Spatial segregation of sympatric marten and fishers: The influence of landscapes and species-scapes

5 authors, including:

Jason T. Fisher
University of Victoria
99 PUBLICATIONS **3,472** CITATIONS

SEE PROFILE

Bradley Anholt
University of Victoria
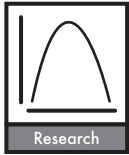**96** PUBLICATIONS **5,728** CITATIONS

SEE PROFILE

John Paul Volpe
University of Victoria
65 PUBLICATIONS **2,849** CITATIONS

SEE PROFILE

Spatial segregation of sympatric marten and fishers: the influence of landscapes and species-scapes

Jason T. Fisher, Brad Anholt, Steve Bradbury, Matthew Wheatley and John P. Volpe

J. T. Fisher (jason.fisher@albertainnovates.ca), Alberta Innovates – Technology Futures, Ecosystem Management Unit. no. 3-4476 Markham St., Victoria, BC V8Z 7X8, Canada. JTF also at: Univ. of Victoria, Dept of Biology, PO Box 3020, Station CSC, Victoria, BC V8W 3N5, Canada. – B. Anholt, Univ. of Victoria, Dept of Biology. PO Box 3020, Station CSC, Victoria, BC V8W 3N5, Canada. BA also at: Bamfield Marine Sciences Centre, Box 100, Bamfield, BC V0R 1B0, Canada. – S. Bradbury, Fish and Wildlife Div., Government of Alberta. Edson, AB T7E 1T2, Canada. – M. Wheatley, Provincial Parks Div., Government of Alberta. Hinton, AB T7V 2E6, Canada. – J. P. Volpe, Univ. of Victoria, School of Environmental Studies, PO Box 3060, STN CSC, Victoria, BC V8W 3R4, Canada.

Co-occurring species are rarely considered as a factor influencing habitat selection. However, niche theory predicts that sharing resources, predators, and other interspecific interactions can limit the environmental conditions under which a species may exist. How does the spatial distribution of one species affect that of another within shared landscapes? We tested whether sympatric marten *Martes americana* and fishers *M. pennanti* in a mountain landscape in Alberta, Canada exhibit local-scale spatial segregation, beyond differential habitat selection. We modelled marten and fisher distribution in relation to remotely-sensed habitat data and species co-occurrence, using generalized linear models and information-theoretic model selection. Marten and fishers selected different habitat types and showed different responses to habitat fragmentation. Even after accounting for these differences, the absence of one species significantly explained the occurrence of the other. We conclude that the spatial distribution of marten and fishers influences habitat selection by each other at landscape scales, and hypothesize that this pattern may result from competition in a spatially heterogeneous environment. Species-habitat models that consider only resources may fail to capture key predictors of species' occurrence. Reliable prediction and inference requires that ecologists expand from landscapes to also include species-scapes: a spatial plane of species interactions that combines with resources to drive species' distributions.

Landscapes are varied mosaics of different patch types that together influence how species are distributed within them (Dunning et al. 1992, Wiens et al. 1993). Landscapes then are also mosaics of species, each with their own spatial distribution, each potentially affecting the distribution of other species sharing that landscape. Although the conceptual importance of interspecific interactions is fundamental to ecology, these interactions are often overlooked as a factor influencing species' habitat selection and distribution at landscape scales. Carrying capacity within habitat patches can be limited by resource competitors, apparent competitors that share a predator, or interference competition between species. Interspecific interactions may modulate patterns of species' occurrence, so should be included as a key variable in habitat selection models. We ask the question: does including the spatial distribution of a potential competitor improve our ability to predict species occurrence within shared landscapes?

Recent studies have examined the role of spatial heterogeneity in facilitating species coexistence on a landscape (Chesson 2000, Amarasekare 2003), many echoing Grinnell's (1917a, b) and MacArthur and Levins' (1964) emphasis on

geographic variation in limiting resources. Species coexistence in space can result from the interplay between species' limiting factors, dispersal ability, competitive ability and dominance hierarchy, and the spatial dispersion of resources in the local and regional landscapes (Amarasekare 2003). For example, coexistence may occur through selection of different habitats (Fedriani et al. 1999) despite ubiquitous distribution of shared prey across habitats. Alternatively, species with overlapping niches may segregate in space as a result of population processes and differences in dispersal, thus partitioning resources and avoiding competition (Shigesada et al. 1979, Pacala and Levin 1997). Together these mechanisms ultimately manifest as spatial patterns of species distribution across a landscape.

Understanding patterns of species co-occurrence, and their relationship to the distribution of resources (or, by proxy, land-cover types) in a landscape, is a key first step toward elucidating the mechanisms behind those pattern (Kotliar and Wiens 1990, Dunning et al. 1992, Wiens et al. 1993). For most species-habitat models, landscapes are typically viewed as patchy mosaics of discontinuously distributed resources. Resource availability, usually quantified as

physical habitat characteristics (e.g. vegetation, elevation, moisture, slope, aspect, etc.), forms the conceptual heart of most habitat selection studies (Hall et al. 1997, Manly et al. 2002). However, habitat necessarily includes more than physical characteristics or even resources; it integrates an individual's lifetime interactions with competitors, predators, parasites, and mates (Wiens et al. 1993, Morris 2003). Though interspecific competition is fundamental to niche theory, species-habitat models rarely include species interactions, with some exceptions (Aunapuu and Oksanen 2003, Morris 2003, Harrington and Macdonald 2008, Vanak and Gompper 2010). It may be necessary to broaden the definition of landscapes to include species-scapes: a spatial plane of species interactions that combines with resources and habitat structure to drive species' distributions. Species coexistence (or conversely, segregation) may be an important but overlooked measure in habitat selection studies.

