RESEARCH ARTICLE



Can landscape heterogeneity promote carnivore coexistence in human-dominated landscapes?

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Abstract

Context Interspecific competition can limit species distributions unless competitors partition niche space to enable coexistence. Landscape heterogeneity can facilitate niche partitioning and enable coexistence, but land-use change is restructuring terrestrial ecosystems globally with unknown consequences for species interactions.

Objectives We tested the relationship between landscape heterogeneity and carnivore co-occurrence in

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Wisconsin Department of Natural Resources, Bureau of Natural Heritage Conservation, 107 Sutliff Avenue, Rhinelander, WI 54501, USA natural and human-dominated ecosystems to assess the landscape-mediated impacts of anthropogenic change on coexistence.

Methods We used boosted regression trees to model the distributions and co-occurrence of two competing forest carnivores, American martens and fishers, at two contrasting sites in the Great Lakes region, USA: a "natural" site largely devoid of human impacts and a "human-dominated" site with substantial development and a history of land-use change. We assessed the importance of climate and habitat variables for each species, measured spatial niche overlap, and quantified co-occurrence as a function of compositional (patch richness), configurational (landscape shape), and topographical (elevation range) heterogeneity per site.

Results We observed significant differences in the effect of heterogeneity on co-occurrence between sites. The natural landscape exhibited little niche overlap and co-occurrence had a significant, positive relationship with heterogeneity. Conversely, the human-dominated site exhibited high niche overlap with variable effects of heterogeneity on co-occurrence. Elevation, snowpack, and development had strong, contrasting effects on marten and fisher distributions, suggesting that differential use of habitat and anthropogenic features facilitates coexistence.

Conclusions Heterogeneity can facilitate coexistence, but too much may undermine carnivore coexistence in human-dominated landscapes where habitat and space are limited. Moreover, future climate change will likely erode niche partitioning among martens and fishers, with particularly strong consequences for coexistence in human-dominated landscapes and at range boundaries.

Keywords Camera trap · Chequamegon National Forest · Climate change · *Martes americana* · Mustelid · *Pekania pennanti* · Roads · Snow tracks · Voyageurs National Park

Introduction

Biotic interactions are important regulators of species' distributions (Peterson et al. 2011; Wisz et al. 2013). Interspecific competition, in particular, can govern the distribution of organisms when coexistence is unattainable (Bowers and Brown 1982; Erlinge and Sandell 1988; Wisz et al. 2013). To maintain stable coexistence, competitors must partition niche space by varying their use of space, time, or resources (Chase and Leibold 2003; Letten et al. 2017). Coexistence theory predicts that spatial heterogeneity can facilitate niche partitioning by providing additional niche axes that enable coexistence through interspecific variation in fitness, dispersal, or access to shared resources (Macarthur and Levins 1964; Chesson 2000). While this relationship is scale-dependent (Chesson 2000; Amarasekare 2003), empirical evidence has shown that landscape heterogeneity can indeed promote coexistence in natural ecosystems (Menge and Menge 1974; Kotler and Brown 1988; Palmer 2003). However, climate and land-use change are restructuring these ecosystems with widespread consequences for landscape heterogeneity, competitive interactions, and species' distributions (Robertson et al. 2013; Gámez-Virués et al. 2015; Perović et al. 2015).

Mammalian carnivores exhibit strong agonistic interactions and their distributions are often regulated by interspecific competition (Donadio and Buskirk 2006; Fisher et al. 2013; Santulli et al. 2014). Consequently, numerous coexistence mechanisms have been proposed, including spatial and temporal segregation, differential habitat and resource selection, behavioral avoidance, and intraguild predation (Table 1 in Manlick et al. 2017b). In natural systems, landscape heterogeneity facilitates these mechanisms and promotes coexistence (Durant 1998; Darimont et al. 2009; Fisher et al. 2013). Nevertheless, carnivores increasingly inhabit human-dominated landscapes that simultaneously create heterogeneity in some niche axes while homogenizing others (McKinney and Lockwood 1999; Cardille and Lambois 2010; Radeloff et al. 2015). The effect of landscape heterogeneity on carnivore coexistence in these novel ecosystems is poorly understood (Manlick et al. 2017b), and excessive heterogeneity in human-dominated landscapes could ultimately inhibit competitor coexistence (Palmer 1992). Indeed, increasing evidence suggests that human agency is intensifying carnivore competition (Lewis et al. 2015; Cruz et al. 2018; Smith et al. 2018). At the same time, however, the restoration of carnivores to human-dominated landscapes is increasingly promoted as a means to restore ecosystem processes and lost species interactions (Chapron et al. 2014; Ripple et al. 2014), but the potential for increased interspecific competition among reintroduced species in these landscapes is rarely assessed (Manlick et al. 2017b).

