



Niche compression intensifies competition between reintroduced American martens (*Martes americana*) and fishers (*Pekania pennanti*)

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Carnivores exhibit strong interspecific competition and partition niche axes to minimize agonistic interactions. Niche partitioning, though, is contingent upon resource heterogeneity, and recent landscape homogenization may limit the abilities of carnivores to partition niche space. The negative fitness consequences associated with niche overlap may be particularly problematic for repatriating carnivores, and could delay the recovery of rare or endangered species. American martens (*Martes americana*) and fishers (*Pekania pennanti*) are the most commonly translocated carnivores in North America and both were reintroduced to a highly modified landscape in Wisconsin, United States. To date, fishers have flourished while martens remain endangered. To assess the role of competition in marten recovery, we used a combination of occupancy modeling, point pattern analyses, and stable isotope analyses to assess 5 coexistence mechanisms: spatial segregation, dietary segregation, temporal avoidance, and differential use of habitat and snow features. Over 7 years, we observed consistently high fisher occupancy and consistently low marten occupancy. Moreover, martens and fishers overlapped in their use of space and time, and neither exhibited habitat preferences. Isotopic analyses revealed complete dietary overlap, with martens falling entirely within the isotopic niche of fishers. Deep, uncompressed snow, however, had a negative effect on fisher activity. We propose that extensive landscape homogenization has resulted in niche compression and that marten recovery has been limited by increased competition with fishers. Restoration programs often overlook competitive interactions, but our results emphasize the importance of interspecific competition for recovering carnivore populations and highlight the challenge of reconstructing carnivore communities in increasingly homogenized landscapes.

Key words: Great Lakes, intraguild predation, mesocarnivore, mustelid, translocation

Competition is a cornerstone of ecology and integral to understanding the demographic processes that regulate populations (Hutchinson 1957; MacArthur 1972). Interspecific competition is a function of species' overlap along 4 primary niche axes: space, time, resources, and predators (Chesson 2000). Consequently, competitors partition niche axes to facilitate coexistence, but such partitioning is contingent upon heterogeneity within the niche space (Amarasekare 2003). Contemporary trends in landscape and resource homogenization (McKinney and Lockwood 1999) could therefore lead to dramatic changes in available niche space (Moss et al. 2016), and, in an extreme form, even niche collapse (Layman et al. 2007b). Moreover, if organisms are unable to partition niche

space in a homogenized landscape, coexistence can only be attained through fitness consequences that reduce competition for shared resources (Amarasekare 2003). In the face of rapid global change, such processes could be especially problematic for rare or endangered species already occurring at low population densities.

Mammalian carnivores typically occur at low densities and are of particular conservation concern due to declining global population sizes and the disproportionate influence they exert on ecosystem processes (Estes et al. 2011). Among carnivores, an apparent evolutionary outcome of resource partitioning has been character displacement, a phenomenon leading to highly structured use of space and resources among different-sized

carnivores (Davies et al. 2007). When resources are homogenized in space, agonistic interactions among carnivores become more frequent and can lead to interspecific killing, particularly among size-structured guilds such as mustelids (Palomares and Caro 1999; Donadio and Buskirk 2006). Because these interactions are generally asymmetric, subordinate species often modify their realized niches by altering foraging (Harrington et al. 2009), habitat selection (St-Pierre et al. 2006), or activity periods (Bischof et al. 2014). These changes in realized niches can lead to negative fitness consequences, and, ultimately, shifting species distributions (King and Moors 1979). Such processes are particularly problematic for rare species, and competitive interactions on altered landscapes present a significant obstacle for reintroduced and recovering carnivores (Creel 2001).

Carnivore reintroductions are increasingly common, yet the role of interspecific competition in the success of reintroductions is still poorly understood (Linnell and Strand 2000; Hayward and Somers 2009). American martens (*Martes americana*; hereafter martens) and fishers (*Pekania pennanti*) are the 2 most commonly reintroduced carnivores in North America (Powell et al. 2012), but they are often direct competitors and can exhibit strong competitive interactions (reviewed by Krohn et al. 1997). Competition between these mid-sized forest carnivores is particularly notable in altered systems at the southern edge of their distributional overlap, where the majority of reintroduction attempts have occurred (Krohn et al. 1997; Powell et al. 2012).

Martens and fishers were reintroduced throughout much of the Great Lakes region following their extirpation in the early 20th century due to widespread habitat degradation and unregulated trapping (Williams et al. 2007). The southern border of both species ranges now occur in Wisconsin, United States, where extensive restoration efforts have led to successful reestablishment of fishers (Williams et al. 2007). Recovery of martens, however, has been limited (Manlick et al. 2016), and they remain a state-endangered species. Interestingly, martens and fishers in Wisconsin exhibit comparable habitat selection at the home-range scale (Wright 1999), and both preferentially

select for similar fine-scale habitat features (e.g., northern white cedar [*Thuja occidentalis*] and eastern hemlock [*Tsuga Canadensis*])—McCann et al. 2014). Moreover, diets of martens in Wisconsin lack many preferred prey items and are akin to those of fishers regionally (Clem 1977; Powell 1979; Carlson et al. 2014). Such nutritional limitation and dietary overlap are predicted to enhance agonistic interactions among mesocarnivores (Donadio and Buskirk 2006; Carlson et al. 2014), and intraguild predation of martens by fishers has indeed been documented (McCann et al. 2010).

Recently (2008–2010), martens were translocated to the Chequamegon National Forest (hereafter, Chequamegon) in northern Wisconsin to augment a remnant population from a previous reintroduction (Woodford et al. 2013). Population recovery, however, was not achieved, and the mechanisms limiting martens in Wisconsin remain unclear (Manlick et al. 2016). Herein, we evaluate the potential role of interspecific competition in limiting marten recovery in Wisconsin. Competitive interactions among mustelids like martens and fishers are widespread (Palomares and Caro 1999), and numerous hypotheses have been generated to explain coexistence among competing species (Table 1). Specifically, an inverse relationship between marten and fisher occurrences has been observed in several sympatric populations and coexistence has been attributed to mechanisms that reduce competition for shared resources, such as spatiotemporal segregation, differential habitat selection, and contrasting use of snow-cover characteristics (Krohn et al. 1997; Fisher et al. 2013). Alternatively, Rosenzweig (1966) hypothesized that martens and fishers maintain coexistence via dietary segregation, similar to sympatric weasels. Additional mechanisms observed for weasels, including intraguild predation and metapopulation dynamics (Table 1), may also facilitate coexistence among martens and fishers, but have received little attention. Nevertheless, previous tests of such hypotheses have focused on competitive interactions in the core of the ranges of martens and fishers (but see Krohn et al. 1997; Zielinski and Duncan 2004) rather than in the modified landscapes regularly targeted for carnivore reintroductions. Wisconsin, however, has

Table 1.—Hypotheses for mechanisms regulating coexistence in mustelids.