Species coexistence is scale-dependent; species can coexist at the small scale of the local community (Hanski and Gilpin 1997), or at larger scales of metacommunities (Wilson 1992). Coexistence at the larger, 'regional' scale of the metacommunity (sympatry) may be facilitated by spatial segregation at smaller, local scales (Amarasekare 2003). If one species uses local space unoccupied by its competitor, this small-scale spatial partitioning could be facilitating co-occurrence on the same landscape. This spatial segregation should be measurable as a reduced occupation probability by one species when the other is present. We hypothesized that spatial segregation could be occurring for two sympatric mustelid species – marten *Martes americana* and fisher *Martes pennanti* – in mountain landscapes in the Canadian province of Alberta. These two species have been a subject of investigations of sympatry since Grinnell's time (Rosenzweig 1966, see also Zielinski and Duncan 2004).

Martes ecology

Marten and fishers are mid-size generalist predators in the Mustelidae with large areas of sympatry across forested regions of North America (Zielinski and Duncan 2004, Williams et al. 2009). Both species are distributed throughout sub-alpine, montane, and boreal forests of western Canada but have experienced substantial range retractions since European colonisation (Laliberte and Ripple 2004). There is little evidence of a dominance hierarchy between these species (see references in Krohn et al. 1997). Fishers' mean body mass (3118 g) is over three times that of marten's (839 g; Holling 1992). Though differing in body size, high dietary overlap has been observed in some sympatric populations of these species (Zielinski and Duncan 2004). Consequently, several authors suggest that marten and fishers compete directly for food and space (reviewed by Zielinski and Duncan 2004), but this remains an untested hypothesis. Conversely, Rosenzweig (1966) proposed that inherent body-size differences create differences in diet (through differential prey exploitation) that permit coexistence of marten and fisher.

American marten occur throughout North American boreal and mixed-transitional forests (Clark et al. 1987). Marten are primarily carnivorous, and prey on small mammals such as shrews, mice, and southern red-backed voles (*Sorex* spp., *Peromyscus* spp., *Clethrionomys gapperi*). Red squirrels, flying squirrels, snowshoe hares, and grouse constitute martens' largest prey (*Tamiasciurus hudsonicus*, *Glaucomys* spp., *Lepus americanus*, *Bonasa* spp.; Thompson and Colgan 1987). Eggs, berries, and carrion are also opportunistically consumed. Marten are generally limited by food availability throughout the year, particularly in winter. Marten's primary predators include felids, canids, owls, (*Bubo* spp.) and larger mustelids (reviewed by Clark et al. 1987). Marten are typically associated with older, closed-canopy forests, and substantial data exist that marten are sensitive to anthropogenic forest fragmentation (Hargis and Bissonette 1997, Chapin et al. 1998, Hargis et al. 1999; see review by Fisher and Wilkinson 2005). Krohn et al. (1997) suggest marten populations may be limited by fishers in some regions.

Fishers occur throughout North American boreal, coastal, mixed-transitional, and Carolinian forests (Powell 1981). They prey upon shrews *Sorex* spp., mice *Peromyscus* spp., southern red-backed voles *Clethrionomys gapperi*, red squirrels *Tamiasciurus hudsonicus*, flying squirrels *Glaucomys* spp., and snowshoe hares *Lepus americanus* (Powell 1979, Arthur et al. 1989, Bowman et al. 2006). The fisher is one of the few species to prey heavily on porcupines *Erethizon dorsatum* where available. Fisher adults are not often preyed upon, but compete with canids, felids, and raptors for prey and carrion (Powell 1981). Fishers inhabit both coniferous and deciduous forests, though they may seasonally prefer coniferous over deciduous stands (Arthur et al. 1989, Powell 1994). Though they most often occur in older closed-canopy forests, they occupy other forest types if prey are available (reviewed by Powell 1981, Arthur et al. 1989, Weir and Harestad 2003). Very few data exist on fishers' response to habitat alteration (reviewed by Fisher and Wilkinson 2005), but the few available studies suggest fishers avoid young successional forest stages (Weir and Harestad 2003), and are sensitive to habitat fragmentation (Carroll et al. 1999).

Based on marten and fisher ecology we predicted that, within a shared landscape, these species would select different landcovers (habitat patches), topography (indexing snow depth in the region), and degrees of habitat fragmentation. We also predicted that marten and fishers segregate at small scales beyond differential habitat selection. We tested the hypotheses that spatial distribution of marten and fishers within a shared landscape is explained by 1) composition of naturally occurring landcover patches; 2) habitat fragmentation and disturbance; and additionally 3) absence of the competitor.

