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Resource limitations and competitive interactions affect carnivore community composition at different ecological scales in a temperate island system

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Abstract: Selective pressures (i.e. resource limitation and competitive interaction) that drive the composition of ecological communities vary, and often operate on different ecological scales (ecological variables across varying spatial scales) than observed patterns. We studied the drivers of distribution and abundance of the American marten (*Martes americana*) and the carnivore community at three ecological scales on a Great Lakes island archipelago using camera traps. We found different drivers appeared important at each ecological scale and studying any of the three scales alone would give a biased understanding of the process driving the system. Island biogeography (resource limitation) was most important for carnivore richness, with higher richness on larger islands and lower richness as distance from the mainland increased. Marten presence on individual islands appeared to be driven by island size (resource limitation) and human avoidance (competitive interaction). Marten abundance at camera trap sites was driven by the cascading effect of coyotes (*Canis latrans*) on fishers (*Pekania pennanti*) (competitive interaction). Incorporating three ecological scales gave novel insights into the varying effects of resource limitation and competitive interaction processes. Our data suggests that ecological communities are structured through multiple competing ecological forces, and effective management

and conservation relies on our ability to understand ecological forces operating at multiple ecological scales.

Keywords: American marten; camera trap; carnivores; community ecology; island biogeography; *Martes americana*; scale.

Introduction

Understanding the effect of scale is essential to determining the drivers of distribution, abundance, and diversity of species within and among ecological communities (Levin 1992, Ruggiero et al. 1994). However, ecological patterns are often driven by ecological processes that operate on different spatial scales (Levin 1992). The selective pressures that affect a meta-community may be different than those that affect a local community, species or individual (Levin 1992, Leibold et al. 2004). The diversity and structure of ecological communities are usually driven by varying combinations of resource limitations and competitive interactions (Hairston et al. 1960, Power 1992), however, one process can outweigh the other depending on the ecological scale (ecological variables across varying spatial scales) at which it is studied (Levin 1992). It is therefore important to determine the factors that affect distribution and abundance of species and communities at multiple ecological scales.

Resource limitations and competitive interactions structure ecological communities differently. Resource limitation processes include ecosystem productivity, which often dictates the availability of food and other resources (Hairston et al. 1960, Oksanen and Oksanen 2000), which are often a limiting factor for populations (Power 1992, Carlson et al. 2014). Competitive interaction processes include direct and indirect competition (Emerson and Gillespie 2008, Levi and Wilmers 2012), where intra- and inter-specific competition structure communities through competition over resources and the ability to exploit niches (Hairston et al. 1960, Emerson and Gillespie 2008). Carnivores also structure the distribution

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and abundance of subordinate species in ecological communities through predation and the fear of predation (Brown et al. 1999, Levi and Wilmers 2012).

Island biogeography is a resource limiting process that affects the availability of resources, species diversity and abundance. Island biogeography has shown that the size and isolation of islands affects both abundance and richness of species, as well as immigration and extinction rates (MacArthur and Wilson 1967, Simberloff 1974, Whittaker and Fernandez-Palacios 2007). However, to date there have been limited studies of the effects of island biogeography on either temperate inland communities or complex mammalian species. Most studies of island biogeography have occurred in tropical systems with innately high levels of biodiversity that are concentrated at lower trophic levels (Whittaker and Fernandez-Palacios 2007), with few studies that focus on temperate or inland systems. Temperate inland systems may be affected by island biogeography differently than tropical systems, due to lower levels of diversity and other factors, such as seasonal effects, that can increase stochasticity and variation in temperate ecological communities (Leibold et al. 2004). Factors affecting the distribution and abundance of species that occupy higher trophic levels, including carnivores, can also be more complex (Ripple et al. 2014).

Carnivores are complex species that are important for maintaining ecological function in communities (Estes et al. 2011, Ripple et al. 2014), but whose populations can be affected by many factors. Carnivores tend to have low population densities (Ripple et al. 2014), and their populations and behaviors can be affected by availability of preferred habitat and prey abundance (Carlson et al. 2014, Ripple et al. 2014). They are also affected by sympatric competition with other carnivores that exploit similar food resources and ecological niches (Hairston et al. 1960, Levi and Wilmers 2012). This is especially important for smaller carnivores that attempt to use areas with abundant prey while simultaneously avoiding areas frequently used by dominant sympatric competitors (Lesmesiter et al. 2015, Wang et al. 2015). The complexity of these interactions is highlighted by cascading effects within the carnivore community, where apex carnivores release subordinate small carnivores from competitive pressure by reducing the abundance of dominant mesocarnivores either in the system (Levi and Wilmers 2012) or at a particular resource (Allen et al. 2015).