Mechanism	Hypothesis	Species
Spatial segregation ^{1–4}	Species are sympatric across their range, but spatial niche partitioning of heterogeneous landscapes results in an inverse relationship at local scales.	<i>Martes americana</i> , <i>Pekania pennanti</i> , <i>Mustela</i> spp.
Metapopulation dynamics ⁵	Coexistence is maintained through continuous local extinction and colonization.	<i>Mustela</i> spp.
Snow conditions ^{6–10}	Morphological adaptations of smaller competitor facilitate foraging in winter, thereby fostering an advantage over larger-bodied competitors.	<i>Martes americana</i> , <i>Pekania pennanti</i> , <i>Mustela</i> spp.
Differential habitat selection ^{3,11}	Variation in habitat selection minimizes competitive interactions and facilitates coexistence.	<i>Martes americana</i> , <i>Pekania pennanti</i>
Temporal or behavioral segregation ^{12–15}	Species alter spatiotemporal use of resources to minimize competitive interactions (e.g., alter activity periods or movement).	<i>Neovison vison</i> , <i>Mustela</i> spp.
Dietary segregation ^{6,11,16}	Differing morphology leads to dietary segregation or specialization and reduces competition.	<i>Martes americana</i> , <i>Pekania pennanti</i> , <i>Lutra lutra</i> , <i>Mustela</i> spp.
Intraguild competition and predation ^{6,12,13,16}	Inferior competitors coexist by suppressing or consuming the superior competitors, and reducing pressure on shared resources.	<i>Mustela</i> spp.

Sources: 1) de Vos 1952; 2) King and Moors 1979; 3) Strickland and Douglas 1987; 4) Fisher et al. 2013; 5) Powell and Zielinski 1983; 6) Simms 1979; 7) Raine 1983; 8) Krohn et al. 1995; 9) Krohn et al. 1997; 10) Krohn et al. 2005; 11) Bonesi and Macdonald 2004; 12) Erlinge and Sandell 1988; 13) St-Pierre et al. 2006; 14) Harrington et al. 2009; 15) Bischof et al. 2014; 16) Rosenzweig 1966.

been subject to widespread landscape homogenization (Schulte et al. 2007; Rhemtulla et al. 2009) and provides a natural experiment to assess the effect of competition on recovery of carnivores in modified landscapes.

We characterized competition between reintroduced martens and fishers in Wisconsin by assessing 5 mechanisms of coexistence: spatial segregation, dietary segregation, temporal avoidance, and differential use of habitat and snow features. At the landscape scale we used dynamic occupancy models to assess spatial segregation of martens and fishers, temporal avoidance of fishers by martens, differential habitat selection between species, and differential use of snow-cover characteristics. We then employed spatial point pattern analyses to assess fine-scale spatial partitioning and used stable isotope analyses of hair to estimate dietary overlap. We hypothesized that martens and fishers in Wisconsin use similar habitat and dietary resources (Wright 1999; Carlson et al. 2014; McCann et al. 2014), but facilitate coexistence through spatiotemporal segregation (McCann et al. 2016). Accordingly, we predicted that marten occupancy would decrease at sites occupied by fishers, whereas the larger, dominant fishers would not respond to marten occurrences. Lastly, we hypothesized that spatial segregation is facilitated by differential use of snow features (sensu Krohn et al. 1997), and predicted that movement and detection probabilities of fishers would decrease as a function of snow cover, whereas martens would remain unaffected.

MATERIALS AND METHODS

Sampling.—We surveyed snow tracks each winter (December to March) from 2007 to 2014 in Chequamegon, a study area characterized by consistent snow cover (\bar{x} = 10.6 cm) and subfreezing high temperatures (\bar{x} = -2.89°C). Surveys were conducted on 153 km of maintained roads subdivided into 4 primary transects within the majority of the known distribution of martens in Chequamegon (Fig. 1). We surveyed a minimum of 2 activity periods (i.e., dusk and dawn) after snowfall, generally within 24 h (\bar{x} = 24.6 h), and repeated surveys up to 4 times per winter. Tracks that crossed the roadway were georeferenced for subsequent analyses and identified to species via a combination of morphology, behavior, and straddle width (fishers > 100 mm, martens < 100 mm). Because straddle widths of martens and fishers can overlap, we censored a subset of data (winters 2011–2014) to include only martens < 100 mm and fishers > 110 mm to reduce the probability of misidentification (N. P. McCann, Great Lakes Indian Fish and Wildlife Commission, pers. comm.) and to assess the effects of potential errors in species identification.

Martens and fishers select resources at various scales (Powell 1994; Shirk et al. 2012); therefore, we subdivided all track data into 2 distinct data sets to assess the scale dependency of our analyses. First, the 4 primary transects were subdivided into 50 segments (2.73–3.22 km) and buffered by 1 km in all directions, resulting in 50 individual landscapes (3.9–6.6 km²; Fig. 1; hereafter, “sites”) approximating the size of a typical home range for martens in this region (Wright 1999). Georeferenced tracks

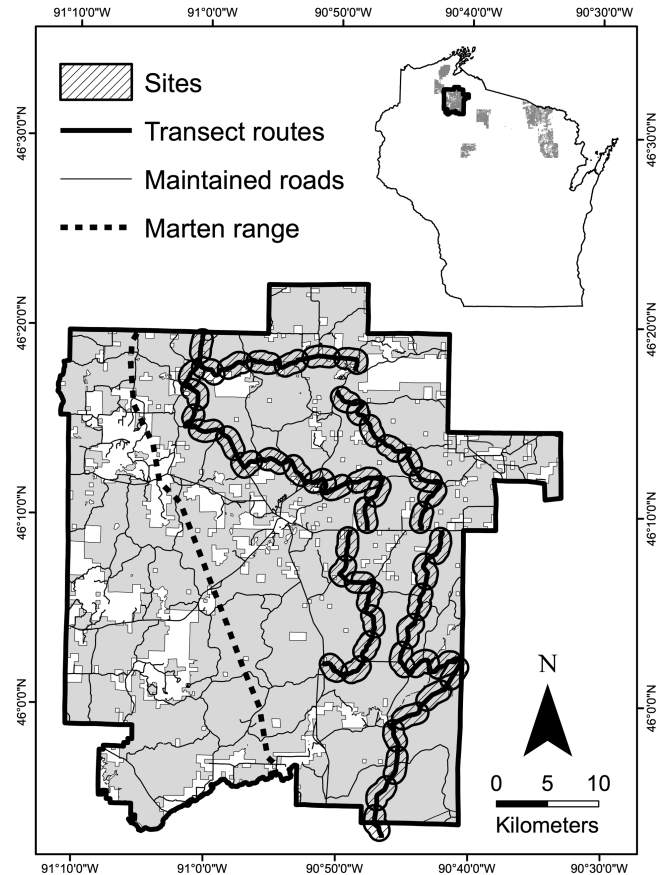


Fig. 1.—Distribution of snow-tracking transects and sites surveyed at the marten (*Martes americana*) home-range scale in the Chequamegon National Forest. The inset map illustrates the location of our study site (black outline) within the national forests (gray) of northern Wisconsin, and the dashed line represents the western extent of known marten distribution in the study region.

were then used to construct site and survey-specific detection–non-detection histories for both species at this marten home-range scale. Similarly, we divided primary transects into 25 segments (5.46–6.45 km) buffered by 1 km in each direction to create 25 individual sites (8.8–12.3 km²) approximating the size of a typical home range for fishers in this region (Wright 1999), with georeferenced tracks used to construct site and survey-specific detection–non-detection histories for both species at this larger, fisher home-range scale. Sites at both scales were indicative of 3rd-order selection (Johnson 1980), and were representative of the broader study area. We used 2011 National Land Cover Data (NLCD—Homer et al. 2015) to quantify land-cover composition and diversity at each site. Because we detected little change between NLCD from 2001 and 2011 (< 1% mean change per site), we used the most current data in our analyses. To account for cover types not included in NLCD but used by martens and fishers (e.g., northern white cedar and eastern hemlock—McCann et al. 2014), we drew an additional lowland conifer land-cover classification from WISCLAND (Reese et al. 2002). Lastly, we obtained forest disturbance records (e.g., harvest, fire, restoration) from the USDA Forest Service Northern Research Station (Rhinelander, Wisconsin) and employed disturbance as an additional land-cover variable.