Material and methods

Study area

Marten and fisher occurrence were sampled in the west-central foothills and Rocky Mountains of Alberta, Canada (Fig. 1). Coniferous forest 80–120 yr old (*Pinus contorta*, *Picea glauca*, *Picea mariana*, and *Abies balsamea*) dominate this landscape, with some small deciduous (*Populus tremuloides*, *Populus balsamifera*) stands occurring throughout. Small
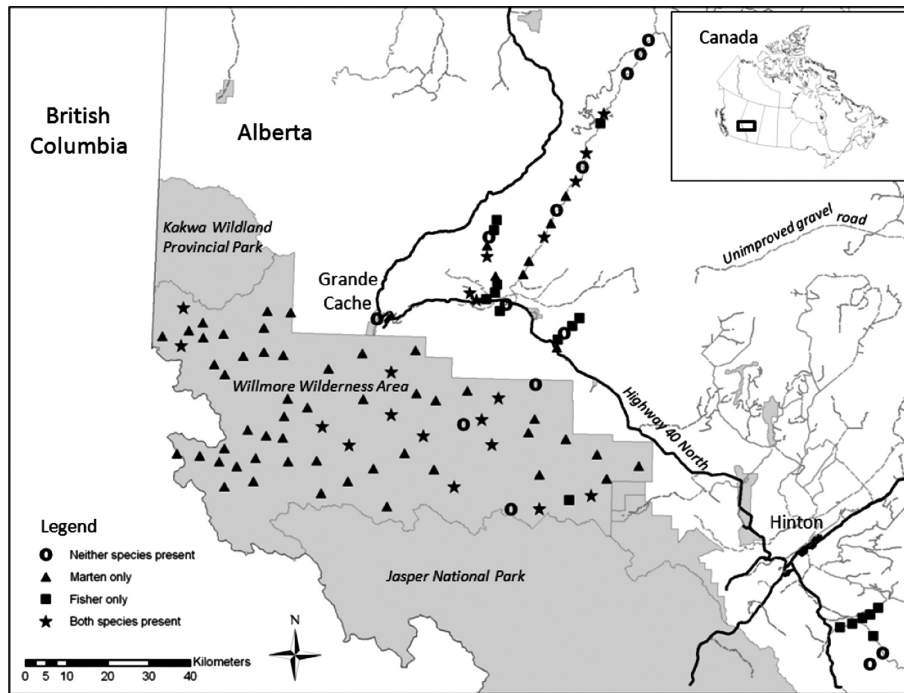
Figure 1. Marten and fisher occurrences were surveyed using non-invasive techniques in the Willmore Wilderness Area and the adjacent Foothills of west-central Alberta, Canada, over a 6400-km² area. We surveyed 120 sites three times (some sites are lost to scale in this figure). Marten were more common than fisher, and the two species co-occurred only sporadically.

stands of black spruce *Picea mariana* with forest floors dominated by Labrador tea *Ledum groenlandicum* and mosses *Sphagnum* spp. occurred in low-lying areas. Pine and mixed stands were often fairly open, with a sparse alder *Alnus crispa* understorey. Younger fire- or harvest-origin stands were embedded within this matrix, as well as deforested linear features (seismic lines) of varying densities and stages of regeneration resulting from oil exploration. Elevation of this landscape ranged from 1200 to 1600 m. A portion of this region, the Willmore Wilderness Area, is a 4600 km² conservation area completely protected from anthropogenic development. The Willmore sits in the Front Ranges of the Rocky Mountains, part of the western Cordilleran system. Topography is rugged, with high peaks, steep-sloped ridges, and valley bottoms. The Rockies grade into the adjacent foothills to the east, with moderately rugged topography. In the foothills, forest harvesting, mining, and oil and gas development have created a mosaic landscape of different forest-seral stages, seismic lines and other linear features, and a high degree of human activity. A limited fur harvest occurred throughout the study area. Marten and fishers are common throughout this region and the eco-regions surrounding them.

Study design

We set carcass-baited sampling sites in December and monitored them monthly until March, during which time food was scarce and thus species detection most likely. Differences in logistical requirements between the remote and roadless Willmore and the road-accessible Foothills necessitated different sample-site placement between areas.

In the Willmore, we used a systematic sampling design constrained by helicopter access and avalanche risk. Sites (n = 66) were placed an average of 5727 m apart (SD 1574 m) in a roughly rectangular grid that covered most of the Park. We sampled 30 sites in 2006–2007 and a different set of 36 sites in 2007–2008, for a total of 66 sites. In the Foothills (n = 54), we deployed sites along a semi-linear transect ca 415 km long using a constrained systematic design that roughly followed the main logging-road access in the region. We constrained sampling to forested areas with logistically feasible access; we omitted wetlands, areas immediately adjacent to main highways, and areas in the immediate vicinity of current industrial activity. Within these constraints, sample sites were placed an average of 4335 m apart (SD 5218 m), approximately 50 m from access roads. A total of 120 sites were sampled across a 6400 km² landscape.

Sampling species occurrence

We used two methods to sample mammals, together designed to detect a range of mammal species: non-invasive genetic tagging (NGT) via hair sampling, and camera trapping. NGT used Gaucho barbed wire (Bekaert, Brussels, Belgium) wrapped around a tree baited with whole beaver; individuals would climb the tree for the bait, and leave a hair sample. Hair traps were deployed at all sample sites and we collected hair samples monthly. DNA from hairs was analysed by Wildlife Genetics International (WGI; Nelson, BC, Canada) to identify species. DNA was extracted from hairs using QIAGEN's DNEasy Tissue Kits (QIAGEN, Hilden, Germany) and analysed to identify species using

sequence-based analysis of the 16S rRNA gene of mitochondrial DNA (mtDNA) (sensu Johnson and O'Brien 1997) that was then compared against a DNA reference library of all known mammal species in the region.

Hair trapping may underestimate occurrence. Absence of hair may result from 1) an absent individual, or 2) a present but undetected individual. This problem has ramifications for estimates of species occupancy, density, and habitat use (Mackenzie et al. 2006). To increase detection rate, we combined hair trapping methods with remote camera detection (Gompper et al. 2006, O'Connell et al. 2010). In the Foothills, remote cameras (Trailmaster 1550 Active infra-red remote camera systems; Goodson and Associates, Lenexa, KS, USA) were installed at 11 randomly selected monitoring stations. In the Willmore we deployed Reconyx RM30 (2006–2007) or PM30 (2007–2008) infrared-triggered digital cameras (Reconyx, Holmen, WI, USA) at all 66 sampling sites.