Our focal species was the American marten (*Martes americana*, Turton, 1806). American martens are a small, opportunistic carnivore which are state-endangered in Wisconsin (Woodford and Dumyham 2011, Allen et al. 2018b). Shrews (*Blarina* sp., *Sorex* sp.), lagomorphs

(*Leporidae* spp.), and White-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) carrion compose a major portion of Martens diet (Zielinski and Duncan 2004, Carlson et al. 2014). They are habitat specialists associated with mature northern forests and are of cultural importance to the Ojibwe tribes native to the area (Allen et al. 2018b). Martens were found recently within the Apostle Islands National Lakeshore (APIS) after 50 years of apparent absence (Allen et al. 2018b), prompting questions about their abundance and distribution throughout the system.

We deployed camera traps over 2 years on 13 islands within the Apostle Islands National Lakeshore to document carnivore distribution and abundance. Our objectives were to determine the drivers of distribution and abundance of martens and the carnivore community in a Great Lakes island archipelago. We used an *a-priori* modeling framework to use our knowledge of the system to test biologically relevant hypotheses at three different ecological scales in order to understand the dynamics of carnivores and martens in the system. Our specific objectives were to: (1) determine the drivers of carnivore richness among different islands; (2) determine the drivers of marten presence and absence among different islands; (3) determine the drivers of marten abundance at each camera trap site. We considered potential drivers including competitive interactions with larger carnivores and resource limitation in the form of preferred habitat and prey availability at each scale. Testing the drivers of the abundance and distribution of the carnivore community in a temperate island system at multiple scales has the potential for novel insights into the varying effects of resource limitation and competitive interaction processes, including island biogeography and cascading effects.

Materials and methods

Study area

The Apostle Islands are an archipelago of Pleistocene relict sandstone islands located in southwestern Lake Superior, WI, USA. APIS was established in 1970, protecting 21 of the 22 islands. The archipelago is in the transition zone between northern boreal coniferous forest and deciduous forest, creating diverse vegetative structure (Judziewicz and Koch 1993). Microclimatic conditions and vegetative communities are variable between islands depending on the island size, elevation and location

within Lake Superior (Judziewicz and Koch 1993; Supplementary material 1). The average temperature for the duration of this study was 4.4°C, with minimum and maximum temperatures ranging from -30.0°C to 32.8°C, and mean annual precipitation was 82.8 cm of rainfall and 197.4 cm of snowfall (Allen et al. 2018a). Ice cover in the Bayfield harbor, which is indicative of overall lake trends, has decreased about 3 days/decade over the past 150 years (Howk 2009), and the ice season has begun an average of 11.7 days later and ended 3.0 days earlier every decade since 1975 (Howk 2009).

Field methods

We systematically deployed 91 camera traps (Hyperfire Model, Reconyx, Holmen, WI, USA) on APIS beginning in September 2014 and ending in June 2016, but four of our camera traps did not function and we excluded them from our analyses. To choose target deployment sites, we overlaid a 1 km² grid on satellite imagery of the islands and placed target locations at the center of cells with >50% of surface area on land. On Stockton Island, four deployment locations were randomly omitted due to a shortage of camera traps. In subsequent camera deployments, we adjusted camera trap density (y , cameras/km²) using a power law curve based on island size (x , km²) to ensure smaller islands were surveyed more intensively. We used the following power law curve equation:

$$y = 2.0826x^{-0.369}$$

On Oak Island, two camera trap locations were omitted according to our power law curve for camera trap density. We omitted one location that was in an area of high human use and a second location due to access issues (e.g. steep ravine). For some of the smaller islands (i.e. Cat, Devils, Ironwood, Raspberry and North Twin) we relaxed our >50% of grid cell surface area on land to ensure adequate camera trap densities.

