal range limits of Pacific Northwest conifers. *Ecology* 92:1323–1331.
- Ganey, J. L., and W. M. Block. 1994. A comparison of two techniques for measuring canopy closure. *Western Journal of Applied Forestry* 9:21–23.
- Gesch, D., M. Oimoen, S. Greenlee, C. Nelson, M. Steuck, and D. Tyler. 2002. The national elevation dataset. *Photogrammetric engineering and remote sensing* 68:5–32.
- Getz, W. M., S. Fortmann-Roe, P. C. Cross, A. J. Lyons, S. J. Ryan, and C. C. Wilmers. 2007. LoCoH: Nonparametric kernel methods for constructing home ranges and utilization distributions. *PLoS One* 2:e207.
- Getz, W. M., and C. C. Wilmers. 2004. A local nearest-neighbor convex-hull construction of home ranges and utilization distributions. *Ecography* 27:489–505.
- Goslee, S. C., and D. L. Urban. 2007. The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software* 22:1–19.
- Graham, C. H., J. Elith, R. J. Hijmans, A. Guisan, A. T. Peterson, and B. A. Loiselle. 2007. The influence of spatial errors in species occurrence data used in distribution models. *Journal of Applied Ecology* 45:239–247.
- Guisan, A., and W. Thuiller. 2005. Predicting species distribution: Offering more than simple habitat models. *Ecology Letters* 8:993–1009.
- Guisan, A., and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* 135:147–186.
- Guisan, A., N. E. Zimmermann, J. Elith, C. H. Graham, S. J. Phillips, and A. T. Peterson. 2007. What matters for predicting the occurrences of trees: techniques, data, or species' characteristics? *Ecological Monographs* 77:615–630.
- Heikkinen, R. K., M. Luoto, R. Virkkala, R. G. Pearson, and J. Körber. 2007. Biotic interactions improve prediction of boreal bird distributions at macro-scales. *Global Ecology and Biogeography* 16:754–763.
- Hernandez, P. A., C. H. Graham, L. L. Master, and D. L. Albert. 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography* 29:773–785.
- Hik, D. S. 1995. Does risk of predation influence the cyclic decline of snowshoe hares? *Wildlife Research* 22:115–129.
- Holt, R. D. 2009. Bringing the Hutchinsonian niche into the 21st century: Ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences USA* 106:19659–19665.
- Hutchinson, G. E. 1957. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology* 22:415–427.
- IUCN (World Conservation Union). 1998. *Guidelines for re-introductions*. IUCN/SSC Re-introduction Specialist Group, IUCN, Gland, Switzerland.
- Ivan, J., M. Rice, T. Shenk, D. Theobald, and E. Odell. 2011. Predicted lynx habitat in Colorado. Pages 1–17. Unpublished report, Colorado Division of Wildlife, Fort Collins, Colorado, USA. <http://wildlife.state.co.us/SiteCollectionDocuments/DOW/Research/Mammals/Publications/CPWPredictiveLynxMapReport.pdf>