American martens (Martes americana; hereafter, martens) and fishers (Pekania pennanti) are smallbodied forest carnivores and the most widely reintroduced carnivores in North America (Powell et al. 2012). Martens and fishers co-occur throughout the temperate regions of North America and are broadly associated with complex, old growth forests (Ruggiero et al. 1994). Both species exhibit similar habitat preferences and overlapping diets (Zielinski and Duncan 2004; Manlick et al. 2017b), often resulting in direct competition, particularly in human-modified landscapes at the southern extent of their distributional overlap where intraguild predation is common (Krohn et al. 1997; McCann et al. 2010). Sympatric populations often partition space, time, or micro-habitat features, thereby minimizing competitive overlap (Fisher et al. 2013; McCann et al. 2017a; Zielinski et al. 2017). In particular, differential use of snow features - stratified by elevation - likely enables coexistence throughout much of their range (Zielinski et al. 2017). For instance, fishers utilize mixed cover types at low elevations throughout their range, while martens generally exploit deep, uncompressed snow in conifer forests via morphological adaptations that minimize foot loading (i.e., low body mass/foot surface area; Krohn et al. 1995; Fisher et al. 2013). Recent studies have hypothesized that landscape heterogeneity promotes these differences and may facilitate marten-fisher coexistence through increased niche partitioning (Fisher et al. 2013; Manlick et al. 2017b).

We tested the relationship between landscape heterogeneity and marten-fisher coexistence in natural and human-dominated landscapes of the Great Lakes region. First, we modeled the distributions of martens and fishers in two contrasting ecosystems - humandominated landscapes of the Chequamegon National Forest in Wisconsin, USA (hereafter, CNF) and natural landscapes of Voyageurs National Park in Minnesota, USA (hereafter, VNP). We then estimated spatial niche overlap and the probability of cooccurrence for martens and fishers at each site. Lastly, we modeled co-occurrence as a function of compositional, configurational, and topographic heterogeneity for each site and compared the relationship between heterogeneity and coexistence across natural and human-dominated landscapes. Both sites occur within the historical range of martens and fishers and are characterized by mixed temperate forests and consistent snow cover. The CNF is located along the southern boundary of marten-fisher overlap in the region and is characterized by widespread disturbance following European settlement. Both martens and fishers were reintroduced to the CNF in the late twentieth century, but, despite decades of intensive management, martens remain a state-endangered species (Manlick et al. 2017a) while fishers have expanded across the region (Pokallus and Pauli 2015). In contrast, VNP has experienced considerably less ecological change (Goring et al. 2016; Goring and Williams 2017), being a federally protected National Park since 1975. Regional surveys also show substantially higher ratios of marten to fisher abundance in the VNP area compared to the CNF (Erb 2015; Manlick et al. 2017b; Woodford 2017). The CNF and VNP therefore provide a natural comparison to test the relationship between landscape heterogeneity and cooccurrence in natural versus human-dominated systems. We predicted that niche overlap would be higher in the modified landscapes of CNF than in the preserved VNP due to limited resource availability (Manlick et al. 2017b), but we predicted that the probability of co-occurrence in both sites would increase with landscape heterogeneity.

Methods

Study sites

Our study focused on the Great Divide District of the CNF (1851 km^2) and the entirety of VNP plus state and federal forests bordering the southern boundary of the park (1642 km^2).

The CNF is a multi-use forest dominated by deciduous forest and woody wetlands, with evergreen and mixed forest interspersed (Fig. 1a; Table 1). Historical logging and continued anthropogenic disturbances have heavily altered CNF forests, and historically conifer-dominated systems are now comprised largely of mixed hardwoods (e.g., sugar maple [Acer saccharum], yellow birch [Betula alleghaniensis], and aspen [*Populus* spp.]; Rhemtulla et al., 2007; Schulte et al., 2007). These novel CNF forests have severely reduced taxonomic and structural heterogeneity (Schulte et al. 2007; Rhemtulla et al. 2007, 2009). Indeed, diverse forests of large, structurally complex trees have been replaced by smaller trees, increased stem densities, and reduced total basal areas (Rhemtulla et al. 2009; Goring et al. 2016). However, widespread development has also increased landscape heterogeneity through fragmentation (Hawbaker et al. 2006; Gonzalez-Abraham et al. 2007), and our CNF study region now contains > 2,750 km of maintained roads and motorized vehicle trails (e.g., snowmobile; Fig. 1a, b). Conversely, VNP is dominated by five large lakes with evenly distributed deciduous, evergreen, and mixed forests, as well as woody wetlands (Fig. 1c, d; Table 1). Though VNP has also seen changes in forest composition, including deciduous forests replacing conifers (mainly Populus spp.; Goring et al. 2016; Paulson et al., 2016), the CNF experiences continued human pressure and now contains an order of magnitude more developed lands than VNP (Table 1). Moreover, VNP contains a combined 770 km of roads and trails, approximately one quarter of what is present in the CNF. Though both systems are characterized by cold winters with consistent snow cover, VNP also maintains 1.5 times more snowpack than the CNF (i.e., snow-water equivalent; Table 1).