All sampling was conducted with approval from the University of Wisconsin–Madison Animal Care and Use Committee (#A01519-0-10-12) and adhered to the guidelines set forth by the American Society of Mammalogists (Sikes et al. 2016).

Occupancy models.—To assess spatiotemporal segregation and differential use of habitat and snow characteristics, we used site detection–non-detection histories for martens and fishers at both scales in dynamic, single-species occupancy models in program PRESENCE (Hines 2006). These models use secondary sampling periods (i.e., repeat surveys) nested within primary sampling periods (i.e., each winter) to estimate survey-specific detection probability (p) and annual occupancy (ψ), colonization (γ), and extinction (ϵ) while accounting for unequal sampling within each period (MacKenzie et al. 2006). Within this framework, ψ is estimated for year 1 and derived for all subsequent years using γ and ϵ , all of which can be modeled as a function of covariates (MacKenzie et al. 2003). Co-occurrence models were explored but were not included because they failed to converge. Prior to analyses, we tested for multicollinearity among environmental covariates and spatial autocorrelation among detections using Moran's I and spline correlograms in the *ncf* package of Program R (Bjørnstad 2005).

We developed a suite of 12 a priori detection models (Table 2) to 1) account for abiotic factors influencing our ability to detect tracks (e.g., time since last snow); 2) assess the effect of snow on animal movements; and 3) quantify behavioral segregation via temporal avoidance. Abiotic covariates were recorded at the start of each survey or gathered from weather stations and included time since last snow (hours), the previous night's low temperature, survey, season, and transect length. We quantified

snow conditions using precipitation preceding each survey (cm within 24 h) and mean seasonal snow depth (cm) averaged from 3 surrounding weather stations within 40 km of the study area midpoint. Because surveys were conducted ~24 h after snow-fall, we quantified temporal avoidance within this timeframe by reciprocally incorporating the opposing species' detection history as a covariate. We hypothesized that detection probability of martens would decrease in the presence of fishers due to temporal avoidance of the larger-bodied competitor.

Using the best detection models for each species, we modeled ψ , γ , and ϵ with 10 a priori models to assess habitat use and spatial segregation. To quantify differences in habitat use, marten and fisher occupancy were modeled as a function of percent deciduous forest, evergreen forest, mixed forest, shrubland, and lowland conifer, as well as cover-type diversity (i.e., Shannon–Weiner index) and site area (km²). To assess spatial segregation, we modeled ψ as a function of the opposing species by incorporating a yearly, binary covariate representing the presence or absence of that species at each site. We assumed cover types to be static variables and therefore held γ and ϵ constant for all cover-type models. Because forest disturbance and species occurrences vary annually, we modeled initial occupancy as a function of those variables' initial values, while γ and ϵ were modeled seasonally as a function of their annual values. Because data were sparse for some seasons, we did not explore additive models or interactions among covariates to minimize overparameterization. All models for occupancy and detection were applied to the complete data set as well as the censored subset to assess the potential impact of misidentification of tracks on results of models.

To further assess the influence of snow conditions on movements of martens and fishers, we modeled detection with

Table 2.—Detection models for martens (*Martes americana*) and fishers (*Pekania pennanti*) with associated hypotheses, scale of covariates, and the predicted effect on detectability. Models were applied to track data from winters 2008–2014 in Wisconsin, United States.

Model	Hypothesis	Covariate scale	Effect
$p(\cdot)$	Constant detection probability		
$p(\text{Length})$	Probability of detecting a marten or fisher increases with transect length	Site	+
$p(\text{Low})$	Probability of detection decreases with previous night's low temperature due to reduced movement	Survey	–
$p(\text{Precipitation})$	Increased precipitation (i.e., snow within 24 h preceding a survey) decreases the probability of detection due to physical constraints of deep reducing movement	Survey	–
$p(\text{Last snow})$	Detection increases with time since last snow (in hours), due to more time for more tracks to be laid	Survey	+
$p(\text{Seasonal depth})$	Detection decreases with increased snow depth due to reduced movement of martens and fishers	Season	–
$p(\text{Competitor})$	Probability of detecting martens and fishers decreases in the presence of the competing species due to spatiotemporal segregation	Site	–
$p(\text{Low} + \text{Precipitation})$	Additive effects of previous night's low temperature and increased precipitation reduce movement of martens and fishers and decrease detection probability	Survey + Survey	–
$p(\text{Low} + \text{Competitor})$	Previous night's low temperature reduces movement and presence of competing species decreases detection due to spatiotemporal segregation	Survey + Site	–
$p(\text{Precipitation} + \text{Competitor})$	Increased precipitation reduces movement due to physical constraints of deep snow and presence of competing species decreases detection due to spatiotemporal segregation	Survey + Site	–
$p(\text{Season})$	Detection varies annually due to environmental stochasticity not captured by other predictors	Season	+/–
$p(\text{Survey})$	Detection varies by survey due to environmental stochasticity not captured by other predictors	Survey	+/–

additional snow covariates only available for winters 2012–2013 and 2013–2014. Because these contemporary analyses were restricted to 2 seasons, we did not model occupancy due to limited occurrence data over that time. Each winter, we conducted 3 complete surveys and measured snow depth (cm) on the road at the beginning of each survey. In addition, we measured snow depth and density at all recorded tracks and at 40 random locations across sites during each survey, each taken a minimum of 50 m from the road to capture representative snow conditions within the forest. We quantified snow density by dropping a 200-g cylindrical penetrometer from a height of 50 cm and measuring penetration depth (cm—Sultaire et al. 2016). We then pooled all measurements for each survey and used ordinary kriging (116-m resolution; ArcMap v.10.1, ESRI, Redlands, California) to generate interpolated snow surfaces for each survey. For each survey, we calculated mean snow depth and snow density (i.e., penetration depth) per site using the *raster* package in Program R. We again modeled p using the 12 models described above, but developed an additional 6 a priori models to test the effects of snow depth and density on detection probabilities for each species (Table 3). With these more-detailed snow measurements, we evaluated our hypothesis that movement of fishers is hindered by deep snow and predicted that detection probabilities would decrease with snow depth and density (i.e., penetration depth), whereas detections of martens would remain unaffected.