- Kamler, J. F., U. Stenkewitz, U. Klare, N. F. Jacobsen, and D. W. Macdonald. 2012. Resource partitioning among cape foxes, bat-eared foxes, and black-backed jackals in South Africa. *Journal of Wildlife Management* 76:1241–1253.
- Kauffman, M. J., J. F. Brodie, and E. S. Jules. 2010. Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade. *Ecology* 91:2742–2755.
- Kauffman, M. J., N. Varley, D. W. Smith, D. R. Stahler, D. R. MacNulty, and M. S. Boyce. 2007. Landscape heterogeneity shapes predation in a newly restored predator–prey system. *Ecological Letters* 10:690–700.
- Kearney, M., and W. Porter. 2009. Mechanistic niche modelling: Combining physiological and spatial data to predict species' ranges. *Ecology Letters* 12:334–50.
- Kenkel, N. C., and L. Orloci. 1986. Applying metric and nonmetric multidimensional scaling to ecological studies: Some new results. *Ecology* 67:919–928.
- Kertson, B. N., R. D. Spencer, J. M. Marzluff, J. Hepinstall-Cymerman, and C. E. Grue. 2011. Cougar space use and movements in the wildland–urban landscape of western Washington. *Ecological Applications* 21:2866–2881.
- Kharouba, H. M., A. C. Algar, and J. T. Kerr. 2009. Historically calibrated predictions of butterfly species' range shift using global change as a pseudo-experiment. *Ecology* 90:2213–2222.
- Kruskal, J. B. 1964. Nonmetric multidimensional scaling: a numerical method. *Psychometrika* 29:115–129.
- Leathwick, J. R., and M. P. Austin. 2001. Competitive interactions between tree species in New Zealand's old-growth indigenous forests. *Ecology* 82:2560–2573.
- Lima, S. L. 2002. Putting predators back into behavioral predator–prey interactions. *Trends in Ecology and Evolution* 17:70–75.
- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology* 68:619–640.
- Lima, S. L., and P. A. Zollner. 1996. Towards a behavioral ecology of ecological landscapes. *Trends in Ecology and Evolution* 11:131–135.
- Maletzke, B. T., G. M. Koehler, R. B. Wielgus, K. B. Aubry, and M. A. Evans. 2008. Habitat conditions associated with lynx hunting behavior during winter in Northern Washington. *Journal of Wildlife Management* 72:1473–1478.
- Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edition. Kluwer Academic, Norwell, Massachusetts, USA.
- Marzluff, J. M., J. J. Millsbaugh, P. Hurvitz, and M. S. Handcock. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's Jays. *Ecology* 85:1411–1427.
- Mather, P. M. 1976. Computational methods of multivariate analysis in physical geography. Wiley, London, UK.
- McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MjM Software, Gleneden Beach, Oregon, USA.
- McKelvey, K. S., Y. K. Ortega, G. M. Koehler, K. B. Aubry, and J. D. Britnell. 2000. Canada lynx habitat and topographic use patterns in North Central Washington: A reanalysis. Pages 307–336 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires, editors. *Ecology and conservation of Lynx in the United States*. University Press of Colorado, Boulder, Colorado, USA.
- Meaney, C. 2002. A review of Canada lynx (*Lynx canadensis*) abundance records from Colorado in the first quarter of the 20th century. Report, Colorado Department of Transportation, Denver, Colorado, USA.
- Meier, E. S., F. Kienast, P. B. Pearman, J. Svenning, W. Thuiller, M. B. Araújo, A. Guisan, and N. E. Zimmermann. 2010. Biotic and abiotic variables show little redundancy in explaining tree species distributions. *Ecography* 33:1038–1048.
- Menéndez, R., A. González-Megías, O. T. Lewis, M. R. Shaw, C. D. Thomas, and D. Granada. 2008. Escape from natural enemies during climate-driven range expansion: A case study. *Ecological Entomology* 33:413–421.
- Minchin, P. R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. *Vegetation* 69:89–107.
- Moorcroft, P. R., M. A. Lewis, and R. L. Crabtree. 1999. Home range analysis using a mechanistic home range model. *Ecology* 80:1656–1665.
- Murray, D. L., S. Boutin, M. O'Donoghue, and V. Namst. 1995. Hunting behaviour of a sympatric felid and canid in relation to vegetative cover. *Animal Behaviour* 50:1203–1210.
- O'Donoghue, M., S. Boutin, C. J. Krebs, D. L. Murray, and E. J. Hofer. 1998. Behavioural responses coyote and lynx to the snowshoe hare cycle. *Oikos* 82:169–183.
- Paine, R. T. 2010. Macroecology: Does it ignore or can it encourage further ecological syntheses based on spatially local experimental manipulations? *American Naturalist* 176:385–393.
- Parmesan, C. 2006. Ecological and evolutionary ecological to recent responses climate change. *Annual Review of Ecology and Systematics* 37:637–669.
- Peterson, A. T., J. Soberón, R. G. Pearson, R. P. Anderson, E. Martínez-Meyer, M. Nakamera, and M. B. Araújo. 2011. *Ecological niches and geographic distributions*. Princeton University Press, Princeton, New Jersey, USA.
- Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190:231–259.
- Phillips, S. J., and M. Dudík. 2008. Modeling of species distributions with Maxent: New extensions and a comprehensive evaluation. *Ecography* 31:161–175.
- Phillips, S. J., and J. Elith. 2013. On estimating probability of presence from use–availability or presence–background data. *Ecology* 94:1409–1419.
- R Development Core Team. 2012. R: A language and environment for statistical computing. Version 2.15. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- Schmitz, O. J. 2005. Behavior of predators and prey and links with population-level processes. Pages 256–278 in P. Barbosa and I. Castellanos, editors. *Ecology of predator–prey interactions*. Oxford University Press, Oxford, UK.
- Schmitz, O. J. 2010. Spatial dynamics and ecosystem functioning. *PLoS Biology* 8:e1000378.
- Schmitz, O. J., V. Krivan, and O. Ovadia. 2004. Trophic cascades: The primacy of trait-mediated indirect interactions. *Ecology Letters* 7:153–163.
- Schmitz, O. J., E. Post, C. E. Burns, and K. M. Johnston. 2003. Ecosystem responses to global climate change: Moving beyond color mapping. *BioScience* 53:1199–1205.
- Schoener, T. W. 1968. The *Anolis* lizards of Bimini: Resource partitioning in a complex fauna. *Ecology* 49:704–726.
- Schurr, F. M., et al. 2012. How to understand species' niches and range dynamics: A demographic research agenda for biogeography. *Journal of Biogeography* 39:2146–2162.
- Schweiger, O., J. Settele, O. Kudrna, S. Klotz, and I. Kuhn. 2008. Climate change can cause spatial mismatch of trophically interacting species. *Ecology* 89:3472–3479.
- Sexton, J. P., P. J. Mcintyre, A. L. Angert, and K. J. Rice. 2009. Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution, and Systematics* 40:415–436.
- Shenk, T. M. 2005. Post release monitoring of lynx (*Lynx canadensis*) reintroduced to Colorado. Page 22. Fort Collins, Colorado, USA.