Sampling

In the CNF, we surveyed winter snow tracks (November-April) along 153 km of maintained forest roads from 2001 to 2014 following Manlick et al. (2017b). All surveys occurred a minimum of 2 activity periods (i.e., dusk and dawn) after snowfall to ensure opportunities for animal movement, and we repeated surveys up to 4 times per winter. We georeferenced all tracks that bisected surveyed roads (Fig. 1a, b) and identified marten and fisher tracks using a combination of morphology, behavior, and straddle width (Manlick et al. 2017b; McCann et al. 2017b). Tracks separated by > 500 m were assumed to be separate detections (Manlick et al. 2017b). In VNP, we deployed camera traps from 2007 to 2017, resulting in 298 unique sampling locations and > 25,000 trap nights. Reconvx cameras (Silent Image, PC900; Holmen, WI, USA) were stationed along corridors, including snowmobile trails, ungroomed hiking trails, game trails, and small forest roads, and all traps were deployed during the snow season to optimize detection of forest carnivores. Sites were baited with deer (Odocoileus virginiana) or beaver (Castor canadensis) carcasses wired to a tree 3-5 m from the camera station. Cameras were deployed annually to maximize the geographic extent of surveys throughout the study area. Cameras operated from 1–210 days ($\overline{x} = 60.02$) and species observations were identified visually by VNP staff. Unique detections of martens and fishers were defined as images captured > 30 min from a previous observation. All detections were limited to snow-on season (October-April) for comparison to CNF snow-track surveys (Fig. 1c, d). All sampling adhered to the ethical guidelines established by the American Society of Mammalogists (Sikes 2016).

Table 1 Mean values (SD) of landscape variables (1–10 km² scales) for Chequamegon National Forest (CNF) and Voyageurs National Park (VNP) used to predict marten (*Martes americana*) and fisher (*Pekania pennanti*) distributions

	1 km ²		5 km^2		10 km ²	
Variable	CNF (<i>N</i> = 1976)	VNP (<i>N</i> = 1762)	CNF (<i>N</i> = 410)	VNP (<i>N</i> = 378)	CNF (<i>N</i> = 217)	VNP (<i>N</i> = 206)
Elevation (m)	438.95 (20.47)	357.75 (17.63)	439.02 (19.61)	357.82 (17.04)	438.01 (21.36)	357.67 (17.18)
Maximum temperature (°C)	2.42 (0.20)	1.00 (0.14)	2.42 (0.2)	1.00 (0.14)	2.42 (0.2)	1.01 (0.14)
Minimum temperature (°C)	-8.94 (0.12)	-11.02 (0.11)	-8.94 (0.11)	-11.02 (0.1)	-8.93 (0.12)	-11.02 (0.09)
Snowpack (kg/m ²)	24.89 (5.31)	39.85 (4.79)	25.11 (5.6)	39.84 (4.69)	25.19 (5.86)	39.98 (4.67)
Edge density	148.23 (49.31)	130.61 (66.88)	150.62 (36.13)	128.78 (59.84)	150.59 (32.25)	123.98 (61.07)
Largest patch index (LPI)	43.19 (20.78)	47.90 (25.79)	32.44 (18.47)	39.65 (24.91)	28.64 (17.18)	38.37 (26.5)
Deciduous forest (%)	36.05 (23.63)	15.58 (16.91)	36.28 (18.96)	15.41 (14.21)	37.24 (17.83)	15.08 (13.65)
Deciduous forest LPI	28.23 (24.61)	10.34 (14.75)	22.84 (20.17)	7.95 (11.47)	20.79 (19.13)	6.68 (9.75)
Development (%)	2.95 (3.42)	0.17 (0.67)	3.02 (2.19)	0.18 (0.48)	2.99 (1.76)	0.18 (0.43)
Development LPI	2.40 (3.07)	0.13 (0.54)	2.03 (1.89)	0.10 (0.28)	1.76 (1.47)	0.09 (0.22)
Evergreen forest (%)	9.14 (10.39)	10.63 (13.66)	9.06 (8.14)	10.10 (10.81)	8.83 (7.06)	9.48 (9.71)
Evergreen forest LPI	5.02 (7.60)	6.58 (10.79)	2.96 (4.29)	4.04 (6.08)	2.22 (3.03)	3.01 (4.42)
Mixed forest (%)	11.66 (8.74)	19.21 (15.99)	11.63 (6.72)	18.36 (13.5)	11.52 (5.97)	17.43 (12.21)
Mixed forest LPI	5.23 (5.63)	12.07 (13.57)	2.84 (3.1)	8.31 (9.33)	2.05 (2.25)	6.75 (7.27)
Shrub (%)	5.49 (5.87)	2.93 (6.11)	5.42 (4.18)	2.96 (4.61)	5.45 (3.84)	2.98 (4.28)
Shrub LPI	2.37 (3.65)	1.87 (4.52)	1.26 (1.75)	1.19 (2.36)	0.92 (1.13)	0.91 (1.64)
Water (%)	4.65 (12.28)	22.37 (32.04)	4.81 (9.71)	21.08 (26.92)	4.56 (7.77)	19.28 (24.07)
Water LPI	4.26 (11.94)	21.59 (31.99)	3.91 (9.26)	19.75 (26.98)	3.27 (6.86)	17.61 (24.13)
Woody wetland (%)	28.32 (20.39)	19.09 (22.26)	28.00 (16.00)	19.01 (19.98)	27.50 (14.92)	18.29 (18.47)
Woody wetland LPI	21.13 (20.19)	14.54 (22.03)	15.91 (14.97)	11.88 (19.65)	13.71 (12.77)	10.38 (17.4)