We used standardized procedures and targeted fine-scale landscape features to maximize detections of carnivores (i.e. camera trap height, orientation, focal area structure) while placing camera traps (O'Connell et al. 2011). From each target deployment location, we walked concentric circles until we intersected animal sign, a clearing, trail or other site with above-average probability of capturing large mammals. We typically selected more open areas that contained a downed tree with few branches. We set the camera traps 0.75–1 m off the ground and 3–7 m away from the chosen site, and programmed camera traps

to take a series of 3–5 photos when they detected motion and no refractory period between trigger events. On each island, we randomly assigned a lure treatment to half of the camera trap sites for that island. These sites received a commercial predator trapping scent lure (Caven's Gusto, Minnesota Trapline Products Inc., Pennock, MN, USA) during the first 6-month deployment, and later we rotated sites and all previously non-lured sites received lure during the second 6-month deployment. Effectively, scent lure was present at half of sites in any given season to account for seasonal variation in detection. We placed aerial call lures (~3–4 m) and local lures (on downed woody vegetation) to draw carnivores into the camera traps detection area. We returned to each camera trap at approximately 6-month intervals to replace batteries and memory cards. We measured habitat variables which may influence carnivore communities through spatial data layers in a GIS (ArcMap 10.3; ESRI 2014). Vegetative characteristics were calculated within a 100 m buffer around each camera site using an open access data layer, Wiscland 2.0 (Wiscland 2016). Within each buffer, we calculated the proportion of the habitat that was composed of pine, mixed hardwood, and northern hardwood (see Wiscland 2.0 user guide for classification details).

Statistical analyses

We used program R version 3.3.1 (R Core Team 2016) for all of our statistical analyses. To calculate total trap nights, we first determined if a camera trap was fully operational for the duration of its deployment. Based on natural breaks in the distribution of days between capture events, if a camera trap did not take a photo in >28 days we assumed that it malfunctioned due to low battery power or extreme temperatures, and these periods were excluded from our calculations. If the camera trap resumed taking multiple photos after a >28-day period of no detections, we considered it reactivated.

We defined a photo event as any series of photos (as programmed) triggered by a human or wildlife species. To avoid pseudo-replication, we considered consecutive photo captures of the same species within 30 min to be the same event (Naing et al. 2015, Wang et al. 2015). We totaled the number of independent events (E) for each species, and determined their relative abundance (RA) at each camera trap as:

$$RA = (E / TN) \times 100$$

where TN is the total number of trap nights that the camera trap was operational. We calculated carnivore

species richness as the number of terrestrial carnivores documented on a given island.

We used a series of *a-priori* generalized linear models (GLMs) with standardized variables (Table 1), using a suite of models to understand the drivers of three dependent variables at different scales: carnivore richness at the island level, marten presence/absence at the island level, and marten abundance at the site level. We compared models using Akaike information criterion (AIC) weight, using AICc values in each of our models due to low sample sizes (Burnham and Anderson 2002). When interpreting models we considered any model with $\Delta\text{AIC} < 2$ to have substantial support and any model with $\Delta\text{AIC} < 4$ to be biologically relevant (Burnham and Anderson 2002).

Table 1: Individual variables considered in creating *a-priori* models of carnivore richness, marten presence, and marten abundance on the Apostle Island National Lakeshore, WI, USA.

Name	Symbol	Description
Bobcat abundance	BCAB	RA of bobcats at camera trap site
Coyote abundance	CYAB	RA coyotes at camera trap site
Deer abundance	DEAB	RA of deer at camera trap site
Elevation	ELEV	The maximum elevation (m) of the island
Fisher abundance	FIAB	RA of fishers at camera trap site
Gray wolf abundance	GWAB	RA of gray wolves at camera trap site
Hardwood habitat	HAHA	Area of hardwood habitat within 100 m radius
Human abundance	HUAB	RA of people at camera trap site
Inter-island distance	ISDI	Distance to the nearest island (km)
Island size	ISSZ	Total area of the island (km ²)
Lagomorph abundance	LGAB	RA of lagomorphs at camera trap site
Mean coyote abundance	MCAB	Mean RA coyotes across camera trap sites on island
Mean fisher abundance	MFAB	Mean RA of fishers across camera trap sites on island
Mean human abundance	MHAB	Mean RA of people across camera trap sites on island
Mixed hardwood habitat	MIHA	Area of mixed hardwood habitat within 100 m radius
Mainland distance	MLDI	Distance to mainland Wisconsin
Mean trap nights	MTRP	Mean number of trap nights across camera traps on island
Pine habitat	PIHA	Area of pine habitat within 100 m radius
Red fox abundance	RFAB	RA of red foxes at camera trap site
Squirrel abundance	SQAB	RA of squirrels at camera trap site
Trap nights	TRAP	Number of trap nights at camera trap site

RA, relative abundance.