We combined the two datasets to yield presence/absence (using either method) of marten and fisher within each of the 3 sampled months. We summed presences across 3 months to yield a 0–3 count of species occurrence at each site. This measure provides presence/absence information as well as indexing residency at each site during the sampling period.

Habitat and statistical analyses

Habitat is defined here as coarse-resolution landcover types that have been reclassified from satellite imagery into categories describing landscape features of ecological importance to wildlife. We used a LandSat thematic-mapped GIS land cover dataset incorporating digital elevation models (DEMs) classified using a habitat-identification algorithm (McDermid et al. 2009). This dataset yielded 16 potential land-cover types, constituting the spatial grain of analysis. Of these 16, seven variables were hypothesized to be of ecological importance to marten and fisher, and were sufficiently represented in the landscape to allow modelling (Table 1). These included closed conifer forest, moderate conifer forest, open conifer forest, mixedwood forest, open wetland, upland shrubs, and upland herbaceous habitats; McDermid et al. (2009) describe these in further detail.

We used ArcGis 9.3 (Environmental Systems Research Inst., Redlands, CA, USA) Spatial Analyst to geo-reference each sampling site on the habitat GIS layer. We quantified habitats around each sampling site at a spatial scale appropriate for each species. Fisher et al. (2011) tested a range of 20 spatial scales and found that habitat quantified within a 500-m radius (78.5-ha area) best predicted fisher occurrence; no best scale was found for marten so we used the 500-m scale for comparability. We calculated the percent of each land-cover type using a combination of spatial analysis routines (written in Arc-View ver. 3.x Spatial Analyst) and the Regional Analysis function of Patch Analyst, an extension to ArcView (< http://flash.lakeheadu.ca/wrrempel/patch >). Additionally, we used digital map inventories to calculate seismic line densities (km km^{-2} of area) to represent oil and gas exploration activity contemporary with our study. We also measured the ruggedness of our landscapes using a topographic ruggedness index (TRI; Riley et al. 1999). The TRI calculates the amount of elevation difference between adjacent cells of a digital elevation model, in this case a 25-m digital elevation model data from the Alberta Base Dataset. Finally, we obtained GPS-derived elevation for each of our sample sites.

We modeled marten occurrence counts against fisher occurrence counts and habitat data using generalized linear models (GLM) in R statistical software (ver. 2.13.0; R Core Development Team) with Poisson errors and log-link function (Crawley 2007). Resulting models were ranked using an information-theoretic approach to model selection (Burnham and Anderson 2002), based on Akaike's information criterion (AIC) score and AIC weights. We used a two-prong approach to model building. First, because we had no a priori hypotheses about species' selection of landcover types, we modelled only the seven landcover variables and species co-occurrence using a stepwise AIC-based model (step-AIC function, MASS package for R software) to identify the best-fit model from these candidate sets. Second, we used this parsimonious landcover model and added variables representing a priori hypotheses about the effects of topography and disturbance on species occurrence. From this global set, the models with the highest AIC weights were taken as the best models describing species occurrence, and we used model averaging (Burnham and Anderson 2002) to calculate parameter estimates from these models. We conducted deviance tests (Faraway 2006) to assess each top

Table 1. Independent variables used in marten and fisher habitat selection models. Full descriptions of the variables are given in McDermid et al. (2009) and Riley et al. (1999; terrain ruggedness). Variables represent the proportion of each land-cover type within a 500-m radius around sampling sites, except elevation at the sampling site.

Category	Code	Variable	Description
Landcover variables	DCON	Dense conifer forest	>75% conifer with >60% crown closure
	MCON	Moderate conifer forest	>75% conifer with 50–75% crown closure
	OCON	Open conifer forest	>75% conifer with 6–49% crown closure
	MFOR	Mixed forest	26–74% broadleaf forest, no specified crown closure
	OWET	Open wetland	<6% crown closure, wet moisture regime
	SHRUB	Upland shrubs	>25% shrub cover, <6% tree cover, with dry-mesic moisture regime
	HERB	Upland herbaceous	<25% shrub cover, <6% tree cover, with dry-mesic moisture regime
Disturbance variables	REGEN	Regenerating area	fire and timber harvest <10 yr old
	SEISMIC	Seismic line density	km of line km^{-2} of area
Topographic variables	RUGGED	Terrain ruggedness	topographic ruggedness index
	ELEV	Elevation	metres above sea level at the sampling site

model's goodness of fit. We also calculated evidence ratios (ER; Anderson 2008) to weigh support for the inclusion of species as a model variable:

$$ER = \frac{\Sigma AIC \text{ weights for models that include species}}{1-(\Sigma AIC \text{ weights for models that include species})} \quad (1)$$

Finally, we conducted Fisher's exact test for differences in expected co-occurrences of marten and fisher across sites, and a χ^2 test on counts within species to examine differences in repeated occurrences across months.

Results

In the foothills, we obtained 346 hair samples, including 38 marten and 160 fisher hairs. Cameras detected 15 marten occurrences and 20 fisher occurrences. In the Willmore, we obtained 491 hair samples, including 183 marten and 36 fisher hairs. We obtained 115 488 photographs of various species in 6 months of sampling (Fisher et al. 2011). Across the study area marten were detected at 85 of 120 sites (71%); fisher were detected at 48 of 120 sites (40%; Table 2). Species distributions were patchy across the shared landscape (Fig. 1).