Point pattern analysis.—To explore potential fine-scale spatial partitioning, we pooled all track locations recorded for martens and fishers across years and analyzed them as marked point processes with an observation window restricted to the sites surveyed. We employed Ripley's univariate L -function with an isotropic edge correction to assess clustering within each species, and a bivariate L -function to assess interactions between species (Ripley 1991). We then performed 999 Monte Carlo simulations to quantify the pointwise critical envelope for each process, and employed a goodness-of-fit test under the null hypothesis of complete spatial randomness (CSR—Loosmore and Ford 2006). All analyses were conducted in the R package *spatstat* (Baddeley and Turner 2005).

Stable isotope analysis.—To assess dietary segregation, we used the isotopic signatures of martens collected from 1991 to 2013 ($n = 27$; 8M, 8F, 11 unknown sex) generated by Carlson et al. (2014), and analyzed hair samples of fishers from the 2013 and 2015 Wisconsin furbearer harvests ($n = 37$; 19M, 16F, 2 unknown sex). All samples analyzed were restricted to locations within the distributional overlap of martens and fishers in Wisconsin. Because both species synthesize hair in autumn, isotopic analysis of hair represents assimilated fall diet for each individual (Pauli et al. 2009). Samples were prepared sensu Pauli et al. (2009) and analyzed at the University of Wyoming Stable Isotope Facility. Results are presented as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios, in parts per thousand, relative to the international standards Vienna-Peedee Belemnite and atmospheric nitrogen. In this framework, a $\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ plot of raw isotopic values represents the resources that an organism consumes, and samples analyzed across years or seasons capture the dietary niche breadth of a population or community (Layman et al. 2007a; Newsome et al. 2007). These isotopic niches can be used to assess dietary niche relationships among consumers. Accordingly, we used the R package SIAR (Parnell et al. 2010) to calculate the isotopic niches of martens and fishers using standard ellipses corrected for small sample size (SEAc—Jackson et al. 2011), and quantified dietary niche partitioning via the measured overlap in isotopic niches.

RESULTS

We detected a total of 87 marten tracks and 115 fisher tracks over 7 winters of primary sampling and 297 site-level sampling occasions at the marten home-range scale. We did not detect spatial autocorrelation among marten occurrences at either 5 km (Moran's $I = -0.03$, $P > 0.05$) or 10 km (Moran's $I = -0.02$, $P > 0.05$), nor did we find strong evidence of spatial autocorrelation among fisher occurrences at 5 km (Moran's $I = -0.02$, $P > 0.05$) or 10 km (Moran's $I = 0.03$, $P > 0.05$). Spline correlograms also revealed minimal spatial autocorrelation at distances > 5 km (Supplementary Data SD1), and no environmental covariates used in our analyses were correlated ($r < 0.6$). Moreover, we did not detect any scale dependency and models were robust to

Table 3.—Detection models for martens (*Martes americana*) and fishers (*Pekania pennanti*) incorporating snow conditions with description of the associated hypothesis, scale of covariates, and predicted effect on detectability. Models were run in addition to 12 original a priori detection models and applied to track data from 2013 to 2014 from Wisconsin, United States.

Model	Hypothesis	Covariate scale	Effect
$p(\text{Road Depth})$	Detection probability increases with snow depth on road because tracks are more visible	Survey	+
$p(\text{Depth})$	Detection probability decreases at sites with deeper snow due to reduced movement, particularly for the less snow-adapted fishers	Site	–
$p(\text{Density})$	Detection increases at sites with denser snow (i.e., more compact) due to increased ability to move across snowpack, particularly for the less snow-adapted fishers	Site	+
$p(\text{Depth} + \text{Density})$	Deep, uncompacted snow (high depth, low density) reduces detection probability due to limited movement, particularly for the less snow-adapted fishers, while shallow, compact snow increases detectability for both species	Site + Site	+/–
$p(\text{Competitor} + \text{Depth})$	Deep snow decreases movement and presence of competitor decreases detection probability due to spatiotemporal segregation	Site + Site	–
$p(\text{Competitor} + \text{Density})$	Uncompacted snow decreases movement and presence of competitor decreases detection probability due to spatiotemporal segregation	Site + Site	–

potential errors in track identification, as top models remained the same for all scales and data sets. Consequently, only results from the full data set at the finer, marten home-range scale are presented.

Detection probability.—The top detection model for martens was the presence of fishers (Table 4); however, contrary to

Table 4.—Top models of detection probability (p) for martens (*Martes americana*) and fishers (*Pekania pennanti*) in Wisconsin, United States (2008–2014). The highest-ranking model for each species was incorporated into subsequent occupancy models. ΔAIC_c = difference between model AIC_c and lowest AIC_c in the model set; w_i = Akaike model weight; k = number of estimable parameters.

Species and models	ΔAIC_c	w_i	k
American marten			
$p(\text{Fisher presence})$	0	0.293	5
$p(\cdot)$	1.28	0.1545	4
$p(\text{Low temperature} + \text{Fisher presence})$	1.57	0.1337	6
$p(\text{Precipitation} + \text{Fisher presence})$	2.3	0.0928	6
$p(\text{Transect length})$	2.84	0.0708	5
Fisher			
$p(\text{Precipitation} + \text{Marten presence})$	0	0.66	6
$p(\text{Precipitation})$	2.89	0.16	5
$p(\text{Marten presence})$	3.93	0.09	5
$p(\text{Precipitation} + \text{Low temperature})$	5.48	0.04	6
$p(\text{Low temperature} + \text{Marten presence})$	7.28	0.02	6

our prediction, the relationship was positive ($\beta = 0.74 \pm 0.38$). Marten detection probability was nearly 2 \times greater in the presence of fishers ($p = 0.44 \pm 0.10$) compared to the absence of fishers ($p = 0.27 \pm 0.06$; Fig. 2a). Similarly, the top model for fisher detections included a positive relationship with presence of martens ($\beta = 0.78 \pm 0.33$; Fig. 2a) as well as a negative association with precipitation preceding each survey ($\beta = -0.35 \pm 0.15$). As precipitation increased, estimates of fisher detection decreased from 0.36 to 0.08 in the presence of martens and from 0.21 to 0.04 in the absence of martens (Figs. 2a and 3a).

Contemporary (2012–2014) detection models for martens yielded a top model with constant detection probability, supporting our hypothesis that martens would be unaffected by snow, but no model in the suite garnered clear support over the others (Table 5). Contemporary detection models did not, however, indicate a response of fishers to snow depth (Table 5), but supported the hypothesis that fishers would respond negatively to snow density (i.e., penetrometer depth; $\beta = -0.15 \pm 0.07$; Fig. 3b).