To determine the drivers of carnivore richness at the island level we tested among seven *a-priori* models (Table 2). We used a Gaussian GLM with an identity link for each model, with the richness of carnivores as our dependent variable. To determine the drivers of marten presence/absence at the island level we tested among six *a-priori* models (Table 2). We used a binomial GLM with a logit link for each model, with whether martens were detected on a given island as our dependent variable. To determine the drivers of marten abundance at the site level we tested among seven *a-priori* models (Table 2). We used zero-inflated Poisson (ZIP) models in the *pscl* package (Zeileis et al. 2008, Jackman 2015), because ZIP models effectively account for the presence of non-informative, structural zeros in a binomial model followed by a Poisson model with non-informative zeros accounted for. We held trap nights and island size constant as predictors of non-informative zeros in the binomial process, and changed the variables as noted in Table 2 for each model in the Poisson process.

Results

We had 87 functioning camera traps, with a mean of 6.7 (± 2.3 SE) camera traps per island (range = 1–30), and our density averaged 1.23 (± 0.19 SE, range = 0.74–3.08) functioning camera traps/km². We collected 93,515 photographs (not including time-lapse photographs) across 18,761 trap nights. This included 3592 wildlife events, of which 1076 were carnivore events. We documented 88 marten events on five of 13 islands (Figure 1). We detected 13 other mammal species or groups, including black bear (*Ursus americanus* (Pallas, 1780)), bobcat (*Lynx rufus* (Schreber, 1777)), coyote (*Canis latrans* (Say, 1823)), fisher (*Pekania pennanti* (Erxleben, 1777)), gray fox (*Urocyon cinereoargenteus* (Schreber, 1775)), lagomorphs, common raccoon (*Procyon lotor* (L., 1758)), red fox (*Vulpes vulpes* (L., 1758)), squirrels (*Sciuridae* spp.), weasels (*Mustela* spp.), white-tailed deer and gray wolf (*Canis lupus* (L., 1758)). The most commonly detected classifications were squirrels ($n = 1506$), black bears ($n = 581$) and lagomorphs ($n = 359$), while the least common were raccoons ($n = 5$) and weasels ($n = 1$) (Supplementary material 2).

Our top model for carnivore richness (Figure 1), Immigration Island Biogeography ($w\text{AIC}_c = 0.57$), had twice as much support as any other model to explain the distribution of carnivore richness among islands (Table 3). Among the variables in the model, island size had a positive coefficient ($\beta = 0.19$), while distance to mainland had a negative

Table 2: Our *a-priori* models at three ecological scales on the Apostle Island National Lakeshore, WI, USA.