Marten spatial distribution was best explained by landcover, fragmentation, and fisher occurrence. Deviance tests suggest the three best-supported models (models 9, 10, 11) fit the data (p = 0.523, 0.591, 0.503, respectively). These best models suggested that marten occurred more often in landscapes with more open conifer forest, less mixedwood forest, less regenerating area, lower seismic line density, and fewer fisher occurrences (Table 3, 4). There was five times more evidence supporting fisher occurrence as explaining marten distribution than not supporting it (ER = 5.4; Table 3).

Fishers' spatial distribution was best explained by landcover and marten occurrences. Deviance tests suggest the three best-supported models (models 3, 4, 5) fit the

data (p = 0.944, 0.939, 0.949, respectively). These best-supported fisher models suggested fishers occurred more often within landscapes containing less dense and moderate conifer forest, less open wetland, more shrub cover, and fewer marten occurrences (Table 4, 5). There was little effect of fragmentation or topography. There was over 36 times more evidence to suggest fisher distribution was explained by marten occurrence, than against it (ER = 36.8; Table 5).

Fisher and marten sometimes occur together, but were less likely to do so than expected by chance. Results of the Fisher's exact test corroborates the generalised linear modelling results, and indicates that the odds ratio derived from expected distributions of marten and fisher occurrences differs from 1 (p = 0.0072; odds ratio = 0.313; 95% CI = 0.126, 0.757). In addition, marten tended to occur consistently at a site (i.e. were detected at all three sampling occasions) more than expected ($\chi^2 = 20.4941$, DF = 2, p < 0.0001). In contrast, fishers were more variable and were detected either once, twice, or thrice at each site with equal frequency ($\chi^2 = 1.125$, DF = 2, p = 0.5698).

Discussion

Marten and fishers are spatially segregated at small scales within this shared landscape, sensu Amarasekare (2003).

Table 2. Contingency table of marten and fisher co-occurrences. The number of monthly occurrences was averaged over three months to yield counts of 0, 1, 2, or 3 occurrences for 120 sites in the Foothills and Rockies Mountains of Alberta, Canada.

		Count of fisher occurrences				
		0	1	2	3	Total
Count of marten occurrences	0	14	4	7	10	35
	1	9	4	2	3	18
	2	13	3	1	2	19
	3	36	8	3	1	48
	Total	72	19	13	16	120

Table 3. Habitat model selection for marten in a mountain and foothills landscape. Models 1–7 were built using stepwise model selection procedures to find the most parsimonious model. Added models (7–12) contain variables describing habitat fragmentation and terrain ruggedness. Model 11 (in bold) is the best-supported.

Model set	Model	Model variables	AIC score	ΔAIC	AIC weight
landcover and fisher	1	DCON + MCON + OCON + MFOR + OWET + SHRUB + HERB + FISHER	364.82	10.08	0.00
	2	DCON + OCON + MFOR + OWET + SHRUB + HERB + FISHER	362.86	8.12	0.01
	3	DCON + OCON + MFOR + OWET + SHRUB + FISHER	361.25	6.51	0.02
	4	OCON + MFOR + OWET + SHRUB + FISHER	360.35	5.61	0.03
	5	OCON + MFOR + OWET + FISHER	359.21	4.47	0.05
best landcover + fisher model	6	OCON + MFOR + FISHER	358.75	4.01	0.07
	7	OCON + FISHER	372.52	17.78	0.00
landcover only	8	OCON + MFOR	366.42	11.68	0.00
global model	9	OCON + MFOR + FISHER + RUGGED + ELEV + REGEN + SEISMIC	357.48	2.74	0.13
landcover and disturbance	10	OCON + MFOR + REGEN + SEISMIC	357.12	2.38	0.15
landcover, disturbance and fisher	**11**	**OCON + MFOR + REGEN + SEISMIC + FISHER**	**354.74**	**0**	**0.51**
landcover and topography	12	OCON + MFOR + RUGGED + ELEV	367.11	12.37	0.00
landcover, topography and fisher	13	OCON + MFOR + RUGGED + ELEV + FISHER	360.66	5.92	0.03
fisher only	14	FISHER	377.72	22.98	0.00

Table 4. Model-averaged parameter estimates for top models predicting marten and fisher occurrence. Marten models 9, 10, and 11 (summed AIC weights = 0.79) and fisher models 3, 4, and 5 (summed AIC weights = 0.71) were averaged.

Species modelled	Parameter	Estimate	Adjusted SE	z value	p
Marten	intercept	0.845	0.283	2.965	0.0030
	FISHER	−0.177	0.089	1.991	0.0465
	OCON	1.049	1.692	0.620	0.5354
	MFOR	−2.452	0.841	2.916	0.0036
	REGEN	−0.662	0.449	1.327	0.1846
	SEISMIC	−193.60	93.16	2.078	0.0377
	RUGGEDNESS	−0.001	0.004	0.383	0.7014
	ELEVATION	0.002	0.004	0.481	0.6305
Fisher	intercept	0.462	0.255	1.813	0.0698
	MARTEN	−0.298	0.097	3.071	0.0021
	DCON	−1.220	0.782	1.559	0.1190
	MCON	−0.792	0.460	1.723	0.0849
	OWET	−5.004	2.259	2.215	0.0268
	SHRUB	3.052	1.125	2.714	0.0066
	MFOR	−0.517	0.871	0.594	0.5526

Similar patterns of segregation have been noted in other species ranging from black and grizzly bears (Apps et al. 2006) to grassland ants (Albrecht and Gotelli 2001), and have been implicated as mechanisms for coexistence.