Occupancy probability.—The top occupancy model for both species included percent cover by lowland conifers, but both models were considered uninformative due to regression coefficients with 95% confidence intervals that overlapped zero (Table 6). For both species, the 2nd-ranked model was used

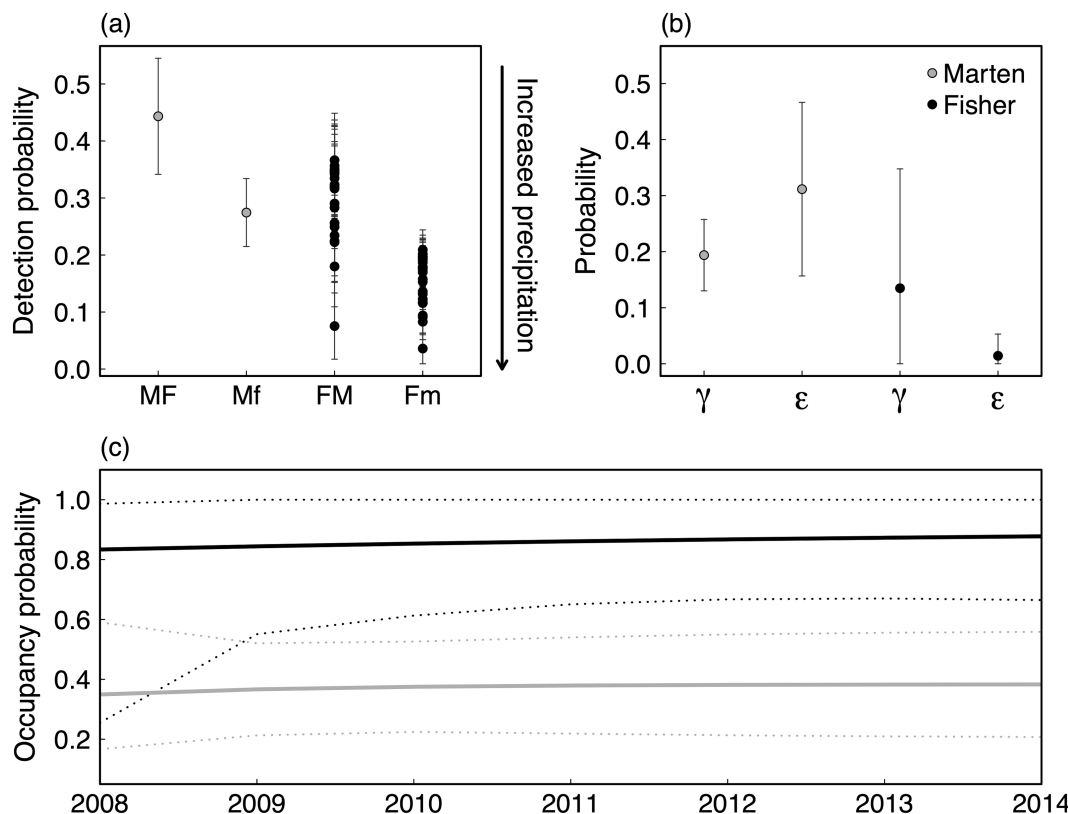


Fig. 2.—Results from top occupancy model for martens (*Martes americana*, gray) and fishers (*Pekania pennanti*, black). (a) Estimated detection probabilities, with SEs, of martens in the presence or absence (MF or Mf) of fishers and fishers in the presence or absence (FM or Fm) of martens. Both species exhibited higher probability of detection in the presence of the competing species, and detection probabilities for fishers also decreased as precipitation increased. (b) Colonization (γ) and extinction (ϵ) probabilities showed an inverse relationship for martens and fishers, though SEs for fishers overlap zero suggesting no extinction or colonization. (c) Seasonal occupancy probabilities from 2008 to 2014 with 95% CIs exhibited stable occupancy for both species over time.

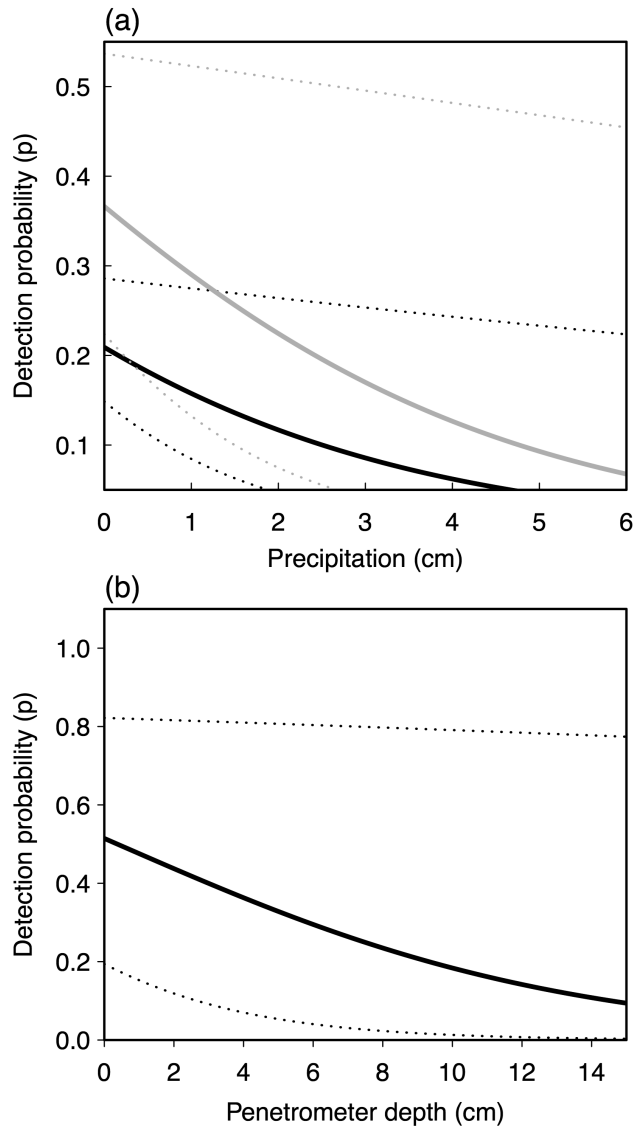


Fig. 3.—Response of detection probability (p) of fishers (*Pekania pennanti*) to snow conditions. (a) Predicted p as a function of precipitation (cm) in the 24 h preceding a survey from 2008 to 2014. Probability of detection of fishers was higher in the presence (gray) than in the absence (black) of martens, but decreased with precipitation regardless. (b) Predicted p as a function of snow density during 2013–2014, as measured by penetrometer depth (cm), indicating p decreased by approximately 0.10 for every 2.5 cm of deep, uncompressed snow. Dashed lines indicate 95% CIs.

to estimate parameters and indicated constant ψ , γ , and ϵ . All subsequent models included covariates with regression coefficients whose confidence intervals overlapped zero and thus did not support either habitat partitioning or spatial segregation between the species (Table 6). Estimates of marten and fisher occupancy were relatively constant over the 7 years despite augmentation of martens, and ranged from 0.35 to 0.38 and 0.83 to 0.88, respectively (Fig. 2c). Marten extinction probability (0.31 ± 0.15) exceeded colonization probability (0.19 ± 0.06), whereas fishers were 10 times more likely to colonize a site (0.13 ± 0.21) than to go extinct (0.01 ± 0.04 ; Fig. 2b). Nevertheless, confidence intervals overlapped zero for both parameters for fishers, suggesting minimal extinction

Table 5.—Top models of detection probability (p) for contemporary martens (*Martes americana*) and fishers (*Pekania pennanti*) in Wisconsin, United States (2013–2014), incorporating snow variables such as snow depth, density, and amount of snow on the roadway. ΔAIC_c = difference between model AIC_c and lowest AIC_c in the model set; w_i = Akaike model weight; k = number of estimable parameters.