Name	Scale	Variables	Hypothesis
Island Size	Richness and presence	ISSZ	Larger islands will have greater carnivore richness and likelihood of martens being present (MacArthur and Wilson 1967, Whittaker and Fernandez-Palacios 2007)
Distance to Mainland	Richness	MLDI	Islands that are closer to the mainland or to other islands will have greater carnivore richness (MacArthur and Wilson 1967, Whittaker and Fernandez-Palacios 2007)
Immigration Island Biogeography	Richness and presence	ISSZ + MLDI	Islands that are closer to the mainland will have greater carnivore richness and likelihood of martens being present (MacArthur and Wilson 1967, Whittaker and Fernandez-Palacios 2007)
Isolation Island Biogeography	Richness and presence	ISSZ + ISDI + MLDI	Larger islands that are closer to the mainland or to other islands will have greater carnivore richness and likelihood of martens being present (MacArthur and Wilson 1967, Whittaker and Fernandez-Palacios 2007)
Island Size and Elevation	Richness	ISSZ + ELEV	Larger islands with broad elevation gradients will provide more ecological niches and increase carnivore richness (Oksanen and Oksanen 2000, Whittaker and Fernandez-Palacios 2007)
Trapping Effort	Richness	TRAP	Carnivore richness is simply based on the number of camera trap nights rather than biological factors
Human Avoidance	Richness and presence and abundance	MHAB (R and P), HUAB (A)	Carnivores avoid human activity and islands/sites with greater human activity will have less carnivore richness, likelihood of marten presence, and marten abundance (Zielinski et al. 2008, Wang et al. 2015)
Direct Competition	Presence and abundance	MFAB (P) FIAB (A)	Competition between fishers and martens for similar resources suggests that islands/sites with higher relative abundance of dominant fishers will be less likely to support martens (Fisher et al. 2012, Zielinski and Duncan 2004)
Cascading Competition	Presence and abundance	MFAB × MCAB (P), FIAB × CYAB (A)	Mesopredator release theory suggests islands/sites with more coyotes will have fewer fishers and, as a result, be more likely to have presence and abundance of martens (Levi and Wilmer 2012, Allen et al. 2015)
Carnivore Avoidance	Abundance	RFAB + CYAB + GWAB + BCAB + FIAB	Sites where the risk of interference competition and mortality from larger carnivores is high will have fewer martens (Brown et al. 1999, Fisher et al. 2012, Lesmesiter et al. 2015, Wang et al. 2015)
Hunted Prey Abundance	Abundance	SQAB + LGAB	Sites with higher abundances of mammalian prey items will have more martens (Zielinski and Duncan 2004, Carlson et al. 2014)
Available Food Abundance	Abundance	SQAB + LGAB + DEAB	Sites with higher abundances of mammalian prey items and carrion to scavenge from will have more martens (Zielinski and Duncan 2004, Carlson et al. 2014)
Habitat Suitability	Abundance	PIHA + HAHA + MIHA	Martens will prefer complex or coniferous upland forest habitats and sites with higher proportions/larger patches of these will support more martens (Gilbert et al. 1997, Thompson et al. 2012)

The scales include carnivore richness at the island level [(richness (R)), marten presence/absence at the island level [presence (P) and marten abundance at the site level [abundance (A)]. We provide the name of the model, the variables included and the hypothesis/reasoning behind the model.

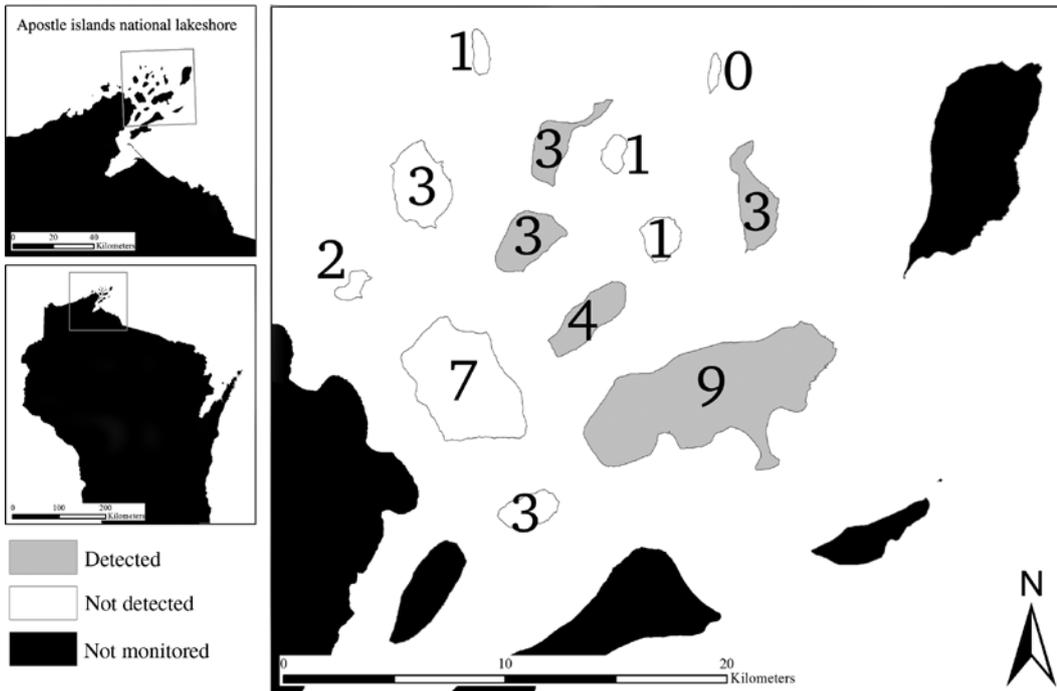


Figure 1: The carnivore richness (indicated by the number associated with an island) and the presence/absence of American martens (indicated by shaded or not for each island) on the Apostle Islands National Lakeshore, WI, USA from September 2014 to June 2016.