Marten and fishers also exhibit differences in habitat selection, a mechanism for coexistence suggested by MacArthur and Levins (1964). Marten were negatively associated with fragmentation and disturbance as expected (Hargis and Bissonette 1997, Chapin et al. 1998, Hargis et al. 1999), whereas fisher showed no response to either. Marten selected conifer forests, and avoided mixedwood forests and disturbed and fragmented areas. Fishers avoided dense to moderate conifer forests and open wetlands, and selected shrub-dominated areas. Marten and fishers' selection of different habitats is evidence that differential habitat selection may in part facilitate their coexistence in this shared landscape. However, their spatial segregation occurs in addition to differential habitat selection. Even after accounting for response to habitats, topography, and fragmentation, the probability of occurrence of each species was negatively predicted by the occurrence of the other.

Sympatry of marten and fisher has been a historical touchstone for discussions of species coexistence and niche partitioning (Rosenzweig 1966, Powell and Zielinski 1983, Zielinski and Duncan 2004). We observed a spatial pattern, but this pattern allows us to generate some hypotheses about its underlying mechanisms. It is possible that the patterns we observed were due to interference competition. Krohn et al. (1997) implicate interference competition, or even intra-guild predation, as contributing to marten and fisher segregation in southern populations. However, evidence for these mechanisms is sparse (see references in Krohn et al. 1997). Further, marten and fisher co-occur frequently enough in our landscapes – 28% of sampling sites – to question exclusion by dominance or interference, and warrant consideration of an alternative explanation.

We hypothesize that spatial segregation may facilitate coexistence of marten and fisher via spatially mediated coexistence (Amarasekare 2003). Different patterns of species distribution are expected to emerge from spatially mediated coexistence, depending on whether the competitive environment is homogeneous or heterogeneous (Amarasekare

Table 5. Habitat model selection for fishers in a mountain and foothills landscape. Models 1–6 were built using stepwise model selection procedures to find the most parsimonious model. Other models (7–12) contain variables describing habitat fragmentation and terrain ruggedness. Model 5 (in bold) is the best-supported.

Model set	Model	Model variables	AIC score	ΔAIC	AIC weight
landcover and marten	1	DCON + MCON + OCON + MFOR + OWET + SHRUB + HERB + MARTEN	275.53	5.38	0.02
	2	DCON + MCON + MFOR + OWET + SHRUB + HERB + MARTEN	273.68	3.53	0.06
	3	DCON + MCON + MFOR + OWET + SHRUB + MARTEN	271.79	1.64	0.15
	4	MCON + OWET + SHRUB + MARTEN	270.83	0.68	0.23
best model	**5**	**DCON + MCON + OWET + SHRUB + MARTEN**	**270.15**	**0.00**	**0.33**
landcover only	6	DCON + MCON + OWET + SHRUB	277.73	7.58	0.01
global model	7	DCON + MCON + OWET + SHRUB + MARTEN + RUGGED + ELEV + REGEN + SEISMIC	274.74	4.59	0.03
landcover and disturbance	8	DCON + MCON + OWET + SHRUB + REGEN + SEISMIC	280.08	9.93	0.00
landcover, disturbance and marten	9	DCON + MCON + OWET + SHRUB + REGEN + SEISMIC + MARTEN	273.06	2.91	0.08
landcover and ruggedness	10	DCON + MCON + OWET + SHRUB + RUGGED + ELEV	276.15	6.00	0.02
landcover, ruggedness and marten	11	DCON + MCON + OWET + SHRUB + RUGGED + ELEV + MARTEN	273.14	2.99	0.07
marten only	12	MARTEN	284.38	14.23	0.00

2003). Spatial niche partitioning (Chesson 2000) – a theoretical mechanism that allows the coexistence of competing species, though with few empirical tests to date (Amarasekare 2003) – occurs in a heterogeneous environment when covariance between competition and environment results in differences in species' competitive ability across space (Holt 1984). In such spatially heterogeneous competitive environments, coexistence at the regional scale and exclusion at the local scale is likely (Amarasekare 2003). Conversely, coexistence may occur in a spatially homogeneous competitive environment if there are differences in the spatial scales at which intraspecific and interspecific competition occur, a phenomenon Murrell and Law (2003) termed heteromyopia (Szabó and Meszéna 2006). In this scenario, conspecifics competitively interact at larger spatial scales than do heterospecifics. This results in aggregation of conspecifics; intraspecific competition then reduces densities of the more common species, such that the less-common competing species can occupy the resultant gaps in the landscape. Put more simply, a patch may provide fishers with sufficient resources unless martens are there, and vice-versa; sometimes there are sufficient resources in a patch for both. Because resources vary in this complex landscape according to land-cover, fragmentation, and topography, multiple factors influence whether any given patch can hold fishers, or marten, or both.

A measure of each species' competitive ability and its variability through space are required to distinguish between these two mechanisms. This study was not designed to test these mechanisms, but we can conjecture based on observed patterns. Since marten and fisher occurrence were predicted by different habitats, it may be reasoned that marten and fishers' competitive ability differed among these habitats. If so, coexistence of marten and fishers may be the result of spatial niche partitioning within a spatially heterogeneous competitive environment. If instead heteromyopia were facilitating coexistence between marten and fisher in this landscape, one would predict: 1) local patterns of intraspecific aggregation and interspecific segregation; 2) a greater degree of aggregation in the more common species than its competitor; and 3) differences in the spatial scales of habitat selection. The first prediction is supported by our data; intraspecific and interspecific patterns of distribution differed within the shared landscape (Fig. 1, Table 2). The second prediction is also supported; marten, the more common species, tended to aggregate and were more abundant where they occurred, but this was not so for less-common fishers. Finally, Fisher et al. (2011) show that the spatial scales at which marten and fisher select habitat may differ.