Species and models	ΔAIC_c	w_i	k
American marten			
$p(\cdot)$	0	0.1244	4
$p(\text{Snow depth on road})$	0.58	0.0931	5
$p(\text{Transect length})$	0.65	0.0899	5
$p(\text{Fisher presence})$	0.71	0.0872	5
$p(\text{Low temperature})$	0.82	0.0825	5
Fisher			
$p(\text{Snow density})$	0	0.2743	5
$p(\text{Marten presence} + \text{Snow density})$	0.95	0.1706	6
$p(\text{Snow depth} + \text{Snow density})$	2.58	0.0755	6
$p(\cdot)$	2.73	0.0701	4
$p(\text{Marten presence})$	3.04	0.06	5

Table 6.—Multi-season occupancy (ψ) models developed to assess niche partitioning in martens (*Martes americana*) and fishers (*Pekania pennanti*) in Wisconsin, United States. The best detection (p) model for each species was included in all occupancy models, and colonization (γ) and extinction (ϵ) were assumed constant for all models when not listed as parameters. ΔAIC_c = difference between model AIC_c and lowest AIC_c in the model set; w_i = Akaike model weight; k = number of estimable parameters. The top-ranked model for both species contained covariate regression coefficients with 95% CIs that overlapped zero; therefore, only the 2nd-ranked models (in bold) were used for further inference.

Species and models	ΔAIC_c	w_i	k
American marten			
$\psi(\text{Lowland conifer}), p(\text{Fisher})$	0.00	0.52	6
$\psi(\cdot), p(\text{Fisher})$	2.50	0.15	5
$\psi(\text{Deciduous forest}), p(\text{Fisher})$	3.83	0.08	6
$\psi(\text{Mixed forest}), p(\text{Fisher})$	4.46	0.06	6
$\psi(\text{Matrix diversity}), p(\text{Fisher})$	4.57	0.05	6
$\psi(\text{Shrub forest}), p(\text{Fisher})$	4.86	0.05	6
$\psi(\text{Area}), p(\text{Fisher})$	5.01	0.04	6
$\psi(\text{Evergreen forest}), p(\text{Fisher})$	5.08	0.04	6
$\psi(\text{Fisher}), \gamma(\text{Fisher}), \epsilon(\text{Fisher}), p(\text{Fisher})$	7.83	0.01	8
$\psi(\text{Disturbed Area}), \gamma(\text{DA}), \epsilon(\text{DA}), p(\text{Fisher})$	8.28	0.01	8
Fisher			
$\psi(\text{Lowland conifer}), p(\text{Marten} + \text{Precip})$	0.00	0.37	7
$\psi(\cdot), p(\text{Marten} + \text{Precip})$	1.52	0.17	6
$\psi(\text{Deciduous forest}), p(\text{Marten} + \text{Precip})$	2.01	0.14	7
$\psi(\text{Shrub forest}), p(\text{Marten} + \text{Precip})$	3.18	0.08	7
$\psi(\text{Evergreen forest}), p(\text{Marten} + \text{Precip})$	3.48	0.06	7
$\psi(\text{Disturbed Area}), \gamma(\text{DA}), \epsilon(\text{DA}), p(\text{Marten} + \text{Precip})$	3.64	0.06	9
$\psi(\text{Marten}), \gamma(\text{Marten}), \epsilon(\cdot), p(\text{Marten} + \text{Precip})$	4.08	0.05	8
$\psi(\text{Matrix diversity}), p(\text{Marten} + \text{Precip})$	4.22	0.04	7
$\psi(\text{Area}), p(\text{Marten} + \text{Precip})$	5.40	0.02	7
$\psi(\text{Marten}), \gamma(\text{Marten}), \epsilon(\text{fixed at zero}), p(\text{Marten} + \text{Precip})$	8.83	0.00	9
$\psi(\text{Mixed forest}), p(\text{Marten} + \text{Precip})$	Did not converge		

and colonization occurred (Fig. 2b). Because extinction probability of fishers approached zero in most models, convergence was not always reached. In particular, ϵ as a function of marten

occurrence did not converge; therefore, we modeled ε as a constant parameter and ε fixed at zero and reported all models (Table 6).

Point pattern analysis.—Ripley's L -function and associated goodness-of-fit tests detected significant clustering among martens ($P < 0.05$; Fig. 4a), but not among fishers ($P > 0.05$; Fig. 4b). Bivariate L -functions also did not detect any dependence of marten locations on fisher locations ($P > 0.05$; Fig. 4c), but fisher locations depended on martens, particularly at distances exceeding 4 km ($P < 0.05$; Fig. 4d).

Stable isotope analysis.—The isotopic niche of fishers was over 1.5 \times greater than that of martens, with SEAc estimates of 3.76 and 2.27, respectively. In addition, significant dietary niche overlap was observed, with the isotopic niche of martens falling entirely within the isotopic niche of fishers (Fig. 5).

DISCUSSION

Our results did not support the spatial niche partitioning, temporal niche partitioning, differential habitat selection, or dietary segregation hypotheses. Indeed, the only difference we detected between martens and fishers was based on snow conditions, and this relationship was not particularly strong. This suggests that martens and fishers in Wisconsin are experiencing significant niche overlap, and that competition is ultimately limiting the recovery of martens. Below, we explore each of these hypotheses individually.

Spatial segregation, temporal avoidance, and differential habitat selection can all facilitate carnivore coexistence, and these mechanisms have been observed in several populations of sympatric mustelids (Table 1). Surprisingly, neither martens nor fishers exhibited strong habitat selection at the scales of our analyses, and our models did not detect either spatial or temporal segregation among these competitors. Instead, both species were more likely to be detected when the other was also present, suggesting spatiotemporal *aggregation* within the 24 h following snowfall. Moreover, the bivariate L -function indicated significant dependence of fisher locations on marten locations, again supporting aggregation between these species. Partitioning, though, could have occurred within more discrete land-cover classes or at spatiotemporal scales finer than we were able to model (McCann et al. 2014, 2016). Indeed, martens and fishers select habitat at various spatial scales (Powell 1994; Shirk et al. 2012), and martens did exhibit significant levels of clustering. Nevertheless, we did not find evidence of scale dependency in our models, and L -functions did not indicate avoidance at any scale. Given that we also found no spatial autocorrelation and parameter estimates within the predicted distributions (Supplementary Data SD2 and SD3), these results appear robust.