Table 3: Results of our model comparisons of carnivore richness at the island level, marten presence/absence at the island level, and marten abundance at the site level, with individual models ranked based on their AIC_w .

Model name	AIC_c	ΔAIC	$wAIC_c$	Cumulative $wAIC_c$
Carnivore richness				
Immigration Island Biogeography	39.29	0.00	0.58	0.58
Island Size and Elevation	40.85	1.56	0.27	0.85
Island Size	42.95	3.66	0.09	0.94
Isolation Island Biogeography	43.85	4.56	0.06	1.00
Distance to Mainland	63.48	24.19	0.00	1.00
Trapping Effort	63.64	24.36	0.00	1.00
Human Avoidance	68.02	28.74	0.00	1.00
Marten presence/absence				
Island Size	21.01	0.00	0.36	0.36
Human Avoidance	21.07	0.16	0.33	0.69
Direct Competition	22.52	1.51	0.17	0.86
Immigration Island Biogeography	23.72	2.71	0.09	0.96
Isolation Island Biogeography	25.48	4.47	0.04	0.99
Cascading Competition	29.30	8.28	0.01	1.00
Marten abundance				
Cascading Competition	246.88	0.00	0.53	0.53
Human Avoidance	248.09	1.21	0.29	0.83
Hunted Prey Abundance	250.61	3.74	0.08	0.91
Available Food Abundance	251.77	4.90	0.05	0.95
Habitat Suitability	252.63	5.76	0.03	0.98
Direct Competition	254.66	7.78	0.01	0.99
Carnivore Avoidance	256.08	9.20	0.01	1.00

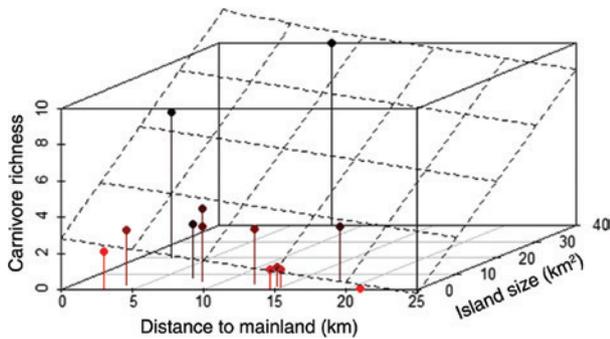


Figure 2: The effects of “Immigration Island Biogeography” (island size and distance from mainland) on carnivore richness on the Apostle Islands National Lakeshore, WI, USA from September 2014 to June 2016.

coefficient ($\beta = -0.11$) (Figure 2). Our second-best model, Island Size and Elevation ($wAIC_c = 0.26$, $\beta_{\text{island size}} = 0.17$, $\beta_{\text{elevation}} = 0.02$), also had substantial support, while our Island Size Model ($wAIC_c = 0.09$, $\beta = 0.22$) was biologically relevant.

Our top models for marten presence (Figure 1) at the island level were Island Size ($wAIC_c = 0.36$, $\beta = 0.07$) and Human Avoidance ($wAIC_c = 0.33$, $\beta = -0.49$) (Table 3).

Direct competition ($wAIC_c = 0.17$, $\beta = -0.01$) also had substantial support, while Immigration Island Biogeography was biologically relevant ($wAIC_c = 0.09$, $\beta_{\text{island size}} = 0.10$, $\beta_{\text{mainland distance}} = 0.10$).

Our top model for marten abundance at the site level (Figure 3), Cascading Competition ($wAIC_c = 0.53$), had nearly twice as much support as any other model to explain the abundance of martens at camera trap sites (Table 3). In this model, both coyotes and fishers had negative coefficients for marten abundance ($\beta_{\text{coyote}} = -0.18$, $\beta_{\text{fisher}} = -1.60$), but their interaction had a stronger positive coefficient ($\beta = 8.59$). Our second-best model, Human Avoidance ($wAIC_c = 0.29$, $\beta = -1.51$), also had substantial support, while Hunted Prey Abundance ($wAIC_c = 0.08$, $\beta_{\text{squirrel}} = 0.02$, $\beta_{\text{lagomorph}} = -0.03$) was biologically relevant.