- Shenk, T. M. 2010. Post release monitoring of lynx (*Lynx canadensis*) reintroduced to Colorado. Page 26. Fort Collins, Colorado, USA.
- Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters* 10:1115–23.
- Thaker, M., A. T. Vanak, C. R. Owen, M. B. Ogdén, S. M. Niemann, and R. Slotow. 2011. Minimizing predation risk in a landscape of multiple predators: Effects on the spatial distribution of African ungulates. *Ecology* 92:398–407.
- Theobald, D. M. 2007. LCaP v1.0: landscape connectivity and pattern tools for ArcGIS. Colorado State University, Fort Collins, Colorado, USA.
- Theobald, D. M., and T. M. Shenk. 2011. Areas of high habitat use from 1999–2010 for radio-collared Canada lynx reintroduced to Colorado. Page 19. Fort Collins, Colorado, USA.
- Tolon, V., J. Martin, S. Dray, A. Loison, C. Fischer, and E. Baubet. 2012. Predator–prey spatial game as a tool to understand the effects of protected areas on harvester–wildlife interactions. *Ecological Applications* 22:648–657.
- Vasconcelos, T. S., M. Á. Rodríguez, and B. A. Hawkins. 2012. Species distribution modelling as a macroecological tool: A case study using New World amphibians. *Ecography* 35:539–548.
- Vashon, J. H., A. L. Meehan, W. J. Jakubas, J. F. Organ, A. D. Vashon, C. R. McLaughlin, G. J. Matula, and S. M. Crowley. 2008. Spatial ecology of a Canada lynx population in Northern Maine. *Journal of Wildlife Management* 72:1479–1487.
- Veloz, S. D., J. W. Williams, J. L. Blois, F. He, B. Otte-Bliesner, and Z. Liu. 2012. No-analog climates and shifting realized niches during the late quaternary: Implications for 21st-century predictions by species distribution models. *Global Change Biology* 18:1698–1713.
- Ward, R. P., and C. J. Krebs. 1985. Behavioural responses of lynx to declining snowshoe hare abundance. *Canadian Journal of Zoology* 63:2817–2824.
- Warren, D. L., R. E. Glor, and M. Turelli. 2008. Environmental niche equivalency versus conservatism: Quantitative approaches to niche evolution. *Evolution* 62:2868–2883.
- Warren, D. L., R. E. Glor, and M. Turelli. 2010. ENMTools: A toolbox for comparative studies of environmental niche models. *Ecography* 33:607–611.
- Warton, D., and G. Aarts. 2013. Advancing our thinking in presence-only and used–available analysis. *Journal of Animal Ecology*. <http://dx.doi.org/10.1111/1365-2656.12071>
- Zarnetske, P. L., D. K. Skelly, and M. C. Urban. 2012. Biotic multipliers of climate. *Science* 336:1516–1518.
- Zavaleta, E., J. Pasari, J. Moore, D. Hernández, K. B. Suttle, and C. C. Wilms. 2009. Ecosystem responses to community disassembly. *Annals of the New York Academy of Sciences* 1162:311–333.
- Zimmermann, N. E., T. C. Edwards, Jr., C. H. Graham, P. B. Pearman, and J. Svenning. 2010. New trends in species distribution modelling. *Ecography* 33:985–989.

SUPPLEMENTAL MATERIAL

Appendix A

Ordination results for fine- and coarse-resolution environmental data at lynx–snowshoe hare encounters ([Ecological Archives A024-011-A1](#)).

Appendix B

Methods used to calculate step length ([Ecological Archives A024-011-A2](#)).