Competitive coexistence of martens and fishers in Wisconsin could be facilitated by partitioning snow features, as reported for sympatric populations in Maine and California (Krohn et al. 1997). Unlike martens, fishers possess high footloads and are

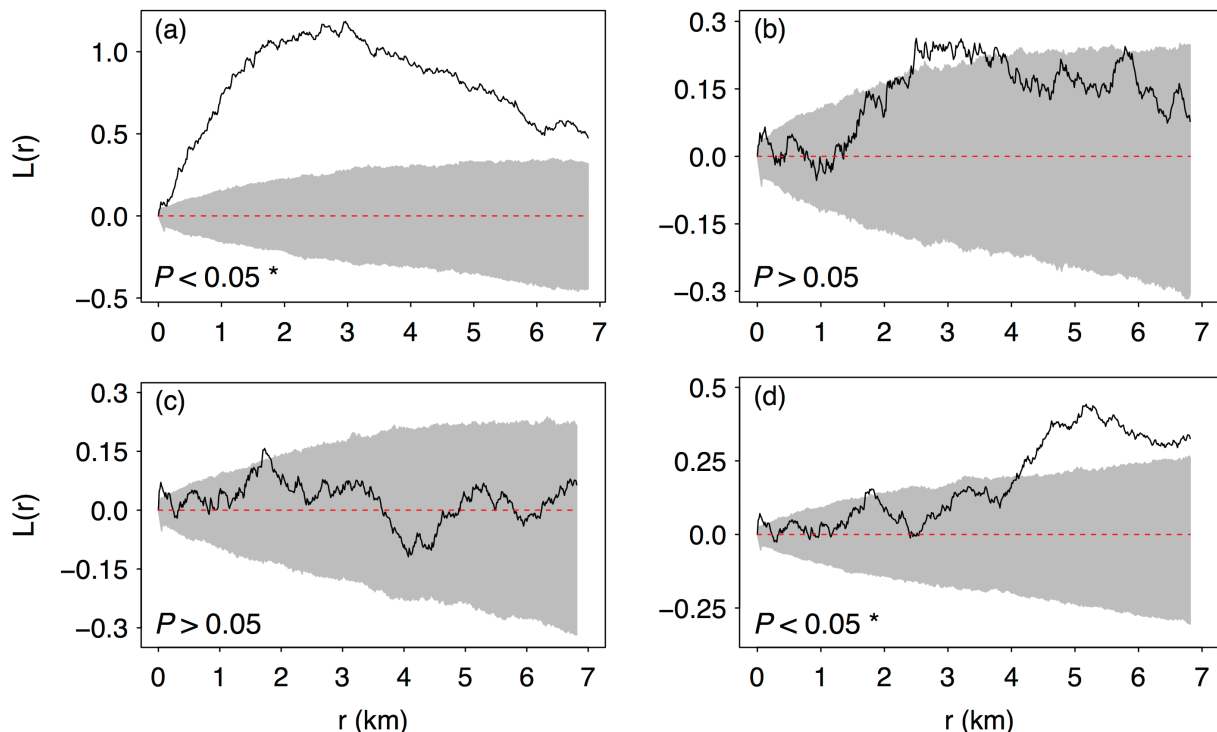


Fig. 4.—Centered L -functions for marten (*Martes americana*, a) and fisher (*Pekania pennanti*, b) track locations, and centered, bivariate L -functions for marten–fisher (c) and fisher–marten (d) interactions in Wisconsin, United States (2008–2014). Solid lines indicate observed spatial relationships, grayed regions indicate 95% confidence envelopes, and dashed red lines represent the theoretical L -function. Significance was derived using goodness-of-fit tests under the null hypothesis of complete spatial randomness. Solid lines above the theoretical L -function indicate spatial clustering, lines below indicate spatial avoidance, and lines outside of the confidence envelope indicate spatial relationships significantly different from random.

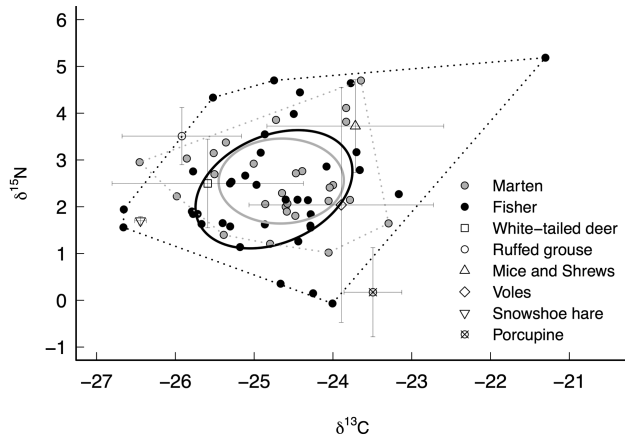


Fig. 5.—Isotopic signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of marten (*Martes americana*) and fisher (*Pekania pennanti*) hair samples from Wisconsin, United States, with convex hulls (dashed lines) and standard ellipses (SEAc; solid lines) to illustrate niche width. The isotopic niche of fishers encompassed that of martens, indicating complete dietary overlap of martens with fishers. For qualitative assessment, marten and fisher samples were corrected for trophic enrichment (Roth and Hobson 2000) and overlaid with potential prey (open symbols—Carlson et al. 2014).

not snow specialists (Krohn et al. 2005). For such species, the energetic costs of locomotion in snow is significant (Crête and Larivière 2003), and Krohn et al. (1997) hypothesized that deep, uncompressed snow imposes strong fitness consequences on fishers resulting in spatial partitioning of snowy landscapes and reduced competition with martens. Our results support this hypothesis and show that movement by fishers decreased following precipitation in our 7-year analysis and at sites with deep, uncompressed snow in our contemporary analysis. Martens, meanwhile, did not respond to snow conditions in any analysis. Because fishers possess a high surface area-to-volume ratio that increases metabolic and foraging demands (Powell 1979), such limited movement could reduce foraging opportunities and impose fitness consequences that promote coexistence with martens. Alternatively, increased snow could simply provide martens additional foraging opportunities given that hunting success is not affected by snow conditions (Andruskiw et al. 2008). Nevertheless, regional climate models predict dramatic reductions in snow cover and increased snow compaction in Wisconsin (Notaro et al. 2010). Consequently, snow cover collapse in Wisconsin should facilitate movement of fishers, as well as other mesocarnivore competitors (Whiteman and Buskirk 2013), and is likely to erode any partitioning based on snow features.

Species that do not segregate spatiotemporally often exhibit differential resource consumption (Rosenzweig 1966), but we observed complete isotopic niche overlap of martens by fishers. While such overlap could simply be the product of limited isotopic space, prey species exhibit significant isotopic variation and present an appropriate isoscape for inferences on resource consumption (Fig. 5; Carlson et al. 2014). Thus, the observed isotopic similarity is indicative of extensive dietary overlap that may enhance competition when prey are limiting. Indeed, Clem (1977)

showed that dietary overlap between martens and fishers increases substantially over winter as resources become scarce, and our isotopic analyses detected significant dietary overlap in autumn when prey should have been readily available. Given that dietary overlap is a primary predictor of intraguild predation (Donadio and Buskirk 2006), and that fishers are the most common source of winter mortality for martens in our system (McCann et al. 2010), the observed lack of dietary niche partitioning likely intensifies interspecific competition between martens and fishers.

Mustelid coexistence is a complex relationship and can depend on elaborate processes such as competition–colonization trade-offs or intraguild predation (Table 1). While not explicitly considered in our analyses, occupancy models can be used to assess competition–colonization processes using meta-population dynamics among occupied and unoccupied sites (MacKenzie et al. 2006). Our models, however, detected low colonization and extinction probabilities, particularly for fishers, and thus did not support competition–colonization trade-offs as a potential mechanism of coexistence for martens and fishers in Chequamegon at a landscape scale. Intraguild predation of martens by fishers, though, has been reported in our study area (McCann et al. 2010). Such intraguild predation is widespread among carnivores, and is indicative of extensive interference competition that can lead to significant consequences for smaller, subordinate species, including martens (Palomares and Caro 1999). Although intraguild predation can facilitate coexistence indirectly (Rosenzweig 1966), we suggest that competition with fishers may ultimately be limiting recovery of martens in Chequamegon. However, survivorship of adult martens in our system exceeds that of a population at equilibrium (McCann et al. 2010; Buskirk et al. 2012), suggesting that, if competition has limited recovery, it must be influencing other vital rates such as juvenile recruitment (Manlick et al. 2016).