Discussion and conclusion

Our study showed that different processes appeared important at each scale tested and highlights the importance of understanding the drivers of the distribution and abundance of wildlife populations at multiple ecological scales

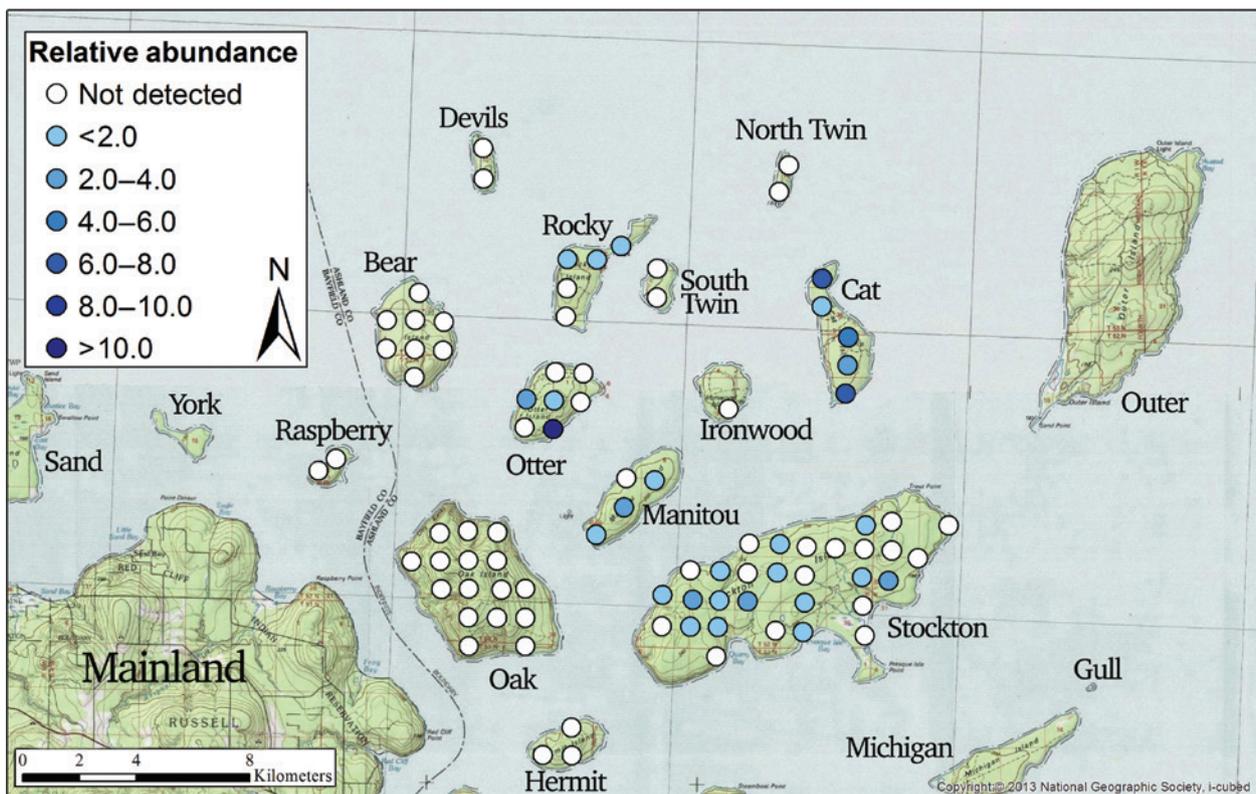


Figure 3: Distribution and relative abundance of American martens detected at camera trap sites on the Apostle Islands National Lakeshore, WI, USA from September 2014 to June 2016.

(e.g. Levin 1992, Ruggiero et al. 1994). Carnivore richness at the island level appeared to be driven by resource limitation (island biogeography; MacArthur and Wilson 1967, Whittaker and Fernandez-Palacios 2007), while American marten presence at the island level appeared to be a combination of resource limitation (island size; MacArthur and Wilson 1967, Whittaker and Fernandez-Palacios 2007) and competitive interaction (human avoidance; Zielinski et al. 2008, Wang et al. 2015), and marten abundance at the site level appeared to be driven by competitive interactions (cascading carnivore interactions; Levi and Wilmsers 2012, Allen et al. 2015). If studied alone, any of our three scales could give a biased understanding of the factors driving the system (e.g. Levin 1992, Ruggiero et al. 1994), but incorporating three levels of ecological scale, gave a more complete picture of the processes behind the abundance and distribution of the carnivore community in a temperate archipelago. Each island likely acts as a local community within the meta-community (Leibold et al. 2004), and communities should be relatively stable in any given moment due to the defined geographic limits of the island. However, it is likely the interaction of these processes on and among islands that move marten distribution and abundance towards an equilibrium (Hairston et al. 1960, Power 1992), and community dynamics will change over time as carnivore species colonize or become extinct from given islands.