Fig. 1 Presences (gray-black) and absences (white) of martens (a, c) and fishers (b, d) in the Chequamegon National Forest (top) and Voyageurs National Park (bottom). Background raster

Species distribution modeling

illustrate underlying land cover from NLCD 2011 and dark lines denote maintained roads

We modeled marten and fisher distributions in CNF and VNP using presence-absence data from each species as response variables. In the CNF, we used all marten and fisher track detections from 2001–2014 as presences. For absences, we subdivided the 153 km of surveyed roads into 1 km transects and identified all transects where martens and fishers were never detected. Using repeated surveys from 2013–2014 (Manlick et al. 2017b), we calculated the per-survey detection probability for martens and fishers as 0.20 and 0.12, respectively. For each species, every transect without a detection from 2001 to 2014 (minimum of 10 surveys) was deemed unoccupied and we randomly generated a point along each unoccupied transect to be used as absences (Fig. 1a, b). For VNP, every camera trap detection of martens and fishers from October–April was used to compile presences. We then calculated daily detection probabilities of 0.11 and 0.07 for martens and fishers, respectively, and restricted absences to sites that were active \geq 14 days

without ever detecting a marten or fisher (i.e., $\geq 98\%$ cumulative probability of detection; Fig. 1c, d).

We modeled marten and fisher distributions using 20 predictor variables to capture the effects of climate (e.g., temperature, snow-water equivalent), elevation, and land cover composition (e.g., % cover) and configuration (e.g., edge density, largest patch index) on marten and fisher occurrence (Table 1). Specifically, we used the USGS National Elevation dataset $(30 \times 30 \text{ m}; \text{Gesch et al.}, 2002)$ to quantify topography and the 2011 National Land Cover Database (NLCD, 30×30 m; Wickham et al., 2013) to quantify land cover variables. All land cover composition and configuration variables were calculated in the program FRAGSTATS (McGarigal et al. 2002). We used the R package *daymetr* (Hufkens et al. 2018) to calculate climate variables from 30-year means (1985-2015) based on Daymet interpolated climate surfaces $(1 \times 1 \text{ km}; \text{Thornton et al., } 2012)$ limited to October-April. To assess scale-dependency, we quantified all predictors within 1, 5, and 10 km² of all locations, and we then gridded CNF and VNP and calculated variables in 1, 5, and 10 km² cells to predict marten and fisher distributions across each study area. Notably, 1 km² was the finest resolution of the climate data and represents habitat use at the patch scale for many forest carnivores (Fisher et al. 2011, 2013), while the 5 km² and 10 km² scales reflect regional marten and fisher home range sizes, respectively (Wright 1999; Dumyahn et al. 2007).

We modeled species distributions and estimated relative variable importance for martens and fishers at each site using Boosted Regression Trees (BRTs) in the R package *dismo* (Elith et al. 2008; Hijmans et al. 2013). BRTs are a machine learning approach that combines large numbers of simple regression trees through boosting techniques to maximize predictive performance (Elith et al. 2008). This approach allowed us to assess the relative importance of variables for each species while also incorporating nonlinear relationships and complex interactions between variables. Moreover, unlike classical regression approaches, BRTs do not require independence in observations, can account for correlation in observations and variables, and they do not rely on a top model for accurate prediction (Elith et al. 2008) - all issues that have plagued the use of snow-track data in species distribution models (Manlick et al. 2017b). We used a bagging fraction of 0.5, a tree complexity of 5 (i.e., up to 5-way interactions), and a learning rate ranging from 0.001 to 0.0001 to ensure > 1000 trees (per Elith et al. 2008). All models were fit using tenfold cross validation via the 'gbm.step' function in *dismo*, and predictive performance was assessed using area under the receiver operating curve (AUC). Models were then used to predict the probability of marten [p(marten)] and fisher [p(fisher)] occurrence across CNF and VNP at the 1, 5, and 10 km² resolutions. Lastly, we used the 'hetcor' function in the R package *polycor* (Fox 2016) to assess the directional relationship between the spatial predictors and species occurrences modeled by BRTs.