Recent evidence suggests intraguild predation can be mediated by landscape and resource heterogeneity (Robinson et al. 2014, sensu Amarasekare 2003). In Wisconsin, widespread spatial (Rhemtulla et al. 2007), structural (Schulte et al. 2007; Rhemtulla et al. 2009), and taxonomic (Schulte et al. 2007; Rhemtulla et al. 2009) homogenization of forests is likely to have altered the competitive relationship between martens and fishers. For example, Schorger (1942) inferred from historical trapping records that martens were far more numerous than fishers throughout Wisconsin prior to European settlement and noted strong spatial segregation, with martens inhabiting the old growth conifer forests of northern Wisconsin while fishers occupied the central Wisconsin hardwoods. Following the conversion of conifer forests to hardwoods through timber harvest, however, fishers gradually replaced martens before both were extirpated via unregulated trapping (Schorger 1942). Forest composition has not changed since the initial extirpation of martens and fishers (Rhemtulla et al. 2009), yet both species were reintroduced to the homogenized forests of northern Wisconsin (Williams et al. 2007). Based on our results and the history of marten–fisher dynamics in Wisconsin, we hypothesize that

landscape homogenization has compressed niche space and enhanced the competitive relationship between martens and fishers via extensive niche overlap (Fig. 6). Specifically, we postulate that reduced habitat availability and structural heterogeneity (Schulte et al. 2007; Rhemtulla et al. 2009), coupled with an increasing loss of snow cover (Saultaire et al. 2016) and a shifting prey base (Rooney et al. 2004; Myers et al. 2009), has collapsed the realized niches of martens and fishers to a

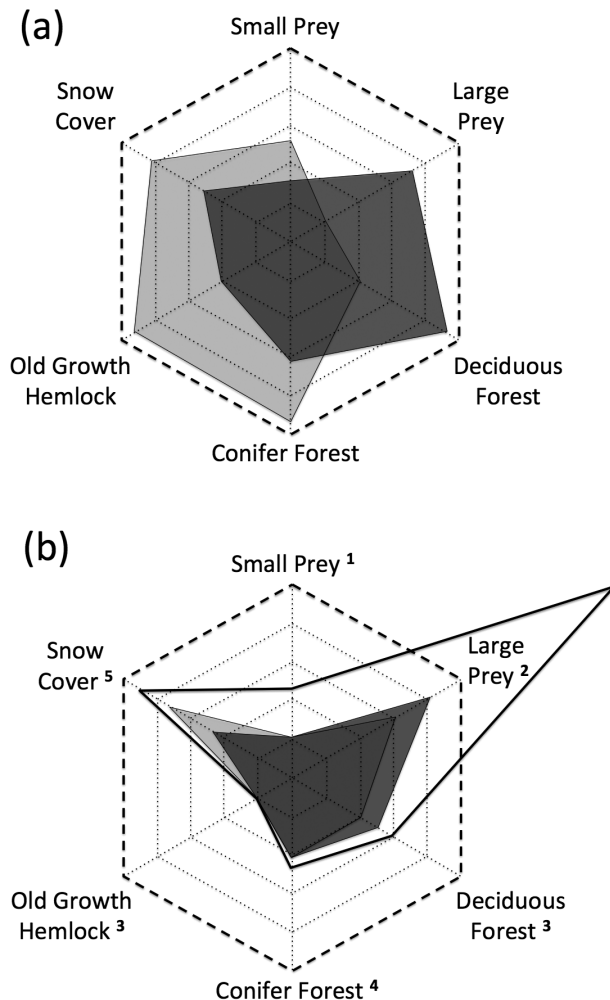


Fig. 6.—A conceptual diagram of niche overlap in martens (*Martes americana*, light gray) and fishers (*Pekania pennanti*, dark gray) for historical (a) and contemporary (b) Wisconsin. Superscripts refer to citations. (a) Hypothesized historical niche space (dashed line) for martens and fishers that facilitated coexistence through differential use of space and resources. Prior to European settlement, martens were more common in the deep snow and old growth conifers of northern Wisconsin, whereas fishers occurred more frequently in the hardwood forests of central Wisconsin (Schorgor 1942). (b) A contemporary niche space estimated by the proportional change of each axis relative to historical baselines (solid line) and derived from empirical studies of the Great Lakes region where structurally complex hemlock stands have decreased 79% (3—Rhemtulla et al. 2009), total conifer cover 57% (4—Rhemtulla et al. 2007), deciduous forests 40% (3—Rhemtulla et al. 2009), snow cover 10% (5—Saultaire et al. 2016), and small mammals 56% (1—Myers et al. 2009). In contrast, large prey such as white-tailed deer (*Odocoileus virginianus*) have increased 2-fold relative to historical abundances (2—Rooney et al. 2004).

fraction of their historical norms and precipitated the observed niche overlap (Fig. 6). To test this hypothesis, future research should focus on quantifying historical niche axes or explicitly comparing niche overlap in homogenized and heterogeneous landscapes.

Our results suggest that competitive interactions among martens and fishers in Wisconsin are a function of niche partitioning that is mediated by landscape and resource heterogeneity. Given the ubiquity of contemporary ecosystem homogenization (Cardille and Lambois 2010), and that reintroduction efforts generally focus on marginalized landscapes (Palmer et al. 1997), the interaction between landscape suitability and interspecific competition should become an increasingly important consideration when restoring carnivore communities. Reintroductions are regularly used to restore carnivore populations, yet even the most thorough guidelines still neglect species interactions, despite continued recommendations (Creel 2001; Stier et al. 2016) and applications to planning of reintroductions (Halsey et al. 2015). Our study highlights the importance of competition for recovering carnivores, and illustrates the difficulties of recreating historical carnivore communities through reintroductions of multiple species. For example, intraguild predation theory predicts that established members of a dominant species will suppress members of the colonizing, subordinate species via strong interference competition (Holt and Polis 1997). Given that martens were reintroduced to Wisconsin following establishment of fishers, our results may have been predicted. Consequently, we urge future restoration programs to consider the order of species reintroductions prior to translocations, and encourage conservation practitioners to promote carnivore recovery and coexistence through the maintenance of diverse habitat and prey resources.

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Spline correlograms of spatial autocorrelation among marten (a) and fisher (b) occurrences at a 1-km lag.

Supplementary Data SD2.—Distribution of maximum likelihood estimates for single-season marten occupancy (ψ) and detectability (p) from 1,000 simulations following Guillera-Aroita et al. (2010). Simulations employed all combinations of the highest and lowest estimated ψ and p , and used the

mean number of repetitions completed for each site ($K = 2$, $N = 50$).

Supplementary Data SD3.—Distribution of maximum likelihood estimates for single-season fisher occupancy (ψ) and detectability (p) from 1,000 simulations following [Guillera-Arroita et al. \(2010\)](#). Simulations employed all combinations of the highest and lowest estimated ψ and p , and used the mean number of repetitions completed for each site ($K = 2$, $N = 50$).

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