Other mechanisms not tested here may facilitate coexistence or conversely, result in segregation. Interference competition and dominance hierarchies not currently documented may behaviourally separate the two. Alternatively, interactions with other species in this diverse ecosystem (e.g. cougars *Puma concolor*, wolves *Canis lupus*, coyotes *Canis latrans*, wolverine *Gulo gulo*, lynx *Lynx canadensis*; Fisher et al. 2011) may affect marten and fisher distribution; these relationships are complex, and we are currently investigating community co-occurrence patterns. Alternatively, differences in martens' and fishers' body size may allow for niche separation through prey differentiation, which in turn permits coexistence, as suggested by Rosenzweig (1966). However, though marten are a third the size of fishers, best evidence suggests that dietary overlap is very high (Zielinski and Duncan 2004), and prey distribution cannot explain the spatial pattern of segregation that we observed. Finally, Powell and Zielinski's (1983) modelling work suggested long-term coexistence of mustelids could occur only through local extinction and recolonisation. No evidence of such patch occupancy dynamics has yet been found for sympatric marten and fisher, and the small distances between our sampling sites (5–7 km) makes this metapopulation dynamic unlikely here. Testing these hypotheses would require us to measure competitive interactions, as well as type and extent of limiting factors, across space (Amarasekare 2003). Doing so across large landscapes is currently logistically prohibitive, but should be a consideration for future research.

Conclusions

Marten and fisher spatially segregate in this shared landscape, and to a greater degree than predicted by differential habitat selection alone. Species interactions have been fundamental to niche theory, from Grinnell (1917a, b), Elton (1927), and Hutchinson (1957) to the present (Chase and Leibold 2003). In contrast, habitat theory has until recently focussed on selection of resources (Hall et al. 1997, Manly et al. 2002, Morrison et al. 2006). Integrating habitat selection theory with interspecific population processes can reveal how species compete and co-occur (Morris 1999, 2003, Morris et al. 2000), and our results illustrate the necessity for this shift. Species-habitat models that consider only resources fail to capture key predictors of species' occurrence. Reliable prediction and inference deriving from ecological research for conservation requires that we expand from landscapes to species-scapes, and include interspecific processes as factors explaining variation in species' distributions.

References

Albrecht, M. and Gotelli, N. J. 2001. Spatial and temporal niche partitioning in grassland ants. – Oecologia 126: 134–141.

Amarasekare, P. 2003. Competitive coexistence in spatially structured environments: a synthesis. – Ecol. Lett. 6: 1109–1122.

Anderson, D. R. 2008. Model based inferences in the life sciences: a primer on evidence. – Springer.

Apps, C. D. et al. 2006. Landscape partitioning and spatial inferences of competition between black and grizzly bears. – Ecography 29: 561–572.

Arthur, S. M. et al. 1989. Habitat use and diet of fishers. – J. Wildl. Manage. 53: 680–688.

Aunapuu, M. and Oksanen, T. 2003. Habitat selection of coexisting competitors: a study of small mustelids in northern Norway. – Evol. Ecol. 17: 371–392.

Bowman, J. et al. 2006. Numerical response of fishers to synchronous prey dynamics. – J. Mammal. 87: 480–484.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd ed. – Springer.

Carroll, C. et al. 1999. Using presence–absence data to build and test spatial habitat models for the fisher in the Klamath region, USA. – Conserv. Biol. 13: 1344–1359.

Chapin, T. G. et al. 1998. Influence of landscape pattern on habitat use by American marten in an industrial forest. – Conserv. Biol. 12: 1327–1337.

Chase, J. M. and Leibold, M. A. 2003. Ecological niches: linking classical and contemporary approaches. – Univ. of Chicago Press.

Chesson, P. 2000. General theory of competitive coexistence in spatially-varying environments. – Theor. Popul. Biol. 58: 211–237.

Clark, T. W. et al. 1987. *Martes americana*. – Mamm. Species 289: 1–8.

Crawley, M. 2007. The R book. – Wiley.

Dunning, J. B. et al. 1992. Ecological processes that affect populations in complex landscapes. – Oikos 65: 169–175.

Elton, C. 1927. Animal ecology. – Sidgwick and Jackson.

Faraway, J. J. 2006. Extending the linear model with R. – Chapman and Hall.

Fedriani, J. M. et al. 1999. Niche relations among three sympatric Mediterranean carnivores. – Oecologia 121: 138–148.

Fisher, J. T. and Wilkinson, L. 2005. The response of mammals to forest harvesting and fire in the North American boreal forest. – Mamm. Rev. 35: 51–81.

Fisher, J. T. et al. 2011. Body mass explains characteristic scales of habitat selection in terrestrial mammals. – Ecol. Evol. 1: 517–528.

Gompper, M. E. et al. 2006. A comparison of noninvasive techniques to survey carnivore communities to survey carnivore communities in northeastern North America. – Wildl. Soc. Bull. 34: 1142–1151.

Grinnell, J. 1917a. The niche relationships of the California thrasher. – Auk 34: 427–433.

Grinnell, J. 1917b. Field tests of theories concerning distributional control. – Am. Nat. 51: 115–128.

Hall, L. S. et al. 1997. The habitat concept and a plea for standard terminology. – Wildl. Soc. Bull. 25: 173–182.