Co-occurrence, overlap, and heterogeneity

We calculated the probability of marten-fisher cooccurrence [p(co-occur)] as p(marten) × p(fisher) for each cell at each resolution in both CNF and VNP. We also estimated the realized spatial overlap of martens and fishers in CNF and VNP at each scale by calculating the similarity of species distributions. Specifically, we used the Expected Shared Presences (ESP) of each species following Godsoe (2014) and Godsoe and Case (2015) where $ESP = \frac{2\sum_{j} P_{1j} P_{2j}}{\sum_{j} (P_{1j} + P_{2j})}$, *j* is each cell, and P_{1j} and P_{2j} are p(marten) and p(fisher) in each cell, respectively. This metric ranges from 0 (no overlap) to 1 (complete overlap) and calculates a generalized Sørensen similarity of two species geo-

graphic distributions (Godsoe 2014). To test the relationship between marten-fisher cooccurrence and landscape heterogeneity in each study site, we modeled p(co-occur) at each scale as a function of three independent heterogeneity metrics to capture variability in landscape composition, landscape configuration, and topographic complexity. Specifically, we quantified patch richness (i.e., the number of land cover classes in each cell) to measure compositional heterogeneity and landscape shape index (LSI; i.e., patch aggregation and complexity) to capture the heterogeneity of land cover configuration in each cell. All land cover metrics were calculated in FRAGSTATS. Topographic heterogeneity was measured as the range of elevation in each cell using the National Elevation dataset. We used analysis of covariance (ANCOVA) to test for differences in the relationship between landscape heterogeneity and cooccurrence by site (i.e., site \times heterogeneity interactions) and for differences in intercepts (i.e., variation in mean co-occurrence by site). To do this, we combined data from both sites and normalized all covariates to range from 0-1. If significant interactions were not detected, we removed interaction terms and used more parsimonious additive models to test for differences in intercepts. Lastly, we used ordinary least squares regression (OLS) in the R stats package (R Core Team 2019) to explore the independent relationship between co-occurrence and landscape heterogeneity within each site. To account for potential spatial autocorrelation, we also modeled the relationship between heterogeneity and co-occurrence within each site using generalized additive models (GAMs) with a smoothed spatial covariate. We used the 'bam' function in the R package mgcv (Wood 2015) with a Gaussian process and 50 knots for each spline.

Results

We detected 128 marten and 249 fisher presences in the CNF from 2001 to 2014. Along the 153 km of surveyed roads, 91 transects had no marten detections and were used to generate marten absences, compared to only 39 transects without a fisher detection (Fig. 1a, b). In VNP, we detected marten presence at 61 camera locations and fisher presence at 73 locations, resulting in 152 and 137 absences for martens and fishers, respectively (Fig. 1c, d). Predictive performance of BRTs was high for all models (all AUC > 0.94).

Species distributions and overlap

Variable importance from BRTs revealed that elevation was the strongest predictor for martens in the CNF, with a positive relationship at all scales (Fig. 2a–c). Marten detections further exhibited a strong, positive interaction between elevation and snow-water equivalent (i.e., snowpack) at all scales (Appendix S1). In addition, martens responded positively to large patches of contiguous land cover at the finest resolution (i.e., patch scale; 1 km²) but showed contrasting responses to large patches and high proportions of specific land cover types at the courser home range scales (Fig. 2a–c, Appendix S1). Conversely, elevation and snow had a negative effect on fisher occurrences in the CNF at all scales, with particularly strong effects at the finest scale (Fig. 2ac; Appendix S1). Notably, the strongest indicator of fisher occurrence at the intermediate resolution (5 km²) was human development, while avoidance of wetlands and water bodies appeared to drive fisher distribution at the largest scale. In total, martens and fishers showed contrasting responses to the most influential variables at all scales (e.g., elevation, snow, development). Nevertheless, predicted fisher occurrence was nearly ubiquitous across the study area, while martens were restricted to isolated pockets (Fig. 3a, b). Consequently, predicted co-occurrence was high for all cells occupied by martens (Fig. 3c), resulting in an ESP (i.e., distribution overlap) of 0.59, 0.51, and 0.52 for the 1, 5, and 10 km^2 scales, respectively.