Island biogeography is a critical theory in ecology, used to explain the distribution and abundance of wildlife species (MacArthur and Wilson 1967, Simberloff 1974, Whittaker and Fernandez-Palacios 2007). The effects of island biogeography on carnivore richness in APIS were pronounced, with higher richness on larger islands and lower richness as the distance from the mainland increased. This is an important confirmation that island biogeography is a powerful force in both temperate and inland island systems, as well as with complex mammalian species such as carnivores. Carnivore species in APIS may be dependent on periodic influxes from the mainland or larger islands to maintain their populations, due to demographic stochasticity and the genetic effects of small population size (Whittaker and Fernandez-Palacios 2007, Emerson and Gillespie 2008), as well as the difficulty of dispersal for terrestrial carnivores in island systems. Given the importance of island biogeography in this system, distance from the nearest island had less effect than might be expected (MacArthur and Wilson 1967, Whittaker and Fernandez-Palacios 2007). This is potentially because there was little variation in the distances between the islands that we studied (Supplementary material 1). Inter-island distance may become more important in

the dynamics of the carnivore community in APIS in the future, however, as ice cover likely affects immigration and emigration, and a warming climate appears to be leading to declining ice cover in the system (Howk 2009).

The factors driving American marten presence and absence on islands was our most equivocal, and possibly most complex, ecological scale. This intermediate scale may be the most complex scale if it is where resource limiting (i.e. island size) and competitive interaction (i.e. human avoidance and direct competition with fishers) processes intersect. Island size is likely important as a measure of the resources available (MacArthur and Wilson 1967, Simberloff 1974); while human avoidance (Lesmesiter et al. 2015, Wang et al. 2015), and to a lesser degree direct competition (Zielinski and Duncan 2004, Fisher et al. 2012), were also important, and may interact with island biogeography in complex ways. This was evidenced by martens being absent from Oak Island, which is the second largest island in our study, but also very close to the mainland with a corresponding high human presence and substantial fisher abundance. The interaction of these processes may be responsible for martens more often being found on islands farther from the mainland, and potentially increasing the importance of immigration between islands for martens.

As a small carnivore, American martens are affected by competition with dominant sympatric competitors that exploit similar resources, most notably fishers (Zielinski and Duncan 2004, Fisher et al. 2012). At the camera trap site scale, the abundance of martens appears directly driven by competitive interaction processes but appears to be part of a behavioral cascade (e.g. Allen et al. 2015, Lesmesiter et al. 2015), wherein coyotes appear to spatially limit fisher abundance and release martens from the competitive pressure of fishers. Our other model at the camera trap site scale with substantial support was human avoidance, and human avoidance and direct competition were also the important competitive interaction processes driving marten presence at the island level. These competitive interactions suggest that some aspect of an ecology of fear (Brown et al. 1999), where martens are affected by humans and dominant sympatric competitors (e.g. Fisher et al. 2012, Lesmesiter et al. 2015, Wang et al. 2015) seems to drive marten abundance at the site level.

The importance of resource limitation and competitive interaction processes varied depending on the ecological scale we studied (e.g. Levin 1992, Ruggiero et al. 1994). American martens are notable as the only state endangered mammal in Wisconsin (Woodford and Dumyahn 2011, Allen et al. 2018b), and our results show that it is important to account for multiple scales for effective

management and conservation of species (e.g. Ruggiero et al. 1994). Our study was based on a small snapshot in time (2 years) that likely leads to a relatively stable system, however, studying the carnivore community over a longer time period could show trends in extirpation from and recolonization of islands (Simberloff 1974, Whittaker and Fernandez-Palacios 2007). It is important for future studies to move towards long-term monitoring to elucidate trends in carnivore community dynamics on the islands and mechanisms for how resource limitation and competitive interaction processes affect carnivore populations and communities over time in island systems.

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