Hanski, I. and Gilpin, M. 1997. Metapopulation biology: ecology, genetics and evolution. – Academic Press.

Hargis, C. D. and Bissonette, J. A. 1997. Effects of forest fragmentation on populations of American marten in the intermountain west. – In: Proulx, G. et al. (eds), Martes: taxonomy, ecology, techniques, and management. Provincial Museum of Alberta, pp. 437–451.

Hargis, C. D. et al. 1999. The influence of forest fragmentation and landscape pattern on American martens. – J. Appl. Ecol. 36: 157–172.

Harrington, L. A. and Macdonald, D. W. 2008. Spatial and temporal relationships between invasive American mink and native European polecats in the southern United Kingdom. – J. Mammal. 89: 991–1000.

Holling, C. S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. – Ecol. Monogr. 62: 447–502.

Holt, R. D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. – Am. Nat. 124: 377–406.

Hutchinson, G. E. 1957. Concluding remarks. – Cold Springs Harbour Symp. Quant. Biol. 22: 415–427.

Johnson, W. and O'Brien, S. J. 1997. Phylogenetic reconstruction of the Felidae using 16S rRNA and NADH-5 mitochondrial genes. – J. Mol. Evol. 44: S98–S116.

Kotliar, N. B. and Wiens, J. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. – Oikos 59: 253–260.

Krohn, W. B. et al. 1997. Relations among fishers, snow, and martens in California: results from small-scale spatial comparisons. – In: Proulx, G. et al. (eds), Martes: taxonomy, ecology, techniques, and management. Provincial Museum of Alberta, pp. 211–232.

Laliberte, A. S. and Ripple, W. J. 2004. Range contractions of North American carnivores and ungulates. – BioScience 54: 123–138.

MacArthur, R. and Levins, R. 1964. Competition, habitat selection, and character displacement in a patchy environment. – Proc. Natl Acad. Sci. USA 51: 1207–1210.

MacKenzie, D. I. et al. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. – Elsevier.

Manly, B. F. J. et al. 2002. Resource selection by animals, 2nd ed. – Kluwer.

McDermid, G. J. et al. 2009. Remote sensing and forest inventory for wildlife habitat assessment. – For. Ecol. Manage. 257: 2262–2269.

Morris, D. W. 1999. A haunting legacy from isoclines: mammal coexistence and the ghost of competition. – J. Mammal. 80: 375–374.

Morris, D. W. 2003. Toward an ecological synthesis: a case for habitat selection. – Oecologia 136: 1–13.

Morris, D. W. et al. 2000. Measuring the ghost of competition: insights from density-dependent habitat selection on the coexistence and dynamics of lemmings. – Evol. Ecol. Res. 2: 41–67.

Morrison, M. L. et al. 2006. Wildlife–habitat relationships: concepts and applications, 3rd ed. – Island Press.

Murrell, D. J. and Law, R. 2003. Heteromyopia and the spatial coexistence of similar competitors. – Ecol. Lett. 6: 48–59.

O'Connell, A. F. et al. 2010. Camera traps in animal ecology. – Springer.

Pacala, S. W. and Levin, S. A. 1997. Biologically generated spatial pattern and the coexistence of competing species. – In: Tilman, D. and Karieva, P. (eds), Spatial ecology: the role of space in population dynamics and interspecific interactions. Princeton Univ. Press, pp. 204–231.

Powell, R. A. 1979. Ecological energetics and foraging strategies of the fisher (*Martes pennanti*). – J. Anim. Ecol. 48: 195–212.

Powell, R. A. 1981. *Martes pennanti*. – Mamm. Species 156: 1–6.

Powell, R. A. 1994. Effects of scale on habitat selection and foraging behaviour of fishers in winter. – J. Mammal. 75: 349–356.

Powell, R. A. and Zielinski, W. J. 1983. Competition and coexistence in mustelid communities. – Acta Zool. Fenn. 174: 223–227.

Riley, S. J. et al. 1999. A terrain ruggedness index that quantifies topographic heterogeneity. – Int. J. Sci. 5: 1–4.

Rosenzweig, M. L. 1966. Community structure in sympatric Carnivora. – J. Mammal. 47: 602–612.

Shigesada, N. et al. 1979. Spatial segregation of interacting species. – J. Theor. Biol. 79: 83–99.

Szabó, P. and Meszéna, G. 2006. Spatial ecological hierarchies: coexistence on heterogeneous landscapes via scale niche diversification. – Ecosystems 9: 1009–1016.

Thompson, I. D. and Colgan, P. W. 1987. Numerical responses of martens to a food shortage in northcentral Ontario. – J. Wildl. Manage. 51: 824–835.

Vanak, A. T. and Gompper, M. E. 2010. Interference competition at the landscape level: the effect of free-ranging dogs on a native mesocarnivore. – J. Appl. Ecol. 47: 1225–1232.

Weir, R. D. and Harestad, A. S. 2003. Scale-dependent habitat selectivity by Fishers in south-central British Columbia. – J. Wildl. Manage. 67: 73–82.

Wiens, J. A. et al. 1993. Ecological mechanisms and landscape ecology. – Oikos 66: 369–380.

Williams, B. W. et al. 2009. Noninvasive hair sampling and genetic tagging of co-distributed fishers and American martens. – J. Wildl. Manage. 73: 26–34.

Wilson, D. S. 1992. Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. – Ecology 73: 1984–2000.

Zielinski, W. J. and Duncan, N. P. 2004. Diets of sympatric populations of American martens (*Martes americana*) and fishers (*Martes pennanti*) in California. – J. Mammal. 85: 470–477.