In VNP, variable importance for martens and fishers was similar to the CNF. Specifically, snowwater equivalent was the primary driver of fisher occurrence, exhibiting strong negative effects at all scales (Fig. 2d-f). Interestingly, martens also displayed a negative overall relationship with snow (Fig. 2d-f), though this response was largely driven by strong, negative associations at the highest snow depths (Appendix S2). Moreover, martens did not exhibit strong associations with any particular variables but responded positively to a number of different land cover types, including evergreen forest, shrubland, and woody wetlands. In total, detections of both species were associated with a diversity of cover types, resulting in patchy distributions across VNP (Fig. 3d, e). Consequently, predicted co-occurrence was low across the park (Fig. 3f) and ESP estimated a distributional overlap of 0.37, 0.37, and 0.36 for the 1, 5, and 10 km² scales, respectively.

Co-occurrence and heterogeneity

The relationship between co-occurrence and landscape heterogeneity differed significantly between CNF and VNP for landscape shape and richness at the patch scale (1 km^2), but the significance of these interactions decreased at coarser resolutions (Table 2, Fig. 4). However, the effect of patch richness (i.e., composition) was consistently different between sites, with less co-occurrence in the CNF as patch richness increased. Models also detected significant differences in intercepts for all metrics at all scales, indicating



Fig. 2 Relative importance (%, out of 100) of the five most important variables from boosted regression trees for martens (light grey) and fishers (dark grey) in the Chequamegon National Forest (**a**–**c**) and Voyageurs National Park (**d**–**f**) at the 1 km², 5 km², and 10 km² scales. Pluses indicate positive

mean co-occurrence was consistently higher in the CNF than VNP (Table 2, Fig. 4). Our OLS regressions and GAMs yielded nearly identical results for each site (Table S1) – co-occurrence increased significantly with all heterogeneity metrics at all scales in VNP, while heterogeneity was largely insignificant to co-occurrence in the CNF (Fig. 4). Co-occurrence in the CNF did, however, increase significantly with topography (i.e., elevation range) at the finest scale and with complex landscape configurations (i.e., LSI) at the larger scales (Fig. 4; Table S1).

Discussion

Landscape heterogeneity is predicted to limit niche overlap and facilitate competitor coexistence. We tested the generality of this prediction using sympatric populations of martens and fishers in the contrasting natural and human-dominated ecosystems of VNP and CNF. We detected little niche overlap in VNP and found that co-occurrence increased significantly with all forms of landscape heterogeneity. Conversely, we observed high niche overlap and variable impacts of

relationships and minuses indicate negative associations between species and variables. Relative importance of variables differed across scales; see supporting appendices for complete model results

landscape heterogeneity on co-occurrence in the human-dominated landscape of CNF, with co-occurrence actually decreasing as a function of patch richness across scales. Our results support the hypothesized relationship between landscape heterogeneity and coexistence in natural ecosystems, but imply a tipping point at which landscape complexity inhibits coexistence in human-dominated systems (sensu Palmer 1992). For instance, we observed positive responses of co-occurrence to complex topography and landscape configurations in both the CNF and VNP, particularly at the coarser home range scales, but we also detected consistently negative effects of patch richness on co-occurrence in the CNF where richness is correlated with development and agriculture (r > 0.6). This suggests that while complex topography and patch configuration may promote coexistence, land-use change that alters the underlying land cover composition (e.g., development) could undermine such facilitation by limiting habitat availability. Human-dominated landscapes present this challenge en masse, as novel land cover like development and agriculture are increasingly prevalent. For instance, edge density, development, and agriculture were all



Fig. 3 Predicted probability of marten occurrence (a), fisher occurrence (b) and co-occurrence (c) in the Chequamegon National Forest, and probability of marten occurrence (d), fisher

occurrence (e) and co-occurrence (f) in Voyageurs National Park at the 5 km^2 scale

higher in the CNF while large patches of contiguous forest were more common in VNP, particularly for preferred habitats like mixed and evergreen forest that were consistent drivers of marten and fisher distribution. Ultimately, our results show that human-dominated landscapes present a challenge in balancing the positive effects of landscape heterogeneity on competitor coexistence while also maintaining adequate habitat and resources.

Climate and land-use change

We found that elevation and snow were significant drivers of marten and fisher distribution in both the CNF and VNP, with contrasting effects on each species. For example, the interaction between elevation and snowpack had a strong positive effect on marten distribution in the CNF at all scales, while both elevation and snowpack restricted fisher occurrences. Likewise, elevation had a positive impact on marten distribution in VNP, while snowpack was the primary driver of fisher occurrence at all scales, largely restricting detections to sites with $< 40 \text{ kg/m}^2$ (i.e., mean snow-water equivalent; Table 1, Appendix S2). Sites with > 40 kg/m² snowpack ($\sim 1 \text{ m of snow}$ assuming snow density = 50 kg/m^3 ; Roebber et al. 2003) were notably rare in the CNF, likely contributing to the ubiquitous presence of fishers across the study area. Ultimately, these results are consistent with the positive effect of topographical complexity on coexistence, and with previous research illustrating the differential impact of snow on martens and fishers in montane systems (e.g., Krohn et al. 1995; Krohn et al. 1997; Zielinski et al. 2017). Thus, our findings support the hypothesis that elevation and snow mediate the distributions and coexistence of martens and fishers, even at relatively low elevations.

Fishers in the CNF selected for low intensity development, a land cover category driven by an extensive road network that further reduces snowpack

	1 km^2				5 km^2				$10 \ \mathrm{km^2}$			
Heterogeneity	CNF	VNP	Slope	Intercept	CNF	VNP	Slope	Intercept	CNF	VNP	Slope	Intercept
Landscape shape	4.75 (1.23)	4.26 (1.67)	< 0.001	< 0.001	9.42 (2.01)	8.20 (3.34)	0.505	< 0.001	12.96 (2.55)	10.80 (4.83)	0.388	< 0.001
Patch richness	6.55 (1.24)	5.88 (2.00)	< 0.001	< 0.001	8.44 (1.21)	7.65 (2.14)	< 0.001	< 0.001	9.22 (1.29)	8.16 (2.51)	0.006	< 0.001
Topography	30.87 (16.16)	26.90 (18.67)	0.203	< 0.001	44.89 (23.74)	39.07 (22.89)	0.207	< 0.001	53.60 (29.21)	43.90 (25.69)	0.004	< 0.001

and likely facilitates the movement of fishers and other mesopredators (Whiteman and Buskirk 2013; Manlick et al. 2017b; Zuckerberg and Pauli 2018). While this result could have been driven by road surveys favoring the detection of larger-bodied species along maintained roads, multiple lines of evidence suggest this was not the case for our study. First, despite the larger number of fisher detections, average marten detection probabilities (0.20-0.43) exceeded the average fisher detection probabilities (0.11-0.34) across all spatiotemporal scales (Manlick et al. 2017b). Furthermore, with > 2500 km of maintained roads, CNF landscapes contained an average of 3% developed lands, mirroring the development surrounding marten (3.6%) and fisher (3.8%) detections and indicating that detections along roads are representative of the broader study site. Interestingly, the CNF approximates mean road density across the United States, while VNP has some of the lowest road densities in the country (Riiters and Wickham 2003; Watts et al. 2007). This suggests that road-snow interactions in the CNF are broadly representative of the potential impact motorized corridors can have on habitat- and snowmediated competition. Previous research has shown that species with high foot loads like fishers and canids exploit compacted snow along motorized corridors, to the potential detriment of snow-adapted prey and competitors (Bayne et al. 2008; Whittington et al. 2011; Gese et al. 2013; Whiteman and Buskirk 2013). Our results support these studies and indicate that development in human-dominated landscapes can support less snow adapted species (e.g., fishers) and erode niche partitioning with snow adapted competitors (e.g., martens). Furthermore, future climate projections estimate significant declines in snowpack for both the CNF and VNP by the end of the twentyfirst century (Notaro et al. 2010, 2014). Such climate changes will favor fishers and other southerly distributed mesocarnivores, likely intensifying competition with martens regionally (Manlick et al. 2017b; Zielinski et al. 2017) and potentially driving martens to regional extirpation (Carroll 2007; Lawler et al. 2012). Nevertheless, our models show that deep snow can also have a negative effect on marten distribution, consistent with recent studies illustrating the costs of deep snow even for specialized species like martens (Martin et al. 2020).



Fig. 4 Relationship between landscape heterogeneity and probability of marten-fisher co-occurrence (OLS) in the Chequamegon National Forest (top, \mathbf{a} - \mathbf{c}) and Voyageurs National Park (bottom, \mathbf{d} - \mathbf{f}) at the 1 km², 5 km², and 10 km²

Landscape heterogeneity and niche partitioning

We estimated niche overlap between martens and fishers at the southern extent of their sympatry in the CNF and over 250 km north in VNP. At our southern site in the CNF, we detected > 1.5 times more niche overlap than in the more northerly VNP, and mean cooccurrence was significantly higher in the CNF at all scales. Range boundary dynamics could have contributed to this observed niche overlap and may have influenced the differential impacts of heterogeneity on co-occurrence observed in the CNF. For example, populations at range boundaries often maintain sparse distributions (Brown 1984), with species capable of exploiting anthropogenic landscapes exhibiting the highest population densities (Channell and Lomolino 2000). We observed similar patterns, including a patchy distribution of martens and the widespread occurrence of fishers selecting for human development in the CNF. Moreover, populations at range boundaries often utilize suboptimal habitat (Lawton 1993), and may even increase niche breadth in the absence of

scales. Solid lines denote significant relationships, dashed lines denote non-significant relationships, and shaded ribbons illustrate 95% confidence intervals

preferred resources (Zielinski and Duncan 2004; Oliver et al. 2009). Our models revealed that both martens and fishers used atypical habitat, including shrubs, wetlands, and development. Consequently, these boundary characteristics may have contributed to the widespread distribution of fishers and the high degree of niche overlap with martens in the CNF. As noted, landscape heterogeneity can help minimize such overlap, but this often occurs via the spatial partitioning of resources (Fisher et al. 2013). We suggest that landscape heterogeneity may have weaker effects on co-occurrence at range boundaries where distributions are constrained and space is limiting, and our results support this hypothesis. Given the high probability of fisher occurrence across the CNF, however, co-occurrence (i.e., $p(marten) \times p(fisher)$) was often a reflection of marten distribution. Thus, our modeled responses of co-occurrence to landscape heterogeneity may have been more indicative of marten habitat selection. Nonetheless, such dynamics are likely prevalent at range boundaries and in anthropogenic landscapes where dominant, more generalist species (e.g., fishers) are widespread and can competitively exclude subordinate species by exploiting a wider degree of resources (Peers et al. 2013). Future studies should continue to explore this relationship between niche breadth and land-use change across species distributions in order to further assess the impact of human-dominated landscapes on coexistence at range boundaries.

While our models clearly illustrate the variable effects of landscape heterogeneity on co-occurrence and niche overlap for these species across ecosystems, there are important limitations to consider. First, because our BRTs did not account for imperfect detection it was essential to correctly identify presences and absences given that pseudoabsences and "background" data can overestimate niche overlap (i.e., ESP; Godsoe 2014). In VNP we used daily detection probabilities to set a conservative threshold and assign absences to camera stations; however, the CNF did not have fixed survey locations so we randomly generated absences along transect segments without a detection during the entire survey period. It is therefore possible that CNF models used informed pseudoabsences which could have inflated niche overlap estimates; however, given our survey-level detection probabilities (Manlick et al. 2017b) it is unlikely that martens and fishers went undetected when present over the entire 14-year survey period. Second, both species distribution models and our regression analyses only incorporated remotely sensed data on climate and land cover variables. These variables relied on coarse cover type classifications, and previous research has shown that both martens and fishers also select for fine-scale habitat features (Buskirk and Powell 1994; Shirk et al. 2014; McCann et al. 2014). Moreover, our data captured the heterogeneity in land cover composition and configuration, but not the underlying structural complexity that is important for both martens and fisher habitat selection (Buskirk and Powell 1994; McCann et al. 2014). Thus, it is possible that martens and fishers select for and partition structural complexity and habitat at finer scales than our analyses, as has been suggested by telemetry-based approaches (McCann et al. 2014). Future studies could incorporate spatial models or animal movements with increasingly available LiDAR data to assess the partitioning of these additional niche axes (Joyce et al. 2019). Lastly, species must partition space, time, or resources to facilitate co-existence, and our results indicate that martens and fishers in VNP partition space and habitat features (e.g., snow) while animals in the CNF do not. Thus, martens and fishers may partition other niche axes to enable long-term coexistence (McCann et al. 2017a), though Manlick et al. (2017b) observed high spatial, temporal, and dietary overlap. Heterogeneity in fine-scale habitats, forest structure, or prey are thus likely to facilitate co-occurrence. Moreover, interactions between resources (e.g., habitat and prey) could also generate environmental heterogeneity, and future research should explore the dynamics of resource availability to assess the mechanisms underlying such heterogeneity.

Conclusions

We revealed potential costs of landscape heterogeneity for carnivore coexistence in human-dominated landscapes, where increased landscape heterogeneity is likely conflated with fragmentation and anthropogenic development. Furthermore, our results suggest human-dominated landscapes can favor species able to exploit these novel landscapes (e.g., fishers), further increasing niche overlap and reducing the potential for coexistence. This is consistent with recent studies illustrating the adverse effects of human agency on carnivore niche partitioning (Lewis et al. 2015; Smith et al. 2018). Nevertheless, carnivore reintroductions are advocated as a potential mechanism to restore ecosystem processes and restructure existing carnivore communities (Ripple et al. 2011, 2014; Chapron et al. 2014), with restoration programs often targeting modified landscapes like the CNF (Navarro and Pereira 2015). We show that interspecific competition is likely among reintroduced carnivores in these human-dominated landscapes and that landscape heterogeneity will not facilitate coexistence, particularly at range boundaries. We encourage wildlife managers to consider these competitive interactions when establishing future carnivore reintroduction programs.

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Data accessibility All data is archived in FigShare (https://doi.org/10.6084/m9.figshare.12724667).

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